Impacts of small- and large-scale drivers of agroecosystems on multi-trophic diversity across the soil surface

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Table of Contents

Summary

Sustaining multifunctionality and stability of ecosystems has become of increasing concern over the last century due to the increased exploitation and degradation of the natural environment by human impacts and rising resource demands. To maintain ecosystem stability and multifunctionality it is essential to more holistically understand the impact of land use in comparison to other drivers across multiple spatial scales on above- and belowground trophic groups. To advance scientific understanding in this regard, my thesis focused on investigating biodiversity responses to land use across the soil surface at multiple spatial grains. While seeking to understand the large- and small-scale drivers and interconnectivity of above- and belowground taxonomic groups that fulfill important ecological functions within agroecosystems. To do so, the thesis is structured into three research topics:

- Firstly, I investigated the generality of scale-dependent responses of biodiversity and its underlying community components (i.e. density of individuals, evenness and aggregation) to land management.
- Secondly, I studied the relative importance of land use (i.e. land management and land use intensity) versus abiotic factors (soil, topography and regional weather conditions) to understand land use impacts on community assembly processes.
- Lastly, I investigated how large- (land cover and weather conditions) and small-scale (local soil and topography) abiotic factors within the agricultural landscapes shape the diversity, composition and connectivity of multiple trophic groups across the soil surface

A novel feature of my research design is the consistent inclusion of both above- and belowground taxonomic groups in scale-explicit analyses, comparing the impact across the soil interface. Research findings from the first topic (**Chapter 2**) add new insight to the complexity of scale-dependency and the underlying components affected by land management. My findings reveal that scale-dependent responses are the norm, rather than the exception, and that responses to land management are context-dependent. Under the second research topic (**Chapter 3**) my results reveal abiotic factors to be more prominent than current land use practices in explaining occurrence patterns of vascular plants and free-living soil fungi species within semi-natural grasslands. Revealing that, despite long-term anthropogenic management, certain managed systems are still driven by small-scale abiotic factors and the local biogeographical context rather than predominantly land management. Findings from the third research topic (**Chapter 4**) revealed a higher importance of landscape-drivers over local-drivers. Here, I found that direct and indirect effects of landscape-level factors, such as the amount of semi-natural habitat, are generally more prominent drivers for both above- and belowground groups than small-scale ones. Furthermore, unexpected links were found between large-scale drivers related to landscape structure on soil microbes (free-living fungi and bacteria), as well as small-scale predictors (e.g. soil texture and pH) on more mobile aboveground groups (wild bees and carabids).

Overall, my research findings provide new insight to the scale-dependence of biodiversity patterns and the multiple drivers shaping agroecosystems. Placed within a policy framing, my work highlights the importance of having policy instruments that allow for contextualized land management plans that take into consideration multiple taxonomic groups and are implemented at multiple spatial scales that are ecologically relevant.

Key words:

above- and belowground biodiversity; scale-dependent responses; community assembly processes; multiple scale drivers; grassland management; environmental context; spatial aggregation; species-abundance distribution; hierarchical joint species distribution modelling; species co-occurrence patterns

Zusammenfassung

Die Erhaltung der Multifunktionalität und Stabilität von Ökosystemen hat im letzten Jahrhundert aufgrund der zunehmenden Ausbeutung und Verschlechterung der natürlichen Umwelt durch menschliche Einflüsse und den steigenden Ressourcenbedarf an Bedeutung gewonnen. Um die Stabilität und Multifunktionalität von Ökosystemen zu erhalten, ist es unerlässlich, die Auswirkungen der Landnutzung auf verschiedenen räumlichen Ebenen auf ober- und unterirdische trophische Gruppen im Vergleich zu anderen Einflussfaktorenganzheitlicher zu verstehen. Um das wissenschaftliche Verständnis in dieser Hinsicht voranzutreiben, konzentriert sich meine Dissertation auf die Untersuchung der Reaktionen der biologischen Vielfalt verschiedener ober- und unterirdischer trophischer Gruppen auf die Landnutzung in verschiedenen räumlichen Maßstäben. Dabei sollen die groß- und kleinskaligen Einflussfaktoren und die Verflechtung der ober- und unterirdischen taxonomischen Gruppen, die wichtige ökologische Funktionen in Agrarökosystemen erfüllen, verstanden werden. Zu diesem Zweck gliedert sich meine Arbeit in drei Forschungsthemen:

- Erstens untersuche ich die Allgemeingültigkeit der skalenabhängigen Reaktionen der biologischen Vielfalt und der ihr zugrunde liegenden Komponenten von Lebensgemeinschaften (d. h. Individuendichte, Artengleichheit [evenness] und Aggregation) auf die Landnutzung.
- Zweitens untersuche ich die relative Bedeutung der Landnutzung (d. h. Landbewirtschaftung und Landnutzungsintensität) im Vergleich zu abiotischen Faktoren (Boden, Topografie und regionale Wetterverhältnisse), um die Auswirkungen der Landnutzung auf die Prozesse der Bildung von Lebensgemeinschaften zu verstehen.
- Schließlich untersuchte ich, wie großräumige (Landschaftsstruktur und Wetterbedingungen) und kleinräumige (lokale Bodenfaktoren und Topografie) abiotische Faktoren innerhalb der Agrarlandschaften die Vielfalt, Zusammensetzung und Konnektivität verschiedener ober- und unterirdischer trophischer Gruppen beeinflussen.

Ein neuartiges Merkmal meines Forschungsdesigns besteht darin, dass ich jedes Mal sowohl ober- als auch unterirdische taxonomische Gruppen in skalenexplizite Analysen einbeziehe. Die Forschungsergebnisse aus meinem ersten Thema (**Kapitel 2**) geben neue Einblicke in die Komplexität der Skalenabhängigkeit und die zugrunde liegenden Komponenten, die von der Landbewirtschaftung beeinflusst werden. Meine Ergebnisse zeigen, dass skalenabhängige Reaktionen eher die Regel als die

Ausnahme sind und dass die Reaktionen auf die Landbewirtschaftung kontextabhängig sind. Im Rahmen des zweiten Forschungsschwerpunkts (**Kapitel 3**) zeigen meine Ergebnisse, dass abiotische Faktoren bei der Erklärung von Vorkommensmustern von Gefäßpflanzen und freilebenden Bodenpilzarten in naturnahen Graslandschaften eine größere Rolle spielen als aktuelle Landnutzungspraktiken. Dies zeigt, dass bestimmte bewirtschaftete Systeme trotz langfristiger anthropogener Bewirtschaftung immer noch von kleinräumigen abiotischen Faktoren und dem lokalen biogeografischen Kontext bestimmt werden und weniger von der Landbewirtschaftung. Die Ergebnisse des dritten Forschungsschwerpunkts (**Kapitel 4**) zeigen, dass landschaftsbedingte Faktoren wichtiger sind als lokale Faktoren. Hier stellte ich fest, dass die direkten und indirekten Auswirkungen landschaftlicher Faktoren, wie z. B. der Umfang naturnaher Lebensräume, im Allgemeinen sowohl für ober- als auch für unterirdische Gruppen wichtiger sind als kleinräumige Faktoren. Darüber hinaus wurden unerwartete Zusammenhänge zwischen großräumigen Einflussfaktoren im Zusammenhang mit der Landschaftsstruktur auf Bodenmikroben (freilebende Pilze und Bakterien) sowie kleinräumigen Prädiktoren (z. B. Bodentextur und pH-Wert) auf mobilere oberirdische Gruppen (Wildbienen und Karabiner) festgestellt.

Insgesamt liefern meine Forschungsergebnisse neue Erkenntnisse über die Skalenabhängigkeit von Biodiversitätsmustern und die vielfältigen Einflussfaktoren, die Agrarökosysteme prägen. Eingebettet in einen politischen Rahmen unterstreicht meine Arbeit die Bedeutung von politischen Instrumenten, die kontextbezogene Landbewirtschaftungspläne ermöglichen, die mehrere taxonomische Gruppen berücksichtigen und auf mehreren räumlichen Skalen umgesetzt werden, die ökologisch relevant sind.

Schlüsselwörter:

Ober- und unterirdische biologische Vielfalt; skalenabhängige Reaktionen; Prozesse der Bildung von Lebensgemeinschaften; Faktoren auf mehreren Skalen; Grünlandbewirtschaftung; Umweltkontext; räumliche Aggregation; Verteilung der Artenvielfalt; hierarchische gemeinsame Modellierung der Artenverteilung; Muster des gemeinsamen Vorkommens von Arten

Chapter 1:

General introduction

Biodiversity and community assembly processes

For centuries the diversity of all living things has been a fascination for naturalists, biologists, ecologists and others studying natural sciences (e.g. Humbolt and Bonpland, 1805). The term 'biodiversity' became more popular in the 1960 and 1970s as a way to describe the variety of living organisms on earth. Initially, it was not well defined, but has since become more commonly considered to encompass the variety of life and its biotic processes. Delong (1996) systematically defined biodiversity as follows, "*Biodiversity is a state or attribute of a site or area and specifically refers to the variety within and among living communities, assemblages of living organisms, biotic communities, and biotic processes, whether naturally occurring or modified by humans. Biodiversity can be measured in terms of genetic diversity and the identity and number of different types of species, assemblages of species, biotic communities, and biotic processes, and the amount (*e.g. *abundance, biomass, cover, rate) and structure of each. It can be observed and measured at any spatial scale ranging from microsites and habitat patches to the entire biosphere*".

The diversity and composition of biotic communities are determined by community assembly processes that have theoretically been described as a set of 'filters' that function hierarchically, at different spatiotemporal scales (Zobel 1997; HilleRisLambers et al. 2012; Kraft et al. 2015). These community assembly processes determine species occurrence patterns. These 'filters' have been considered to include a range of stochastic (random) and deterministic (directional) processes. The initial deterministic ('filtering') step is considered a 'dispersal filter', stating that the occurrence of a species in a specific community is limited by its ability to arrive and potentially colonize a site. The next filter, upon the arrival of a new species, was considered to be the abiotic conditions serving as an 'environmental filter'. The abiotic conditions of the area determine whether or not the species can successfully establish. The final filtering step is the impact of biotic interactions ('biotic filter') on species occurrence and abundance, both intraspecific and interspecific (i.e. individuals of the same species or other species). Understanding community assembly is a fundamental goal in the field of Community Ecology, and has long been a focus of experimental and field-based research. These studies have shown community assemblage processes are less linear and more integrative components than initially proposed (Maire et al. 2012; Spasojevic and Suding 2012; Glassman et al. 2017). Modern coexistence theory thus suggests community assembly processes to be more interlinked with feedback loops from both biotic and abiotic factors to serve as concurrent 'filters' (Mason et al. 2011; HilleRisLambers et al. 2012). Understanding the relative importance of stochastic versus deterministic processes, and how these change with environmental context is important for predicting species assemblages and how they will respond to environmental drivers, including anthropogenic disturbances.

Biodiversity is valuable inherently, for its life supporting ecological functions and processes that are needed to ensure the functioning and resilience of ecosystems (Soliveres et al. 2016b; IPBES 2019; de Bello et al. 2021). Humans, for example, rely on species-rich communities for a range of ecosystem goods and services provided by natural, e.g. for water and air purification, and managed systems, e.g. agroecosystems for food and fodder production. It is, however, less well known how human-use of these systems are altering the underlying community assembly processes (Münkemüller et al. 2020). The impact of land use, for example, would form part of the 'environmental filter' determining the species richness and composition of fauna and flora. However, to what proportion anthropogenic factors, e.g. land management and land use intensity of grasslands, are affecting community assembly processes in comparison to the biogeographical context remains unclear. Unpacking the relative importance of land use on these ecological processes is relevant for understanding the current and future consequences of anthropogenic disturbances on biodiversity and ecosystems (Newbold et al. 2015).

Biodiversity in agroecosystems

The role of biodiversity within managed ecosystems, such as agroecosystems, is of ecological and economic value (IPBES 2019; Oelmann et al. 2021; Senapathi et al. 2021). The agricultural systems themselves are derived from and based on a rich diversity of biological resources (Diaz et al. 2018; Smith et al. 2021). Biodiversity within agricultural systems (also termed 'agrobiodiversity') include both genetic diversity of domesticated crop and livestock, as well as a suite of above- and belowground organisms that fulfill a range of ecological functions and services. It also encompasses a range of ecological services essential for the overall health and functioning of the agroecosystem. The ecological and functional role of agrobiodiversity include aspects such as nutrient cycling, prevention of soil erosion , soil fertility, animal-mediated pollination, natural pest control and reduced risk to disease and pest outbreaks (Harrison et al. 2014; Dainese et al. 2019; Smith et al. 2021).

The increased exploitation of natural resources and land use change over the last century has caused a severe loss of biodiversity, which in turn has detrimental effects on ecological functions and ecosystem services (Foley et al. 2005; Potts et al. 2010; Newbold et al. 2015). The loss of above- or belowground biodiversity reduces the resilience and stability of (agro)ecosystems to provide ecosystem services and increase their vulnerability to extreme events (e.g. drought) and other stressors (Oliver et al. 2015). This in turn will decrease agricultural productivity (e.g. see Dainese et al. 2019), jeopardizing food security, and has a wide range of negative social impacts (Thrupp 2004). Replacing functions that used to be provided by agrobiodiversity by external inputs such as pesticides (e.g. insecticides, herbicides and fungicides) and fertilizers, is not a sustainable alternative. The use of agrochemicals (whether synthetic or natural), for example, is not a viable option as it leads to further disruption of ecosystems (on- and off-site) and its misuse and long-term application presents environmental health risks for current and future generations (Nicolopoulou-Stamati et al. 2016; Tscharntke et al. 2021). Therefore, to move toward more sustainable agricultural production, we need to prioritize the above- and belowground biodiversity that is essential for overall sustainability, including aspects related to agricultural production, ecosystem health and human well-being.

Above- and belowground biodiversity and their interactions

Above- and belowground biodiversity is present in all terrestrial ecosystems. Aboveground biodiversity, including all fauna and flora living predominantly at or above the soil surface include, for example, plants, birds, certain insects, mammals, reptiles, etc. Belowground biodiversity (soil biodiversity), includes an even more diverse range of organisms from micro- to macroscopic ones, such as soil bacteria, fungi and nematodes, earthworms, various insects and moles. Aboveground biodiversity has received much more research attention over the past millennia, while belowground biodiversity has only become the focus of more extensive research in the last decade. The surge of research on soil biodiversity was spurred on as it became increasingly evident how diverse these organisms are and the important role they fulfill in ecological systems (Bardgett and Van der Putten 2014; Smith et al. 2021).

Above- and belowground biodiversity are closely linked and influence the processes and properties of biotic communities and ecosystems (Hooper et al. 2000; Wardle et al. 2004; De Deyn and Van der Putten 2005). The link across the soil interface can be direct, e.g. symbiotic interactions (Van der Heijden et al. 2008; Delavaux et al. 2021), or indirect, such as through soil microbes altering the quality of resources available to plant herbivores or to secondarily root-associated species (Porazinska et al. 2003; Urbanová et al. 2015). The link across the soil interface is typically through plants, and these interactions are often modulated via soil-related mechanisms, for example, via altered edaphic conditions (Schöps et al. 2018). These soil-mediated changes can cause legacy effects (Cuddington 2011) due to plant-soil feedback loops (Bonanomi et al. 2005; Heinen et al. 2020) or from past human-induced disturbances that continue to have an impact on future biotic communities (Gustavsson et al. 2007). These legacy effects can persist over a prolonged time period due to physical or biological changes to the soil (Cuddington 2011).

As above- and belowground organisms are highly interconnected across the soil surface, their close association may result in correlations in how they respond to environmental drivers, such as land management and land use intensity, despite their biological and ecological differences (Allan et al. 2014; Manning et al. 2015; Gossner et al. 2016). For example, according to the multi-taxa study by Gossner et al. (2016) above- and belowground taxon groups responded to land use in a similar way at a large spatial scale in managed grasslands. This was because intense land use resulted in a loss of beta-diversity for multiple trophic groups across the soil surface. However, when investigating the same groups' responses at more local scales (alpha-diversity), the taxa groups had contrasting responses. This scale-dependence highlights the importance of investigating the impact of anthropogenic factors across the soil interface, as well as at multiple scales (e.g. see Le Provost et al. 2021).

Scale-dependent biodiversity patterns

The plurality of how scale is perceived, not only within ecology, but also within and across other scientific disciplines and within a social-economic perspective (e.g. by different stakeholders, Vervoort et al. 2012), increases the complexity of finding effective ways toward biodiversity conservation and sustainability across multiple trophic guilds and multiple ‘scales’. The question of scale goes back many decades and continues to be a relevant question to be addressed with every ecological study. Levin outlines it well, in his award-winning lecture in 1992, which concluded that no single scale is the 'correct' scale for investigation and that all lie along a continuum as the description of any system, especially ecological ones, varies with the scale of observation. There is also a high level of interconnectivity between scales, however, ecological processes and mechanisms that are relevant at one scale are not necessarily active at other spatial scales (Levin 1992).

Biodiversity increases non-linearly with an increase of spatial grain, and is thus considered to be scale-dependent (Levin 1992; Chase et al. 2018). The effect of natural and anthropogenic environmental drivers on biodiversity is also scale-dependent (Hamer and Hill 2000; Gossner et al. 2016), and the effect size of biodiversity change has been shown to change in both magnitude and direction across different scales (Chase et al. 2018). It is thus important to measure multiple scales and components (e.g. richness, abundance, evenness) of biodiversity to understand its scale-dependent change across environmental drivers. Furthermore, it is important to understand what components of biodiversity are changing as this will have a cascading effect on ecological functions and processes.

While the multidimensionality and scale-dependence of biodiversity is appreciated in ecological literature, the effects of natural and anthropogenic drivers on biodiversity are still often examined at only one spatial grain or extent in empirical studies (Chase and Knight 2013; Demalach et al. 2019). The disregard for the scale-dependence of biodiversity has contributed to the high variation observed in results across studies (Chase and Knight 2013; Blowes et al. 2017). For example, in a meta-analysis not all studies use the same spatial grain for sampling, resulting in variation in the respective effect sizes of drivers on biodiversity that clouds our synthetic understanding of biodiversity change (Chase and Knight 2013). For a complete understanding of biodiversity change more comprehensive synthesis is required of the effect environmental drivers have on different components of biodiversity (i.e. richness, abundance, evenness) across multiple spatial scales (e.g. Korell et al. 2021). Insufficient synthesis of the impact of important drivers on biodiversity across multiple spatial scales has caused much confusion, for example, in the debate regarding the impact of land management and land use intensity on biodiversity. Furthermore, impacts of disturbances on different biodiversity components (e.g. species richness, abundance, evenness) may result in similar species-accumulation curves, thus comparing these alone, across communities, offers limited insight into how ecological drivers are altering biodiversity or the underlying processes (Chase and Knight 2013; Blowes et al. 2017), and thus the resulting ecological functions. Only by studying these patterns in more detail, for example, by investigating the changes to different biodiversity components, can the underlying mechanisms, resulting in the observed biodiversity pattern, be disentangled (e.g. see Simons et al. 2017).

Multi-trophic diversity for multifunctionality

Within a single ecosystem there are several trophic levels that collectively perform a suite of ecological functions. These trophic groups are broadly grouped as primary producers, herbivores (primary consumers), predators (secondary and tertiary consumers) and detritivores (decomposers). Species within each trophic grouping together create a network of functions and outputs ('services') within an ecosystem (Daily 1997; Lefcheck et al. 2015). Most ecological functions, and their resulting ecosystem services, are facilitated by service providers at a community or habitat level (i.e. by the entire grassland, forest or wetland), while others are more closely linked to functional groups (e.g. flower visiting insects for pollination, or parasitoids for pest control) or specific species (e.g. certain provisioning services such as a tree species used for timber production) (Harrison et al. 2014). Multi-trophic diversity is required to ensure the full range of ecological functions needed for healthy ecosystems. Functions such as water and air purification, biomass production, decomposition and soil carbon fluxes are performed by the species within and across each of the trophic levels. One to several species could be responsible for any function and one species could also be connected to several functions (Lefcheck et al. 2015; Hanisch et al. 2020). This multitude of interlinked species results in the collective contribution biodiversity has for facilitating multiple ecological functions simultaneously ('ecosystem multifunctionality') (Lefcheck et al. 2015).

The functional importance of above-belowground interactions has become increasingly evident to hold potential value as natural tools for promoting sustainable crop production and suppression of pests and pathogens (Shelef et al. 2020). Thus, studying both above- and belowground biodiversity within agroecosystems is required for moving towards more sustainable management that optimizes on biodiversity-based solutions (e.g. nature-based soultions, see Miralles-Wilhelm, 2021). Ecosystem multifunctionality has been shown to be positively correlated to above- and belowground biodiversity (Gamfeldt et al. 2008; Lefcheck et al. 2015; Soliveres et al. 2016b), despite some functional trade-offs that may occur at species level (e.g. resource acquisitive species vs. conservative species, de Bello et al. 2021) or local-spatial scales (e.g. a trade-off between crop and livestock production vs. regulating services, Maes et al. 2012). The number of species and the identity of the species within and across trophic levels is important for determining the functions performed by biotic communities (Gamfeldt et al. 2008; Harrison et al. 2014). Furthermore, for sustained multifunctionality it is important to have diverse species assemblages across multiple spatial-scales (Zavaleta et al. 2010). The community assemblages should ideally contain both common and locally rare species. Rare species are especially important for ecosystem multifunctionality as they enhance functional diversity and have fewer functional trade-offs (e.g. where one species cancels out the contribution of another) than common species (Soliveres et al. 2016a), while the abundance of common species promotes inter-annual stability of ecosystem services (Senapathi et al. 2021). Moreover, taxonomically diverse species assemblages have higher trait-diversity ensuring ecosystem stability (de Bello et al. 2021) which provides a more consistent supply of ecosystem services (Dainese et al. 2019; Senapathi et al. 2021).

Multifunctionality within agroecosystems

The multifunctionality of ecological systems provides a cohort of ecosystem services, more recently also known under the umbrella term 'Nature's contribution to People', which are fundamental for agricultural production of food, fodder and fiber (Alcamo et al. 2003; Diaz et al. 2018).

Many of these are soil derived (Smith et al. 2021), such as nutrient cycling, for example, which is positively affected by soil microbial diversity which determines what proportion of the organic carbon is broken down (Torsvik and Øvreås 2002). This is a key ecological process on which other ecosystem processes hinge including productivity of various trophic levels and biomass production within agricultural systems. Other important soil-related functions and ecosystem services include, for example, accumulation and transport of nutrients, water infiltration, water storage and availability, detoxification of soils, prevention of soil erosion and soil pathogen suppression (Smith et al. 2021). Arthropod-mediated services relevant to agroecosystems include, for example, pollination and natural pest control. To ensure stability of agricultural production it is important to safeguard a diversity of above- and belowground service-providing organisms across multiple taxonomic (Senapathi et al. 2021) and trophic levels (Soliveres et al. 2016b; Dainese et al. 2019; Snyder 2019).

Remnants of semi-natural habitat within agroecosystems such as edge habitats (e.g. field margins and road verges), provide a range of ecosystem functions and services (e.g. by providing nesting, overwintering sites and shelter for beneficial entomofauna) (Phillips et al. 2019; Bennewicz and Barczak 2020). Edge habitats have been found to provide valuable habitat and refugia to a diversity of plants and animals that is complementary to larger areas of semi-natural vegetation (e.g. managed grasslands) (Suárez-Esteban et al. 2016; Everaars et al. 2018), and serve as important corridors connecting semi-natural areas within the broader landscape (Snyder 2019; Bennewicz and Barczak 2020). Furthermore, they facilitate the foraging of ecosystem service providers, such as pollinators (e.g. wild bees and hoverflies) and natural pest enemies (e.g. parasitic wasps and predators beetles) (Fusser et al. 2017; Everaars et al. 2018) advancing multifunctionality in agroecosystems.

Impact of land use on biodiversity and ecosystem multifunctionality

Within agroecosystems, above- and belowground biodiversity has been under increased risk over the past decades due to land use change (Potts et al. 2010; Newbold et al. 2015; Winkler et al. 2021). This includes agricultural intensification within existing agroecosystems, e.g. increased use of agrochemicals, higher mowing frequencies or livestock densities (Laliberté et al. 2010; Allan et al. 2015; Gossner et al. 2016) and land use change, e.g. conversion of permanent grassland for urban use or to cropland or land abandonment (termination of grassland management) (Nitsch et al. 2012; Bohner et al. 2019).

The impact of land use on biodiversity is not a random process, but rather takes place in a trait-specific manner with a ripple-effect of consequences for community assembly processes and ecological functions (Schweiger et al. 2007; Eskildsen et al. 2015). Land use is likely to be a negative ‘environmental filter’ reducing abundance, species richness, taxonomic and functional diversity, and species interactions of biotic communities across various spatial scales. Rare species, for example, are more vulnerable to land use impacts than more common species due to higher niche specialization, e.g. with specific habitat requirements and narrowly defined host or pollinator associations, and are thus more likely to go locally or regionally extinct. This results in a systematic loss of specialist groups and the increased dominance of common generalists, leading to biotic homogenization of local- and landscape-level communities (Gámez-Virués et al. 2015; Gossner et al. 2016). Biotic homogenization of above- and belowground communities in agroecosystems jeopardizes the system's multifunctionality, and the stability of agroecosystems, making them more vulnerable to environmental and anthropogenic disturbances (Laliberté et al. 2010; Oliver et al. 2015; de Bello et al. 2021).

The continued impact of land use on biodiversity is especially evident within semi-natural grasslands where land use intensification and land abandonment are placing these species-rich biotopes at risk (Nitsch et al. 2012; Bohner et al. 2019). Abandonment of active grassland management, for example, results in a loss of plant species richness due to encroachment by other species, such as medium- to tall grasses and tall herbs (Bohner et al. 2019). While increased land use intensity of grasslands, by higher fertilization rates, mowing frequencies and livestock densities, has a negative impact on species richness across multiple trophic groups, and alters the relationship across these groups (Manning et al. 2015). Furthermore, historical land management of semi-natural grasslands also has a legacy effect on the diversity of multiple trophic groups (Gustavsson et al. 2007; Le Provost et al. 2020). To what extent and by which mechanisms legacy effects of past and current land use are altering current and future biotic communities remains an area of active research. Therefore, where possible, it is important to consider both historic and current land use when studying land use impacts on biodiversity.

Relevance for research across the soil surface

The entire extent of ecosystem multifunctionality is difficult to fully comprehend due to the multiple interacting factors and role players. To more comprehensively understand the connectivity between biodiversity and ecosystem multifunctionality it is necessary to study multiple taxonomic groups and trophic levels across the soil surface simultaneously. Furthermore, more research is needed investigating the effects of anthropogenic disturbances, such as land use, on multiple taxonomic groups and trophic levels across multiple spatial scales. Scale-explicit comparisons across the soil surface would advance our understanding of the scale-dependence of biodiversity responses and how interconnected above- and belowground biodiversity is responding to land use.

Of the multi-taxa studies conducted to understand the effects of land use on biodiversity, many only consider either above- (e.g. de Castro Solar et al. 2015; Manning et al. 2015) or belowground (e.g. Birkhofer et al. 2012; Wakelin et al. 2009) groups. Existing research that has considered the impact of land use on above- and belowground biodiversity of interconnected taxa groups or across trophic levels have mostly been either manipulative experiments (e.g. Liliensiek et al. 2012; Scherber et al. 2010) or meta-analyses of prior research (e.g. Kulmatiski et al. 2008). Only more recently have a few field-based research articles of these interconnections been published (e.g. Billeter et al. 2008; Penone et al. 2018; Le Provost et al. 2021). A multi-taxa study by Gossner et al. (2016) in semi-natural grasslands, for example, found strong similarity in how above- and belowground communities respond to land use, respectively. However, these differed in comparison to each other (above- vs belowground groups). Despite these multi-taxa studies across the soil surface, there are still many uncertainties and unanswered questions regarding land use impacts on biodiversity and ecosystem functioning. It is, for example, still unclear to what extent soil legacy effects of past and current land use practices are impacting different trophic levels across the soil interface. It is also relatively unknown how influential land use is in shaping these communities in comparison to natural community assembly processes. Furthermore, it is important to further unpack how different drivers at local- and landscape-scales are shaping the richness, diversity and composition of multi-trophic communities across the soil surface.

Quantifying the effects of land use components, such as land management and land use intensity, on biodiversity metrics and ecological processes shaping biotic communities is important to inform policy development regarding land management decisions. Within the European Union (EU) the main policy developments regarding land use are set out in the Common Agricultural Policy (CAP) (Pe’er et al. 2017b). The CAP was first implemented in 1962, and consists of two sections (referred to as pillars): Pillar 1, includes ‘direct payments and market-related expenditures’ and Pillar 2 the ‘Rural Development Programme’. The initial aim of the CAP was to stabilize market prices and ensure food security, with only a limited focus on environmental sustainability. Several reforms have attempted ‘greening’ pillar 1 (where the bulk of the budget is), and to expand measures that promote environmental protection and sustainability under pillar 2 (e.g. agri-environment schemes). The success of these measures and subsequent reforms has been extensively questioned and criticized (Pe’er et al. 2017a, 2020), and there is a lack of evidence regarding increasing effectiveness (Batáry et al. 2015). The effectiveness of agri-environment schemes, for example, have been found to be context specific and scale-dependent, often having moderate success, especially locally, within intensive farmland (Batáry et al. 2015), or being ineffective or even detrimental in more extensively farmed areas (Sutcliffe et al. 2015). The promotion of generalized grassland management practices by the CAP, for example, has resulted in the abandonment of traditional management practices that created heterogeneous agricultural landscapes (Dahlström et al. 2013) highly beneficial for biodiversity conservation (Myklestad and Sætersdal 2004). Furthermore, the CAP has been ineffective in protecting permanent grasslands from conversion to arable land (Nitsch et al. 2012; Pe’er et al. 2017a) which has long lasting negative impacts of multifunctionality of agroecosystems (Le Provost et al. 2020). Even under the current CAP reform, it is questionable if it will become more effective in promoting sustainable agriculture in the EU (Pe’er et al. 2020). Further research to making scientific-based recommendations is needed to inform policy development that will more effectively address press environmental issues such as biodiversity loss. One area of research that could provide valuable insight for policy development are studies that consider multiple scales and taxonomic groups across the soil surface.

Aim and scope of thesis

This thesis aimed to investigate above- and belowground components of agrobiodiversity simultaneously and comparatively to enhance the understanding of agroecosystems and the effects anthropogenic factors have on local biotic communities and ecological processes. In doing so, a more holistic impression of the impact agricultural land use has on multi-taxa communities and its consequences for multifunctionality, is attained.

To build on existing research about the effects of land use on ecosystem multifunctionality, I focus my research chapters on addressing several of the knowledge gaps outlined in the previous sections. Firstly, I investigated the occurrence of scale-dependent responses of above- and belowground groups to land use, and study the similarities and dissimilarities in how different trophic groups respond. Additionally, investigating the relative importance of anthropogenic land use related factors (e.g. land management and land use intensity) versus abiotic factors (e.g. local topography, soil, and regional weather conditions) in shaping above- and belowground communities, respectively. And lastly, I consider the different large- and small-scale drivers impacting on multiple trophic communities across the soil surface within agroecosystems.

For the respective research chapters I make use of multi-taxa datasets from biodiversity monitoring conducted within agroecosystems situated in Central Germany, Sachsen-Anhalt (Median Latitude: 51.64; Median Longitude: 11.50; South-bound Latitude: 51.36; West-bound Longitude: 11.03; North-bound Latitude: 52.09; East-bound Longitude: 11.76. The study sites form part of the Terrestrial Observatories in Germany and are representative of a typical Central German, and Central European agricultural landscape (Zacharias et al. 2011). In each of the chapters I maintain a multi-taxa approach across the soil surface to address my respective research questions. The focal taxa groups covered are from several trophic levels that contribute to key ecosystem functions and services, namely:

Aboveground taxonomic groups:

- wild bees (consumers providing, for example, pollination services)
- (flying) ground beetles (consumers providing, for example, pest suppression services)

Soil interface taxonomic group:

- vascular plants (primary producers providing a range of ecosystem functions and services)

Belowground taxonomic groups:

- free-living soil fungi (several trophic roles including, for example, decomposers, pathogens and symbionts providing multiple services, such as, soil structure formation, nutrient cycling, and contributing to plant productivity)
- free-living soil bacteria (mostly decomposers providing multiple services, such as, soil structure formation, nutrient cycling, and plant protection against pathogens)

Outline of research chapters

As previously stated, an overarching theme of my thesis includes looking at above- and belowground components of biodiversity simultaneously. I accomplish this by either individually analyzing the respective taxa groups in the same way for comparison across taxa groups or by analyzing several groups collectively. I systematically investigate the impact of anthropogenic factors on above- and belowground taxonomic groups, first considering the issue of scale, then aspects related to community assembly processes, and lastly studying which direct and indirect drivers are shaping the richness, diversity and composition of multi-trophic communities within agroecosystems. See Figure 1 for a visual overview of the main research topics.

The first research chapter (**Chapter 2**) investigates patterns of biodiversity change of different land management treatments across two spatial grains. This chapter evaluates biodiversity of above- (vascular plants) and belowground (free-living soil bacteria and fungi) taxa groups, within semi-natural grasslands as a case study. I investigate the impact of land management on the classic ‘species richness’ measure, as well as related biodiversity components (i.e., density of individuals, species-abundance distribution, and spatial aggregation) of the respective taxonomic groups at two spatial scales (plot- and site-level).

In the second research chapter (**Chapter 3**), I use a subset of the same grassland dataset used in **Chapter 2** to ask more mechanistic questions of the effects land use has on the diversity of above- (vascular plant) and belowground (free-living soil fungi) taxonomic groups. To do so, I investigate whether the land management and land use intensity or local abiotic conditions or biotic interactions are the main drivers of species co-occurrence patterns of the respective above- and belowground taxa groups. As analysis method, I apply a joint-species distribution model approach to disentangle to what extent land use, abiotic factors and biotic interactions shape the respective taxonomic groups.

In the third research chapter (**Chapter 4**), I investigated how multiple trophic groups across the soil surface are influenced by large- (land cover and weather conditions) and small-scale (local soil and topography) abiotic drivers within agricultural landscapes, as well as the level of connectivity across trophic groups through considering indirect effects of specific factors. For this I compiled structural equation models to assess the importance of different drivers in shaping the species richness, diversity and community composition of five taxonomic groups (wild bees, carabids, vascular plants, free-living soil bacteria and fungi) covering a range of functional roles of relevance for ecosystem multifunctionality.

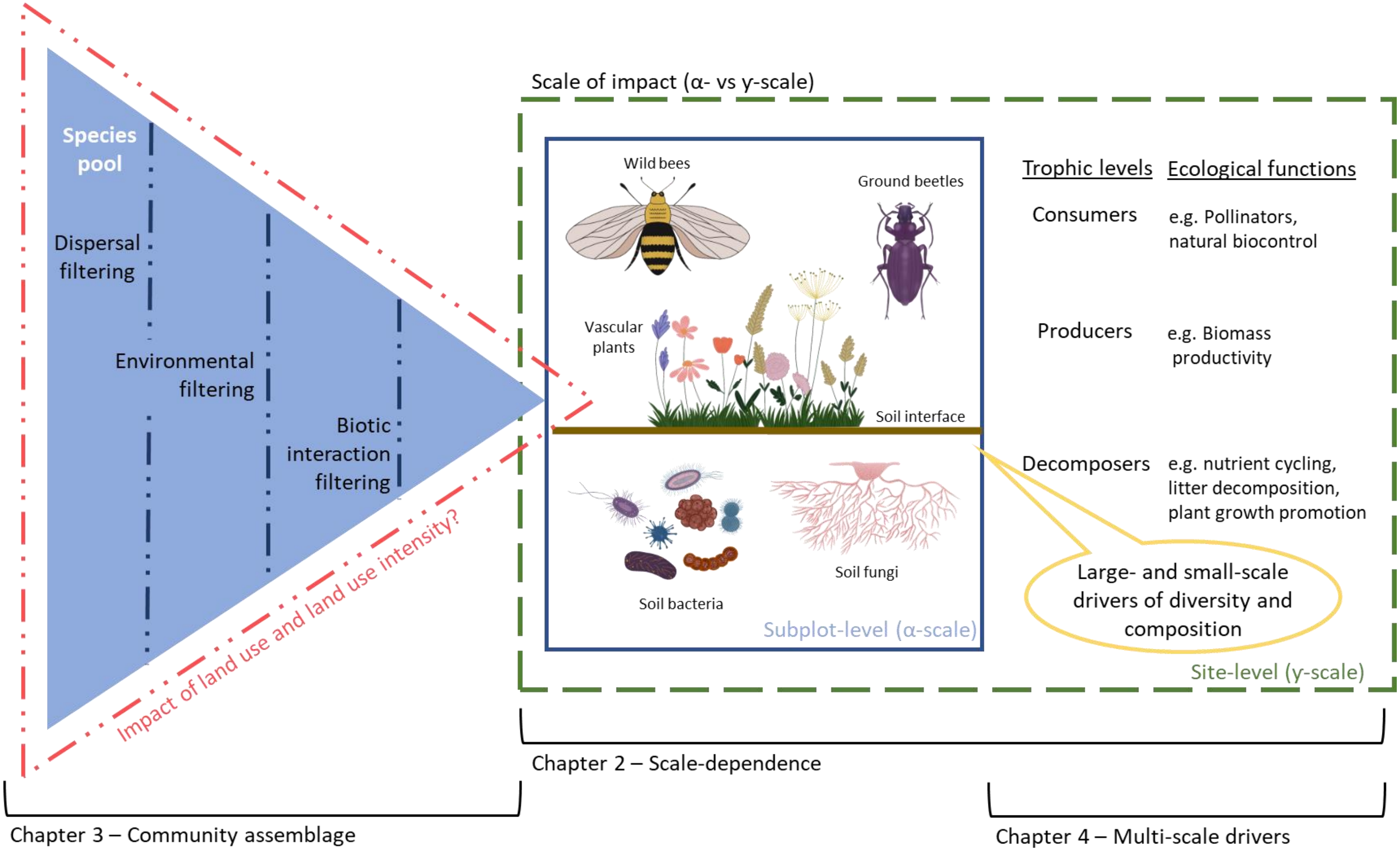

Figure 1. Graphical overview of main thesis topics as covered in the respective research chapters outlined above. Namely investigating the scale-dependence of land management impacts (Chapter 2), the impact thereof on ecological processes shaping community assemblage (Chapter 3), and the multi-scale drivers of trophic diversity for above- and belowground biodiversity relevant for multifunctionality of agroecosystems (Chapter 4). Taxa illustrations by Marija Milanović.

Chapter 2:

Scale-dependent impact of land management on above- and belowground biodiversity

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Scale-dependent impact of land management on above- and belowground biodiversity

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Abstract

1. Land management is known to have consequences for biodiversity; however, our synthetic understanding of its effects is limited due to highly variable results across studies, which vary in the focal taxa and spatial grain considered, as well as the response variables reported. Such synthetic knowledge is necessary for management of agroecosystems for high diversity and function.
2. To fill this knowledge gap, we investigated the importance of scale-dependent effects of land management (LM) (pastures vs. meadows), on plant and soil microbe diversity (fungi and bacteria) across 5 study sites in Central Germany. Analyses included diversity partitioning of species richness and related biodiversity components (i.e., density of individuals, species-abundance distribution, and spatial aggregation) at two spatial grains (α- and γ-scale, 1 m^2 and 16 km^2, respectively).
3. Our results show scale-dependent patterns in response to LM to be the norm rather than the exception and highlight the importance of measuring species richness and its underlying components at multiple spatial grains.

[Correction added on 1 November 2020, after first online publication: Projekt DEAL funding statement has been added.]

4. Our outcomes provide new insight to the complexity of scale-dependent responses within and across taxonomic groups. They suggest that, despite close associations between taxa, LM responses are not easily extrapolated across multiple spatial grains and taxa. Responses of biodiversity to LM are often driven by changes to evenness and spatial aggregation, rather than by changes in individual density. High-site specificity of LM effects might be due to a variety of context-specific factors, such as historic land management, identity of grazers, and grazing regime.
5. *Synthesis and applications:* Our results suggest that links between taxa are not necessarily strong enough to allow for generalization of biodiversity patterns. These findings highlight the importance of considering multiple taxa and spatial grains when investigating LM responses, while promoting management practices that do the same and are tailored to local and regional conditions.

KEYWORDS

above- and belowground taxonomic groups, biodiversity, grassland management, rarefaction curve, scale-dependent responses, spatial aggregation, species-abundance distribution

1 | INTRODUCTION

It is critical to understand how land management (LM) influences the diversity of organisms if we are to maintain, and possibly restore biodiversity and the ecological functions that it provides. Response patterns to these factors depend on the focal taxonomic group considered and the spatial grain of measurement. Taxa are known to respond differently to the same LM gradient (Gossner et al., 2016; Penone et al., 2018), likely due to their different generation times, dispersal abilities, and other life-history characteristics. Effects of LM on biodiversity can become less prominent with increasing spatial grains as environmental variability created by LM decreases through spatial averaging at larger scales of investigation (Levin, 1992) and other environmental factors, such as climate, can increase in importance (Carl, Doktor, & Schweiger, 2016). Therefore, our understanding of the effects of LM on biodiversity would be improved by studies that consider both multiple taxa and different spatial grains.

The scale-dependent effects of LM on observed species richness depend on their effects on its underlying biodiversity components, namely (a) the density of individuals (i.e., species abundance), (b) their relative abundances or the evenness of the community (i.e., species-abundance distribution), and (c) the spatial aggregation of species (Chase et al., 2018; Simons et al., 2017). For example, if LM primarily reduces the density of individuals, the impact on species richness may only be evident at smaller spatial grains since fewer species are observed when there are fewer individuals. However, with increasing grain, the chances of observing at least one individual of rarer species increases. LM may also alter the evenness of communities by changing the availability of specific resources. For instance, nutrient input and/or high access to light in grasslands with intense LM can result in the dominance of species adapted to these conditions (Hülbera et al., 2017; Ignatavičius, Sinkevičius, & Ložytė, 2013). Thus, most individuals sampled at small grains would be those of the dominant species, whereas rare species would be observed at larger grains. Finally, LM can affect the spatial aggregation of species, for example, by altering the heterogeneity of the habitat, presence of different microsites, and by influencing the dispersal of propagules (Baltzinger, Karimi, & Shukla, 2019; Tälle et al., 2016). For instance, a decrease in habitat heterogeneity by specific LM practices has been shown to homogenize biotic communities (Allan et al., 2014; Gossner et al., 2016; Hendrickx et al., 2007). In this case, LM effects on biodiversity would become more apparent at larger spatial grains.

Furthermore, it has also been shown that within an ecosystem different species groups can react differently to environmental drivers and that these differences can be scale-dependent (Gossner et al., 2016; Penone et al., 2018; Schuldt et al., 2015). For example, local species richness of belowground soil biota are less or even positively affected by intense agricultural land use in comparison with aboveground taxa which show a more pronounced negative response (Allan et al., 2014; Gossner et al., 2016). However, at larger spatial scales, responses are more similar between above- and belowground taxa (Gossner et al., 2016). Yet, it remains unclear which biodiversity components (i.e., density of individuals, community evenness, spatial turnover) are causing these taxa-specific scale-dependent responses.

To investigate the scale- and taxa-specific effects of LM on biodiversity and the underlying components, we considered seminatural grasslands in Central Germany under different LMs (pastures vs. meadows). Seminatural grasslands have formed due to historic land use practices and are some of the most species-rich habitats in Europe (Hönigová et al., 2012; Tälle et al., 2016). Seminatural grasslands are of value not only for their rich biodiversity of plant and animal species, but also as productive agroecosystems that provide an array of ecosystem functions and services (Hönigová et al., 2012; Ignatavičius et al., 2013). Traditional management of these grasslands using either low-intensity mowing and grazing is known to support high biodiversity, and it is unclear if one LM type promotes more biodiversity than the other. Increasing the intensity of either LM type, for example, through increased fertilization, mowing frequency or grazing intensity, is well-known to have negative consequences for biodiversity (Dahlström, Iuga, & Lennartsson, 2013; Ignatavičius et al., 2013; Socher et al., 2012; Tälle et al., 2016).

There is high variation across studies in the effects of grassland LM on biodiversity. A meta-analysis by Tälle et al. (2016) found that, within pasture-meadow comparisons, there was only a marginally more positive effect of pasture management in comparison to meadows in species richness of multiple taxa (e.g., insects, plants, earthworms, and spiders). Further analyses found effects to vary by grassland characteristics (e.g., grassland types) and many other factors that vary between studies, such as context-specific differences between different continents, grazer identities, and forms of intensification. The meta-analysis did not explicitly consider the spatial grains of the study, or underlying biodiversity components, which might also explain variation in richness responses to LM. The few studies on the effects of LM on soil microbial communities also show variable results. Some reporting significant shifts in community composition and structure (Patra et al., 2005; Wang et al., 2013), while other studies have found LM to have little to no effect (Bardgett & McAlister, 1999; Harold et al., 2014; Penone et al., 2018).

In the present study, we specifically compare grasslands managed for livestock grazing to those managed for hay production with the aim of explicitly investigating the importance of scale-dependent responses of multiple taxa to these LM types. Our study considers five sites, and each site has replicate grasslands of each LM type. The meadow management of all sites is similar, but the pasture management includes a variety of contexts (e.g., differences in grazing intensities and grazer species). Each study site provides a test to determine how LM influences species richness across taxa and spatial scales (i.e., α- (1 m^2) and γ-scales (16 km^2)), and which component of biodiversity (density of individuals, evenness, and spatial turnover) is most affected by LM. Across all five sites, we can assess whether there is any generality in these responses to LM, or if biodiversity conservation will require consideration of other aspects of the management context.

We expect scale-dependent effects of LM on biodiversity. Since grazers have localized disturbances (e.g., by trampling), we predict more prominent LM effects at the α- and ß-scale resulting in scale-dependent responses in species richness were pastures have higher richness in comparison with meadows. Due to grazer selectivity, we also expect stronger impacts of evenness and spatial aggregation on local species richness and turnover. Second, we expect that more closely linked taxa will have similar response patterns to LM (Bever, Westover, & Antonovics, 1997; Neuenkamp et al., 2018). For example, belowground soil microbe communities that are more directly connected with plant communities (e.g., soil fungi through mutualistic and symbiotic interactions) are expected to resemble plant responses to LM, while organisms with weaker links to plants (e.g., soil bacteria) should respond more independently of LM (e.g., see Hedlund et al., 2004).

2 | METHODS AND MATERIAL S

2.1 | Study area

We selected five study sites which form part of the Terrestrial Environmental Observatories (TERENO) (Zacharias et al., 2011). These sites are also part of the German and European Long-term Ecological Research networks. The latter being initiated in 2009 as part of the former EU FP5 GREENVEINS project (Billeter et al., 2008). Each site is 4 km by 4 km and represents typical agro-ecological landscapes in Central Germany and comparable landscapes across Europe. Sites differ in their extent of agricultural intensity, land management practices, and biophysical characteristics (e.g., mean annual precipitation and temperature; topography, see Frenzel, Everaars, & Schweiger, 2016), including soil chemical properties (Table S1). Unfertilized grasslands, managed predominantly for livestock grazing (pastures) or hay production (mown meadows, henceforth referred to as "meadows"), were identified within each site as the focal system of our study.

The placement of LM types within each site by farmers might be not at random, but based on local site conditions, such as topography or local soil conditions, which could confound our results of LM effects on biodiversity and, moreover, restrict a farmer's flexibility in decision making. We investigated this possibility and found that pastures and meadows did not differ consistently across the different sites in chemical soil properties (Figure S1, Table S2), but did differ in some topography features (e.g., slope) (Figure S2, Table S2).

The initial study design was balanced and nested with three grasslands per LM type per study site, each with a randomly placed sampling plot of 10 m × 10 m. Plots were subdivided into subplots of 1 m^2 from which 10 were randomly selected for sampling plants and soil microbes. Due to in-field limitations and more detailed records from farmers on field-specific management practices, the final data-set consisted of 270 subplots, 120 from meadows and 150 from pastures (Table 1) leading to a slightly imbalanced sampling design. All grasslands were in use as the respective LM type for at least the last 10 years. Meadows had similar mowing frequencies (once or twice), but the grazing intensities of the pastures differed (Table 1). We summarize the land use intensity (LUI) of pastures at each site by their grazing intensity per plot. Specifically, we used equivalent livestock units per hectare per annum standardized across the different grazer species (horse, cattle, sheep, mixed; Table 1) and categorized them to low, intermediate, and high intensity levels. With five sites, we do not have the statistical power to test how grazing intensity influences biodiversity responses to LM across spatial scales. However, these site categories do help with data visualization and discussion.

2.1 | Data collection and processing

Aboveground vascular plants and belowground, fungi and bacteria, were sampled during summer 2014. The finest spatial resolution was at subplot level (α-scale of 1 m^2), which was pooled to reach the γ-scale at site level (16 km^2), with turnover between them as ß-diversity. We did not consider the intermediate grain (plot), but rather focused on the extremes of the scale gradient (i.e. subplot level and site level). Sampling included species richness and species abundances within the respective taxonomic groups per subplot. All vascular plant species were identified to species level, and their cover was visually estimated to the nearest percentage as a proxy for abundance. Nomenclature was cross referenced and updated according to "The Plant List" (2013). Soil microbial communities were sampled per subplot using a standard composite sampling approach whereby 5 soil cores of ca. 6 cm diameter to 10 cm depth (after removal of loose organic matter) have been collected and then pooled in-field and sieved to 2 mm. Of the pooled subplot sample, ten grams of the soil sample was flash-frozen on dry-ice for microbial analysis. A total of 270 soil samples were collected for further processing. An overview of the plant, fungi, and bacterial data is provided in the Table S3.

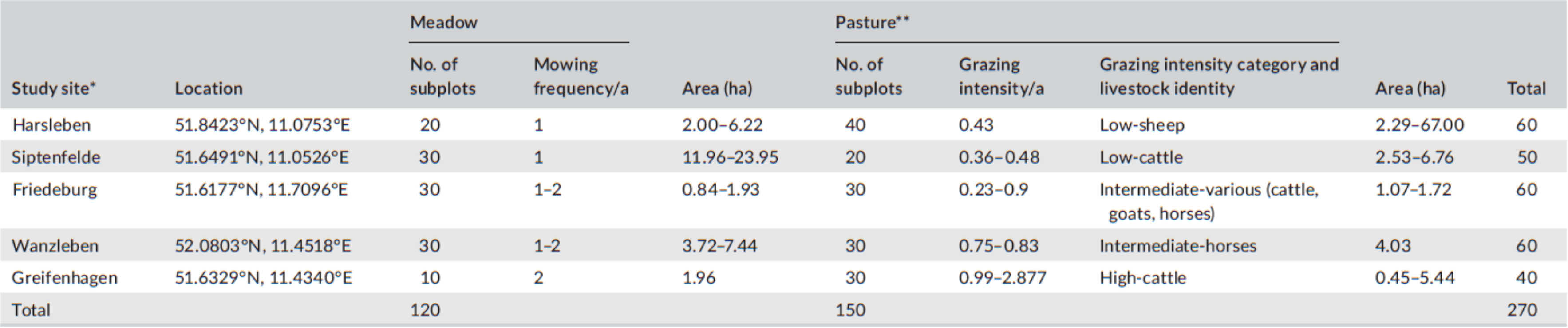
2.2 | DNA extraction, amplicon library preparation, and Illumina MiSeq sequencing

Soil microbial genomic DNA was extracted from 0.25 g of each soil sample using a PowerSoil DNA Isolation Kit (MO BIO Laboratories Inc.). DNA yields were quantified with a NanoDrop ND-8000 spectrophotometer (Thermo Fisher Scientific), adjusted to 10–15 ng/µl, and stored at −20°C. The V4 bacterial 16S rRNA gene fragment was amplified using the universal primer pair 515f and 806r (Caporaso et al., 2010) with Illumina adapter sequences. The PCR condition was initial denaturation at 95°C for 3 min, 25 cycles of denaturation at 98°C for 20 s, annealing at 55°C for 15 s, elongation at 72°C for 15 s, and a final extension at 72°C for 5 min. To generate the fungal amplicon library, seminested PCRs were performed, starting with amplification of the fungal ITS rDNA region using the primer combination ITS1F (Gardes & Burns, 1993) and ITS4 (White et al., 1990). The PCR thermo-cycle conditions were as follows: initial denaturation at 95°C for 5 min, 10 cycles of denaturation at 98°C for 20 s, annealing at 50–60°C for 15 s (−1°C per cycle), followed by elongation at 72°C for 15 s and 2 cycles of denaturation at 98°C for 20 s, annealing at 50°C for 15 s, followed by elongation at 72°C for 15 s. The final extension was carried out at 72°C for 5 min. The ITS2 region was subsequently amplified using 1:10 diluted products of the first PCR and the primer pair fITS7 (Ihrmark et al., 2012) and ITS4 (White et al., 1990). PCR was performed under the following conditions: initial denaturation at 95°C for 5 min, 25 cycles of denaturation at 98°C for 20 s, annealing at 56°C for 15 s, followed by elongation at 72°C for 15 s, and a final extension at 72°C for 5 min. All PCRs were conducted using the proof-reading Kapa Hifi polymerase (Kapa Biosystems). Paired-end sequencing of the equimolar pooled fungal and bacterial amplicon libraries was performed using a MiSeq Reagent kit v3 (2 × 300 bp) on an Illumina MiSeq platform (Illumina Inc.). The raw sequence datasets were deposited in the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) under the accession PRJNA563995.

2.3 | Bioinformatic analysis of the microbial datasets

Sequences from individual samples were de-multiplexed by the Illumina MiSeq Reporter software package v2.5.1.3 and then processed using custom bash scripts on a high-performance computing cluster following the workflow presented in Schöps et al. (2018). Briefly, paired-end reads were merged using PANDASeq v2.8. (Masella, Bartram, Truszkowski, Brown, & Neufeld, 2012) and the assembled reads were quality filtered using MOTHUR v1.39.5. Chimeric sequences were detected using the UCHIME algorithm in de novo mode as implemented in MOTHUR (Schloss et al., 2009). Reads from each sample were pooled, dereplicated, and sorted by decreasing abundance and pre-clustered. The cd-hit-est v4.6.1 algorithm (Fu, Niu, Zhu, Wu, & Li, 2012) was used to cluster sequences into operational taxonomic units (OTUs) at a similarity threshold of 97%. The representative sequences were classified against the UNITE database v7 (Kõljalg et al., 2013) for fungi and against the SILVA database v128 (2016-11-28; Quast et al., 2012) for bacterial sequences using the Bayesian classifier as implemented in MOTHUR (Schloss et al., 2009). Rare OTUs were removed from the dataset to remove the impact of potential sequencing artifacts, OTU inflations and to reduce excessive variability due to extremely low occurrences. The data matrix was filtered to only include OTU's that occurred more than 5 times in at least 1% of the dataset using the "phyloseq" package (McMurdie & Holmes, 2019).

TABLE 1 Summary of land management (LM) and pasture grazing intensity of unfertilized seminatural grasslands managed as pastures or meadows in the Terrestrial Environmental Observatories, Central Germany



		Meadow			Pasture**				
Study site*	Location	No. of subplots	Mowing frequency/a	Area (ha)	No. of subplots	Grazing intensity/a	Grazing intensity category and livestock identity	Area (ha)	Total
Harsleben	51.8423°N, 11.0753°E	20	1	2.00–6.22	40	0.43	Low-sheep	2.29–67.00	60
Siptenfelde	51.6491°N, 11.0526°E	30	1	11.96–23.95	20	0.36–0.48	Low-cattle	2.53–6.76	50
Friedeburg	51.6177°N, 11.7096°E	30	1–2	0.84–1.93	30	0.23–0.9	Intermediate-various (cattle, goats, horses)	1.07–1.72	60
Wanzleben	52.0803°N, 11.4518°E	30	1–2	3.72–7.44	30	0.75–0.83	Intermediate-horses	4.03	60
Greifenhagen	51.6329°N, 11.4340°E	10	2	1.96	30	0.99–2.877	High-cattle	0.45–5.44	40
Total		120			150				270

Note: *Site names refer to the nearest large village.

**Average mowing and grazing intensities per annum of the respective LM types, as well as different grazers present on pastures are indicated. Grazing intensity was standardized as livestock units per hectare per annum (LSU/ha/a). Three grazing intensity categories (low, intermediate, and high) were allocated to the sites based on the LSU/ha/a for increased ease of visualization and discussion of results.

2.4 | Statistical approach

To investigate scale-dependent responses of the three taxonomic groups (plants, fungi, bacteria) to LM, we used the "measures of biodiversity" package ("mobr"; McGlinn et al., 2019) within R (R Core Team, 2019) to calculate biodiversity indices for α-, γ-, and β-diversity and followed the analytical framework as outlined in Chase et al. (2018) and McGlinn et al. (2019). In addition to overall abundance (i.e., % cover of plants and OTU reads of soil microbes) (*N*) and observed species richness (*S*), we also calculated rarefied richness (S_n) investigating whether LM effects on biodiversity were solely caused by differences in *N* or have density-independent effects on species richness. For instance, an effect of LM on *S* but not S_n is interpreted as a sole effect of *N*. Additionally, a measure of community evenness (S_{PIE}) tests whether LM changes the shape of the species-abundance distributions at α-scale and γ-scale. Comparisons of responses of S_{PIE} with that of S_n allow to assess whether the effects of LM on species richness are direct or rather indirectly caused by changes in evenness. At α-scale, species richness was rarefied to the minimum total number of individuals within a subplot across LM type using individual-based rarefaction curves, while for γ-scale, this minimum was multiplied by the number of replicates per LM. The slope at the base of the individual-based rarefaction curves yields the probability of intraspecific encounter (PIE) (i.e., an evenness metric) (Hurlbert, 1971) and is the equivalent to 1 - Simpson's index (Jost, 2006). For better comparisons to *S* and S_n, we converted PIE to an effective number of species (S_{PIE}) (i.e., the number of equally abundant species needed to reach the given species richness) (e.g., Hill, 1973; Jost, 2006, 2007). S_{PIE} captures changes in community evenness, with a particular weight on common species in comparison with changes in *S*, which gives equal weights to all species (McGlinn et al., 2019). S_{PIE} is based on species accumulation curves which cover density, evenness, and (implicitly) spatial extent. Since S_{PIE} is calculated as slope at the basis of these species accumulation curves, it is independent of both species pool and spatial scale. This ensures an unbiased estimation of S_{PIE} at α- and γ-scales, except under significantly altered community aggregation (Chase et al., 2018; McGlinn et al., 2019).

Disentangling the different underlying mechanism determining the response of species turnover (β-diversity) to LM follows in principle the same rationale than for α-diversity and γ-diversity, that is, comparing responses of *S*, S_n, and S_{PIE}. However, since the analyses of α-diversity and γ-diversity indicated a predominant role of evenness, we focused on β-diversity based on S_n and S_{PIE}. We use a multiplicative β-diversity metric to determine β-S_n and β-S_{PIE} (Whittaker, 1960). The influence of spatial aggregation (i.e., intraspecific clustering) can be disentangled using β-S_n, calculated from the same n (i.e., minimum total number of individuals within a subplot) for α- and γ-scales to control for density and species-abundance distribution effects (McGlinn et al., 2019). A high β-S_n relates to an increased spatial aggregation of common and rare species, while controlling for the effect of *N*, while β-S_{PIE} is more representative of aggregation among common species. By comparing β-S_n and β-S_{PIE}, we identify the impact of turnover in evenness on spatial aggregation in comparison with turnover of species. A summary table adapted from Chase et al. (2018) of biodiversity metrics and their descriptions are in the supplementary material (Table S4).

We assessed the effect of LM (pasture vs mowing) on S and the different components of biodiversity separately for each site and taxonomic group. The effect sizes of LM were summarized as relative differences (i.e., log-response ratios) (Hedges, Gurevitch, & Curtis, 1999) and were then quantitatively compared with analyses of variance and permutation tests (perm = 199) (McGlinn et al., 2019). At α-scale, we used one-way analyses of variance (*F*-statistic) to compare observed LM differences to the null hypothesis of no difference. At the γ-scale, where there is only one value per treatment, the average relative difference between treatments was compared to a permuted distribution to determine an equivalent p-value statistic. Permutation (perm = 199) for γ-scale took place on data pooled across LM types. The null distribution was determined by calculating the difference in diversity indices for the LM types per permutation (Chase et al., 2018). Sampling imbalances across LM types were accounted for by standardizing sampling effort by a re-peated resampling procedure across the LM comparisons as needed at three of the five sites, that is, by repeatedly limiting the number of subplots per LM type to the minimum number available across LM types. The number of standardized replicates was determined by the total number of unique plot combinations possible without replacement. Replicated metrics and test statistics from this standardization were averaged using the R package "harmonicmeanp" (Wilson, 2019).

3 | RESULTS

3.1 | General overview

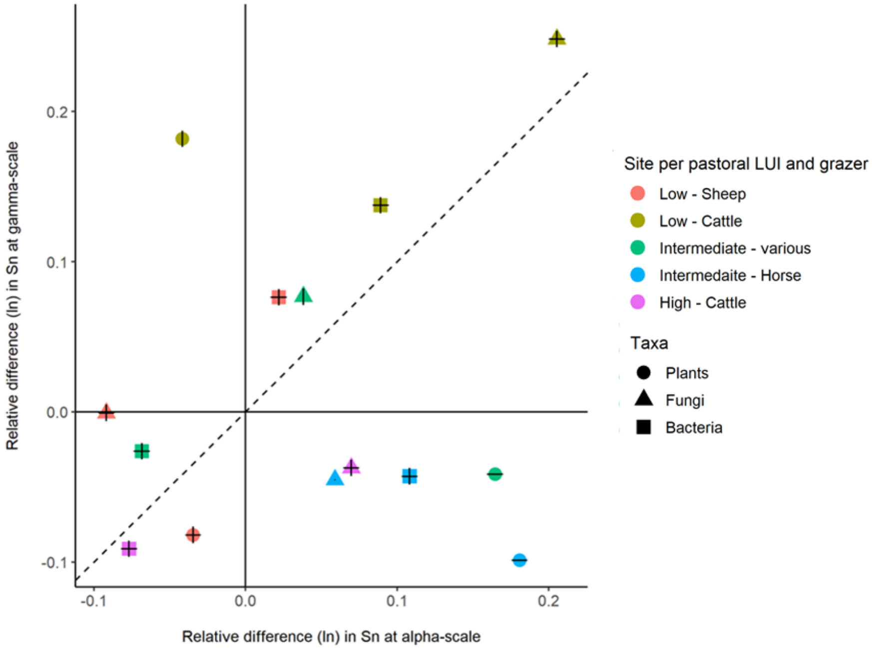
We identified scale-dependent responses of species richness (S) to land management (LM) for all species groups (Figure S3). These effects were only partly defined by differences in overall abundance (N) and remained qualitatively the same for rarefied richness (S_n) (Figure 1, Table S5). Responses of S and S_n to LM were highly site-specific and often not consistent within or across taxa. The underlying biodiversity component resulting in these responses was, however, often driven by a change in species evenness (α- and γ-S_{PIE}), and by turnover across subplots in the identity of the dominant species (β-S_{PIE}) (Figure 2, Table S5). In general, pasture LM increased S_n at sites with intermediate levels of LUI, while at sites with the lowest and highest pasture LUI, the meadow management had higher S_n (Figure 1, bottom left quadrant), especially for plants under the highest grazing LUI (Figure S4). Higher S_n in pastures compared to meadows was more common at the α-scale, but also present at the γ-scale, and often at both (e.g., bacteria and fungi at the low-cattle site; Figure 1).

3.2 | Species richness

The observed responses of S_n to LM included many reversals in direction across scales, as represented by points falling within the top left- and bottom right-hand quadrants of Figure 1. Qualitative scale- dependent responses, that is, with a significant reversal across both scales, included the fungal communities at the sites with low-sheep and high-cattle LUI and in the bacterial community at the site with intermediate-horse LUI (Figure 1). The other scale-dependent responses only had significant LM impact ($p < .05$) at one of the scales for specific taxa groups. These included plants at the sites with intermediate LUI with a LM response at only the α-scale (Figure 1, bottom right-hand quadrant); while plants at the low LUI cattle grazed site only had a LM response at the γ-scale (Figure 1, top left-hand quadrant).

The frequency and direction of the response of S_n to LM was consistent across scales for specific taxa groups at some sites (e.g., plants and bacteria at high-cattle LUI, and bacteria and fungi at low-cattle LUI), but also varied across scales (e.g., fungi at the low- sheep and high-cattle site; and plants and bacteria at the intermediate-horse site) and between the respective taxonomic groups at some sites (e.g., plants and bacteria at the low-sheep site; and bacteria and fungi at intermediate-various site) (Figure 1). Within a few sites, all taxa responded similarly to LM (e.g., pasture management resulted in higher γ-S_n at the low-cattle site, while the LM resulted in lower γ-S_n at the intermediate-horse-grazed site).

Bacteria had a significant change in S_n as response to LM across both scales for all five sites, although with less pronounced scale dependence (Figure 1). Pasture management generally increased α- and γ-S_n of bacteria at the lower LUI, and decreased S_n at the intermediate to highest LUI, with the exception of the horse-grazed sites α-S_n. In comparison, plants and fungi were only moderately less responsive at the respective scales of investigation, and also had site-specific LM



FI G U R E 1 Scale-dependent impact of land management (pasture vs. meadow) observed as a change in the log-response ratio (Relative difference (ln)) in rarefied species richness (Sn) at the α-scale (subplot level, 1 m^2) and γ-scale (site level, 16 km^2) for above- (i.e., plants circles) and belowground taxa (i.e., soil fungi and bacteria triangles and squares, respectively). The log-response ratio between management types was calculated with meadows as reference, thus positive values indicated that S_n is higher in pasture management. Horizontal and vertical bars indicate significant differences (p < .05) in S_n between LM types based on the ANOVA and permutation tests, for α- and γ-scales, respectively. The dashed 1:1 line indicates no scale dependence. Sites are color coded according to pasture land use intensity (LUI) calculated as livestock units per hectare per annum, see Table 1 for more details. The plant community comparison at the highest pasture LUI was excluded as this distorted the scale for other comparisons (α- & γ-scale S_n, −6.4 and −20.0, respectively) (see Figure S1)

outcomes on S_n. Pasture management decreased α- and γ-S_n for plants at sites with the highest LUI (Figure S4) and low LUI, with cattle and sheep grazing, respectively (Figure 1). While at other sites, with low-to-intermediate LUI grazing, plant S_n increased at both scales. The impact on fungal S_n at both scales was the least consistent, with the direction of impact occasionally being in reverse across scales as highlighted before (Figure 1).

3.3 | Biodiversity components resulting in scale- dependent responses

Pasture management mostly increased *N*, with the exception of plants at the low-cattle site (Figure S5). The magnitude of change in *N* across LM types was, however, much lower than the contribution of altered community evenness of common species (α- and γ-S_{PIE}) or the differences in their spatial turnover (β-S_{PIE}) (Figure 2). The direction of altered dominance among common species between the LM types (Figure 2) often reflected the scale-related responses observed in S_n (Figure 1). For example, at the low-cattle site, pasture management increased plant richness at the γ level but not α level (Figure 1), and plant species evenness was also higher with pasture management at the γ level, but not α level (Figure 2).

For all taxonomic groups, changes in community turnover across the two LM types were caused by species turnover (β-S_n) to a lesser extent, while changes in evenness (β-S_{PIE}) contributed the most with some consistency within the respective sites between taxa (Figure 2a, b, d, e, β-S_{PIE} and Figure S6). The relative contribution of altered β-diversity to the change in S_n was usually lower than that of S_{PIE}, with the exception of fungi at the lower LUI (Figure 2a, b). Here, β-S_{PIE} of fungal species either increased (Figure 2a) or decreased (Figure 2b) much more than at other sites or for the other taxa groups. Interestingly, LM occasionally altered β-S_{PIE} in the opposite direction than its impact on S_{PIE} (Figure 2a, b, d).

4 | DISCUSSION

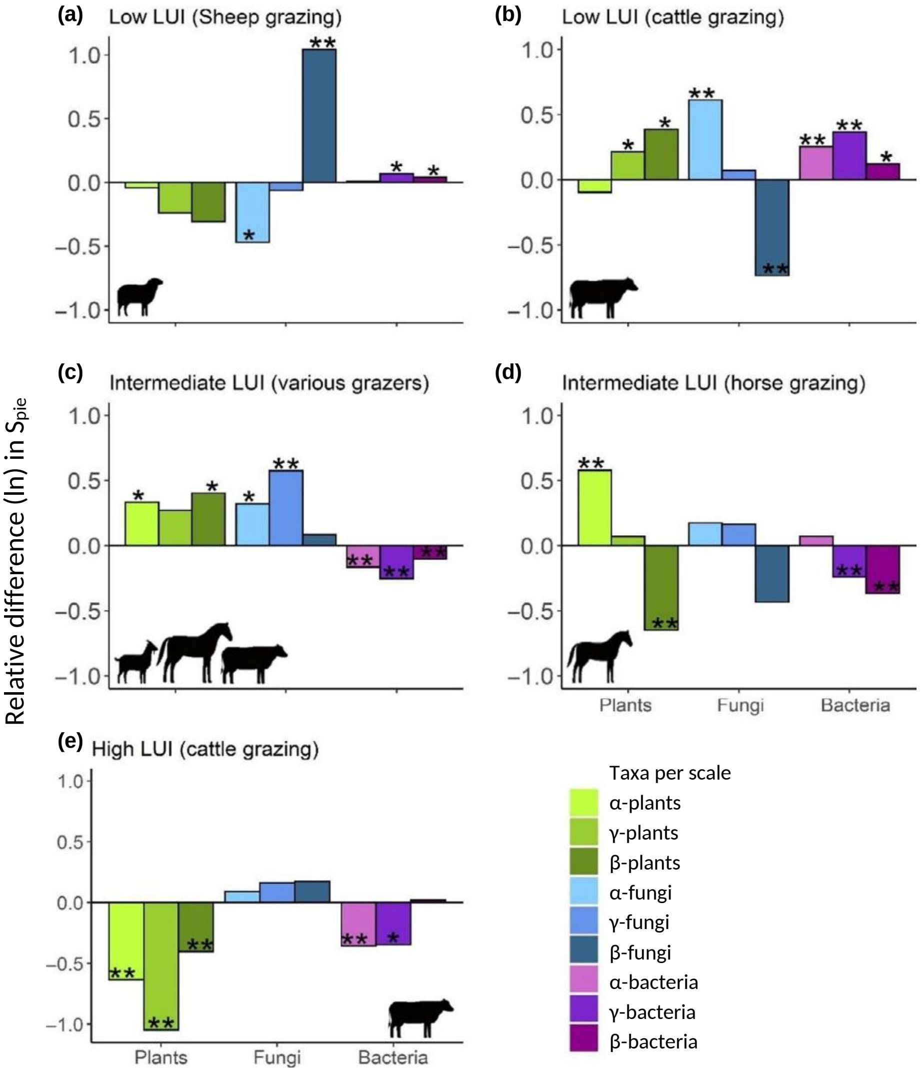
4.1 | General overview

Scale-dependent responses to LM were evident across both above- and belowground taxonomic groups and for all sites, indicated by no LM comparisons falling on the 1:1 line in Figure 1. Our prediction that pasture LM would increase species richness (*S* and S_n) was mostly supported with only a few exceptions. However, the scale-dependent patterns within and across taxa groups were less consistent than expected. In 50% of the cases, we observed a reversal of LM impacts across the α- (1 m^2) and γ- (16 km^2) scale, but the α-scale impact was not necessarily consistently more prominent as we initially predicted. Changes in *S*, irrespective of the directionality, were primarily driven by LM altering community evenness of common species (S_{PIE}), as well as the spatial aggregation of both common and rare species (β-S_n and β-S_{PIE}), rather than changes in species abundance (*N*). Considering our second hypothesis, regarding similarity of scale-dependent LM responses within closer linked taxa groups, our results showed no clear consistency for plants and fungi. LM effects were inconsistent among the sites, suggesting that context-specific factors, such as grazing intensity and grazer identity, might be important. Further, other factors, such as the time and seasonality of grazing or other unmeasured abiotic conditions, may influence biodiversity responses to LM. Our results suggest the need for studies that explicitly sample a variety of context-dependent factors that vary across sites.

4.2 | Scale dependency of LM, and the impact of grazing intensity and grazer identity

The response of S_n to LM was highly scale-dependent, and the direction of the effect varied at different grazing intensities. Pasture management often resulted in higher species richness at the α- and γ-scales at sites with intermediate grazing intensities, while the positive effect of pasture management was in reverse at the lowest and highest grazing intensity sites. These LM results are consistent with the idea that disturbances of intermediate intensity and frequency allow for higher diversity through creating habitat heterogeneity at γ-scale and modulating competition among species at the α-scale (Connell, 1978). Our results coincide with some of the studies in the meta-analyses by Tälle et al. (2016), several of which found grazing, especially in central Europe, to favor higher species richness in grasslands.

The higher S_n in pastures in comparison with meadows was due to an increase in pasture communities' evenness and species turn-over, especially under certain low-to-intermediate grazing intensities. This suggests that the positive impact of pasture management could be a consequence of higher habitat heterogeneity, which likely promotes higher species coexistence and spatial aggregation of habitat specialists. This increase in evenness of pasture communities is in contrast to other grassland studies in the meta-analyses by Tälle et al. (2016) that found mowing, rather than grazing, to increase community evenness. Another noteworthy finding includes the observation that diversity patterns were more strongly driven by a change in common species, and not only due to a loss of rare species. Observations that could be explained by the "niche differentiation hypothesis" (Connell, 1978); with more diversity of habitat niches, more species can coexist as species can spatially be arranged according to their resource needs. Contrastingly, grazing reduced local species richness for most taxa groups at two sites: the pasture with low-sheep grazing intensity and the site with high-cattle grazing intensity.



FI G U R E 2 Scale-dependent impact of land management (pasture vs. meadow) on the log-response ratio (Relative difference (ln)) of effective number of species (S_{PIE}) for above- (i.e., plants, green) and belowground taxa (i.e., soil fungi and bacteria, blue and purple, respectively). The log-response ratios between management types were calculated with meadows as reference at α-scale (subplot level, 1 m^2) and γ-scale (site level, 16 km^2), and β-diversity (scales indicated from lightest to darkest hue) per taxa. Positive values of α- and γ-S_{PIE} indicate that pastures have more even communities compared to meadows, while a positive β-S_{PIE} is representative of higher turnover among common species in pastures. Asterisks' indicate significance differences (**p* < .05; ***p* < .01; ****p* < .001) between management types based on ANOVA and permutation tests, for α- and γ-scales, respectively. Sites are labeled according to pasture land use intensity (LUI) calculated as livestock units per hectare per annum, see Table 1 for more details.

Here, the negative impact on the respective communities was a result of grazing promoting the dominance of only a few species, possibly by selecting plant species with a high tolerance for grazing, excessive trampling, or both (e.g., *Lolium perenne* and *Festuca rubra*). These results suggest even higher site specificity than found by Tälle et al. (2016).

The high-site specificity of the LM impacts can be due to a variety of site-specific factors, such as historic LM, identity of the grazers, grazing regime, soil properties, or topography. Legacy effects of historic LM practices on our grasslands could be resulting in less consistent scale-dependent effects than expected across scales and taxa. It is known that past landscape structure and long-term LM and LUI of an area have a significant role in shaping current biodiversity patterns (Gustavsson, Lennartsson, & Emanuelsson, 2007; Poschlod et al., 1998). Continuity of historic LM, for example, has been found to have lasting effects on the local communities by determining current species pools (e.g., of grassland plants) (Eriksson, Eriksson, & Berglund, 1995; Gustavsson et al., 2007). The study by Gustavsson et al. (2007) found land use of 200 years ago to be a better predictor of biodiversity patterns for both plants and soil microbes than current land use. This suggests LM to have had a time-lagged effect on these communities. Comparable soil chemical properties across LM types at certain sites hint at similar historic fertilizer applications that's effects are still evident. Unfortunately, a lack of historic data prevented us from investigating such potential legacy effects.

A second factor influencing the high-site specificity could be grazer identity, despite previous studies that have shown it to be of lesser importance than grazing intensity in shaping grassland communities (Stewart & Pullin, 2008). The occurrence of site-specific scale-dependent responses, especially for fungi and to some degree plants, suggests that grazer identity may potentially be a prominent factor. Different grazers alter the local microclimate and habitat heterogeneity in distinct ways while also impacting the dispersal patterns of propagules (e.g., via endo- or epizoochory) (Baltzinger et al., 2019; Golan & Pringle, 2017). For instance, the amount and effectiveness of dispersal is correlated with body size (i.e., volume of biomass they consume) and other properties linked to grazer identity, such as feeding habit, behavior, and fur or hair characteristics (Baltzinger et al., 2019). The impact of grazers on community dynamics could seem counterintuitive in both creating higher habitat heterogeneity that leads to higher coexistence (i.e., high β-diversity), while also facilitating dispersal that would lower β-diversity. Our results, contest this, showing that the overall "net" outcome can still be an increase in species richness. In contrast, the less frequent removal of biomass through mowing results in more homogeneous habitat conditions, higher nutrient inputs, and increased competition for light (Hülbera et al., 2017; Ignatavičius et al., 2013). These conditions could result in a shift in species composition, with higher intraspecies competition and increased dominance of species tolerant to these conditions, as our results suggest for instance in the plants and bacterial communities of the high grazing intensity site. Another factor influencing high-site specificity could be grazing regime, for example, continuous versus rotational grazing and extensive versus intensive grazing. Although it is not statistically considered in detail here, these management decisions and the movements of grazers between fields would further influence observed biodiversity patterns and the size of the species pool influencing the richness of the local communities (Poschlod et al., 1998).

We did not find consistent differences in soil chemical properties (Figure S1, Table S2) and only a slight but expected preference for pastures at steeper slopes (Figure S2, Table S2). Thus, soil conditions might not be responsible for site specificity, but on the other hand, this indicates greater flexibility of independent management decisions, within some topographical boundary conditions, strengthening the relevance of our results in terms of conservation.

4.3 | Scale-dependent responses within and across taxa.

The LM response of plants and fungi, as closer associated taxa, was not remarkably more similar to each other in comparison with bacteria as we hypothesized. Our findings are in contrast to previous studies that found more linked LM responses (Hedlund et al., 2004) or consistent responses for above- and belowground taxonomic groups to LM (Gossner et al., 2016; Simons et al., 2017). Our results suggest that these trends are not as simple when multiple spatial grains and highly variable sites are considered. Similarly, Schuldt et al. (2015) found that fungi and bacteria had distinct scale-dependent response rates in species turnover. Together, these results also point to higher complexity of scale-dependent responses of belowground soil microbiota to environmental factors, and advocates for more scale-explicit investigation of soil microbial communities. Similar site-specific factors, as outlined above, could be causing the low consistency of LM responses within and across taxa groups. Legacy effects on the taxa groups could, for instance, be temporally staggered (e.g., due to different turnover rates). Thus, plant communities, for example, could be reflecting LM of a few centuries ago (Gustavsson et al., 2007), while microbial communities, with shorter generation times, could be more representative of current LM responses (Felske & Akkermans, 1998).

5 | CONCLUSIONS

Our results highlight that scale-dependent patterns in responses to land management (LM) are the norm rather than the exception. This emphasizes the importance of investigating the underlying components resulting in these patterns. Despite clear links and interactions influencing diversity patterns of above- and belowground taxa, our findings suggest these links to not be strong enough for generalization of biodiversity patterns. Furthermore, that the simple dichotomy between the two LM types (here pasture and meadow management of grasslands) fails to accurately consider the context specificity of scale- and taxa-dependent responses to LM.

Our findings affirm existing management recommendations advocating low-to-moderate grazing intensities for promoting biodiversity, through creating habitat heterogeneity, and warn against too high grazing intensities which can reduce species richness. Our study provides a first step in our understanding of the management that might promote biodiversity of multiple taxa at multiple spatial scales, but the context dependency highlights the need for more studies that consider multiple scales and taxa within a variety of contexts (e.g., grazing regime, historical land use). For the time being, we recommend that overarching policies, such as the European Common Agricultural Policy (CAP), advance agro-biodiversity conservation by having a framework that allows for local adaptation of management regimes, and prioritizes conservation of multiple taxa, across multiple spatial grains.

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CONFLIC T OF INTEREST

The authors have no conflicting interests to declare.

AUTHOR CONTRIBUTION

Eleonore L. Slabbert: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Software (lead); Validation (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Oliver Schweiger:** Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (supporting); Project administration (supporting); Supervision (equal); Validation (equal); Visualization (supporting); Writing-original draft (equal); Writing-review & editing (equal). **Tesfaye Wubet:** Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Resources (equal); Supervision (supporting); Validation (supporting); Writing- original draft (supporting); Writing-review & editing (supporting). **Antje Kautzner:** Conceptualization (equal); Data curation (equal); Investigation (lead); Project administration (equal); Writing-original draft (supporting); Writing-review & editing (supporting). **Cornelia Baessler:** Conceptualization (equal); Funding acquisition (equal); Investigation (supporting); Project administration (supporting). **Harald Auge:** Conceptualization (equal); Investigation (equal); Validation (supporting); Visualization (supporting); Writing-original draft (supporting); Writing-review & editing (supporting). **Christiane Roscher:** Conceptualization (equal); Investigation (equal); Validation (supporting); Visualization (supporting); Writing-original draft (sup- porting); Writing-review & editing (supporting). **Tiffany M. Knight:** Conceptualization (lead); Formal analysis (supporting); Methodology (equal); Supervision (equal); Validation (equal); Visualization (supporting); Writing-original draft (equal); Writing-review & editing (equal).

DATA AVAIL ABILITY STATEMENT

Plant data is archived on PANGAEA (Kautzner, Auge, Roscher, Baessler & Slabbert, 2020; https://doi.org10.1594/PANGAEA.919343) and the soil microbial data on the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) under the accession PRJNA563995 (Kautzner, Baessler, Auge, Roscher & Wubet, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section, as well as in the Appendix of this thesis.

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Chapter 3:

Abiotic factors are more important than land management and biotic interactions in shaping vascular plant and soil fungal communities

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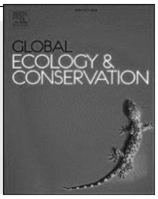

Abiotic factors are more important than land management and biotic interactions in shaping vascular plant and soil fungal communities

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ABSTRACT

Human-induced disturbances to ecosystems cause a direct loss of biodiversity, and also alter the inherent processes that shape ecosystems even after the main disturbance has ceased. Therefore, is it important to understand the ongoing consequences of past and present land use practices on both above- and belowground components of agroecosystems. Our study takes a detailed investigation of what shapes communities in semi-natural grasslands under long-term management as either pastures or meadows. We investigated the relative importance of land use (land management (LM) and land use intensity (LUI)) and abiotic conditions (soil, topographic, climatic) across five grassland sites in central Germany in explaining species occurrence patterns of vascular plants and soil fungi. Analyses included a hierarchical joint-species distribution modeling approach to uncover the role of possible drivers shaping the local communities.

Our results show that abiotic factors are of particularly high importance compared to LM and LUI for both vascular plant and soil fungal communities. In general, the relative importance of explanatory variables was similar across both taxon groups, however, for plant communities, local climate conditions were more important, while for fungal communities the soil variables (e. g., soil acidity and fertility including soil carbon and potassium concentrations) played a more prominent role. Species-specific responses to the respective variables showed some similarity across the taxon groups, however less so than expected given the long legacy of past LM. Here we found that approximately 50% of the plant and fungi species had clear LM preferences and responses to LUI. More plant species were positively related to pasture than meadow management, while the opposite was found for fungal species. Our findings advance the understanding of

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how abiotic conditions and human land use impact local species communities in managed semi-natural grasslands, aiding further research and policy development for conserving multitrophic diversity within these biodiversity rich habitats. Our results highlight the importance of controlling for soil and climate in studying the impact of land use, and of considering the environmental context at both small and larger spatial grains when making land management and biodiversity conservation decisions. In so doing, the complexity of ecological processes within managed systems are accounted for and prioritized, promoting both conservation and ecological functioning of the agroecosystem.

Data availability: Plant data is archived on PANGAEA (Kautzner, Auge, Roscher, Baessler & Slabbert, 2020; https://doi.org10.1594/PANGAEA.919343) and the soil microbial data on the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) under the accession PRJNA563995 (Kautzner, Baessler, Auge, Roscher & Wubet, 2020)

1. Introduction

Ongoing biodiversity loss and the degradation of resulting ecosystem goods and services has become an increasing concern in the past decades. Human-induced impacts due to land use change and increased intensification of agricultural systems continue to become more evident even years after the activity has ceased owing to soil-mediated legacy effects (Gustavsson, Lennartsson and Emanuelsson, 2007; Heinen et al., 2020). These long-lasting impacts elude to the complexity of ecological consequences of land use and management practices that go beyond just the obvious direct loss of natural habitats and biodiversity. It has become increasingly important to understand the ongoing consequences of past and present land use practices in order to better manage agroecosystems for more sustainable production, as well as for conservation and promotion of biodiversity within these novel ecosystems.

The diversity and composition of species found at any given point in time, and spatial scale, is determined by various community assemblage processes that have traditionally been perceived to function in a hierarchical manner (Kraft et al., 2015), or to be inter-linked by feedback loops (HilleRisLambers et al., 2012). The deterministic processes are broadly classified as being environmental and biological, and these serve as 'filters' for certain species occurring in any given area. Environmental filtering is typically considered the first filter, in which abiotic factors such as local (e.g., soil and topography) or biogeographical conditions (e.g., climate) select for species according to their fundamental niche (Sax, Early and Bellemare, 2013). Biotic interactions are considered as a second filter, shaping local community composition, including both intra- and interspecific interactions. Distinguishing between these processes, and their relevant importance, has proven to be challenging in studies of biodiversity patterns (Münkemüller et al., 2020).

Agroecosystems have become the dominant transformed landscapes in Europe and globally, and thus, understanding the effects of LM and LUI on the composition of these ecosystems in addition to the local and biogeographical context is important to sustaining ecosystem services. Several studies have found soil-mediated legacy effects are more important in explaining plant diversity patterns than current land use (Gustavsson, Lennartsson and Emanuelsson, 2007; Heinen et al., 2020), suggesting an important role of biotic filtering. Heinen et al. (2020), for example, found soil-mediated legacy effect are significant drivers of plant communities, especially via fungal-mediated pathways.

Research has clearly demonstrated that LM and LUI significantly influence above- and belowground biodiversity and community composition (Socher et al., 2013; Gossner et al., 2016; Tälle et al., 2016). However, it is still unclear if these anthropogenic changes are more important than local, biogeographical or biotic factors for community assembly. It has been shown, for example, that temporal variability in climate can be a more important driver of vegetation patterns than grazing (Ren et al., 2012) while other studies have found LM to have a strong effect on the richness and composition of plant communities (Socher et al., 2013; Allan et al., 2015). However, studies disentangling the impact of anthropogenic land use, local, biogeographical and biotic factors for both above- and belowground communities within one setting are scarce.

Our study investigates the importance of local (soil, topography) and biogeographical (climate) versus LM and LUI in explaining variation in vascular plants and soil fungi communities using semi-natural grasslands as a study system. While soil fungi represent the belowground aspect, vascular plants link belowground and aboveground biodiversity (Wardle et al., 2004). Semi-natural grasslands, which are managed as meadows (mown) and pastures (grazed), are important for both their conservation and human-use value (Ignatavičius, Sinkevičius and Ložytė, 2013; Dengler et al., 2014). These species-rich habitats emerged due to human use of the landscape under low land use intensity and are the biodiversity richest habitats within the European cultural landscape. Due to intensification and/or abandonment of traditional management, these biodiversity rich habitats are threatened by degradation and biodiversity loss of above- and belowground communities (Socher et al., 2012; Gossner et al., 2016).

Within the community assembly framework, we address environmental filtering by identifying local and biogeographical drivers of species co-occurrence at the community level, and potential biotic filtering by analyzing co-occurrence patterns. We hypothesize that local above- and belowground communities, specifically vascular plants and soil fungi, are influenced by LM and LUI more strongly than by soil, topography and climatic conditions or biotic interactions, because of strong legacy effects of LM in grassland systems managed for long times in the same way. We further hypothesize that vascular plants and soil fungi may have similar responses due to their close association and the legacy effects of LM that have shaped these communities collectively.

2. Materials and methods

2.1. Study site and design

This study was conducted in five sites of the Terrestrial Environmental Observatories (TERENO) network (Zacharias et al., 2011), located in the Central German Lowlands area, in the central German Lowlands observatory Saxony-Anhalt, Germany (Fig. S1). These sites also form part of the German and European Long-Term Ecological Research Network (www.lter-europe.net/). They are located near Friedeburg (FBG), Greifenhagen (GFH), Wanzleben (WAN) Harsleben (HAR) and Siptenfelde (SIP), cover 16 km^2 each, and differ in their landscape features including altitude, slope, soil properties and climatic conditions, as well as in their extent of land use intensity (Table S1; Frenzel et al., 2017).

Data collection took place on grasslands managed by local farmers following local practice for at least the past 10 years continuously as either pastures, for livestock grazing, or mown for hay production (here after referred to as ‘meadows’), both of which unfertilized (See Table S1 for further details). Pasture plots had a gradient of grazing intensity ranging from 0.23 to 2.88 livestock units/ha, whereas meadows were managed more uniformly, being mown for hay production only once or twice a year.

The initial sampling design was balanced with three grasslands per management type per study site that each contained a sampling plot of 10 by 10 m. Each plot was subdivided into a checker board of 1 m^2 subplots of which 10 were randomly selected for sampling. Due to site limitations the final dataset was marginally less balanced with an uneven number of plots across pastures and meadows. Of the 270 subplots samples, 150 were from pastures and 120 from meadows (see Table S1 for further details).

2.2. Data collection and processing

Data collection included two taxonomic groups, with soil fungi as the belowground representatives, and vascular plant species linking below- and aboveground diversity (Wardle et al., 2004). Plants were recorded to species level and their percentage cover per 1 m^2 estimated as a proxy for abundance. Plant species names where initially checked against the 'The Plant List' (2013) and then the Leipzig Vascular Plant Catalogue (Freiberg et al., 2020) for accuracy.

Soil microbial data was also sampled from each subplot, along with soil properties, using composite sampling of 5 cores (6 cm diameter x 10 cm depth) per subplot. Fungal operational taxonomic units (OTUs) were identified with next-generation sequencing. See Slabbert et al. (2020) for further processing details and barcoding procedure. Identification of fungal OTUs are hereafter discussed as species-level identification. Soil variables determined included soil pH (H_2O method); percentage moisture and dry matter content; calcium carbonate ($CaCO_3$) concentration and nutrient concentration (e.g., nitrogen (N), phosphorus (P), potassium (K)), and soil carbon concentration, including total carbon (TC), organic (TOC) and inorganic (TIC) carbon, and the carbon to nitrogen ratio (C:N ratio) using a Vario EL III Element Analyzer. Soil properties were determined using standard methods and are reported as mg per 100 g of soil (VDLUFA, 1991). Long-term climate data (i.e. 30-year average of mean annual precipitation and air temperature) was included as sourced from the weather stations managed by the Helmholtz Centre for Environmental Research – UFZ and the Deutscher Wetterdienst stations at the respective sites. These climatic variables were selected as they represent biogeographical factors impacting the distribution of species across our five sites (Zacharias et al., 2011) and have been found to impact plant (see, e.g., Feeley et al., 2020) and soil fungal communities (Větrovský et al., 2019). To capture more microclimatic differences created by local topography (Hannah et al., 2014) within and across sites we extracted topographical details at subplot-level, from a digital elevation model at 10 m resolution using the raster package (Hijmans and van Etten, 2012).

2.3. Statistical approach

Disentangling the effects of human land use and local and biogeographic factors assumes that their impacts are independent. However, farmers might adapt their management to climatic, topographic and soil conditions. To rule out such potential indirect abiotic effects being assigned to management, we used a Welch *t*-test to test for differences in topography and soil characteristics with respect to LM. We did not find a clear pattern across sites to suggest such adaptive management. See the supplementary material for an overview of the soil properties (Fig. S2) and an overview of topography (Fig. S3).

To disentangle the effects of land use variables, soil, topography and climatic conditions and biotic interactions on community assemblage within grassland ecosystems, we took a hierarchical joint species distribution modelling approach (Ovaskainen and Abergo, 2020), which utilizes residual species co-occurrence patterns, after accounting for species-environment relationships, to improve ecological niche models within a community framework. As a modelling tool we used the Hmsc package (Tikhonov et al., 2021) in R (R Core team, 2021), which fits a multivariate generalized linear mixed effects model with Bayesian inference using the Markov Chain Monte Carlo (MCMC) methods. The Hierarchical Modelling of

Species Communities (HMSC) framework allows for an integrative approach for investigating environmental filtering and species interactions (Ovaskainen and Abergo, 2020). The latent variable approach used enables analysis of large datasets, previously hindered by dimensionality limitations (Ovaskainen et al., 2016). The HMSC framework assumes that the environmental covariates provided are appropriate for representing the environmental filters acting on the communities and that the biotic filtering process can be inferred from the environmentally constrained residuals, presented as species-to-species correlation matrices. Further, the model assumes that residual variation not captured by the environmental or biotic filtering predictors can be attributed to random processes. However, we acknowledge that the residual variation might instead be attributed to unaccounted environmental factors and/or biotic interactions.

We modeled the taxa specific data as presence-absence data using a probit model, with a link scale in which zero means an occurrence probability of 0.5. Due to computational constraints, we filtered out rare species (vascular plants with less than five occurrences across the whole dataset, soil fungi with less than 10). To account for the nested study design, a three-tier random level was included in the model structure (Site | Plot | Subplot). Explanatory variables covered four categories: (i) land use, (ii) topography, (iii) soil, and (iv) climate. For a balanced subsequent aggregated estimation of relative importance, we selected two variables per category. To account for land use we included a categorical land management variable (LM) of grasslands management as either mown meadows or as grazed pastures, as well as a standardized index of "Land use intensity" (LUI) calculated according to Blüthgen et al. (2012), determined at plot-level. As our grasslands where either grazed or mown, and not fertilized, only the relevant section of the Blüthgen et al. (2012) LUI calculation was used based on grazing and mowing intensity over a two year period (2013–2014). The latter was log transformed (log(x+1)) to linearize the relationships. To cover topographical conditions, we used hill shading based on respective slope and aspect values (Horn, 1981) and a topographic position index (tpi) based on elevation, both calculated from the digital elevation model. Tpi is calculated as the difference in elevation between a focal cell and the mean of its eight neighbors and indicates whether the location is in a depression (negative values) or on a peak (positive values; Guisan et al., 1999). Hill shading combines information of slope, aspect and angle and azimuth of the sun and was calculated for the summer season. Hill shading and tpi were calculated per subplot by averaging across all 10 m grid cells. Both indices can serve as good proxies for above- and belowground microclimatic conditions, insolation, temperature and soil moisture in particular, with high relevance for vascular plant and soil fungi performance (Swetnam et al., 2017). To reduce the initial number of 11 soil variables to two, we performed a principal component analysis (PCA) and kept the first two axis (explaining together 72% of the variation). The first axis can be interpreted as representing soil carbon concentration (PC 1: highest loadings for TC and TOC). The second axis (PC 2) represented soil acidity (soil pH), con- centration of plant available potassium (soil K), and to a lesser extent plant available phosphorus. Same as for topography, soil information was represented at the subplot level. Climatic conditions were obtained at the site level and were represented by mean annual temperature and precipitation.

Numeric explanatory variables were checked for collinearity using the Hmisc package (varclus function) (Harrel, 2021), and *t*-tests for the factorial variable and all other variables (e.g., Fig. S2). No considerable colinearity (Pearson correlation coefficient < 0.4) was found. We scaled the numeric variables to have a mean of zero and unit variance, thus making the HMSC (weak) priors generally more applicable. For more details on the HMSC default priors see Ovaskainen and Abergo (2020).

Explanatory power is determined both by the ′Area Under the Curve′ (AUC) and Tjur R^2, the average predicted occurrence probability divided by sampling units with species occurrence minus those

without (Ovaskainen and Abergo, 2020). Predictive power was estimated using two-fold cross-validation in which 50% of the data was set aside as independent test data for assessing model predictability. Key parameters were then estimated using the MCMC method to determine how species occurrence patterns relate to abiotic variables, how dependent species niches are on the species broader taxonomic classifications (grouped to clade level classification for plants (five clades, Table S2) (Chase et al., 2016), and phylum level for fungi (seven Phyla, Table S3) (Köljalg et al., 2013). The HMSC models ran with four MCMC chains at increasing thinning and sample size until satisfactory MCMC convergence was reached, i.e. Gelman and Rubin′s convergence diagnostic′s upper limit is close to 1. For plants this required a burn in phase (transient) of 1250 000 iterations (thin 10,000, sample 250) and for fungi, 12,500 iterations (thin 100, sample 250).
The following measures from the HMSC were interpreted.

To assess the relative importance of abiotic factors, LM and LUI, variance partitioning (VP) took place at species level by estimating variance components for each fixed and random effect. Relative importance is presented as percentage explained variance at com- munity level, first grouped into thematic land use, biogeographical and local categories, and then per fixed effect as they appear in the model. The categories are as follows: Land use (LM and LUI); climate (temperature, precipitation); soil (first two soil PC′s) and topography (tpi and hill shading).

The response of the species to environmental variables β parameter in the Hmsc package (Tikhonov et al., 2021; Ovaskainen and Abergo, 2020) were summarized to indicate the percentage of species with positive and negative responses with a posterior probability of more than 0.85 for tabulation. Additionally, these response effect sizes and directions were also plotted as violin plots per broad taxonomic classification (only results for the vascular plants are shown).

As a final step, we investigated the pair-wise residual co-occurrence patterns (Omega parameter, Ω, in the Hmsc package) as species to species matrices per taxon group to make inferences about the potential impact of biotic interactions for the assembly of vascular plant and soil fungi communities compared to land use and local and biogeographic factors.

3. Results

Across all the plots and semi-natural grasslands 195 vascular plant species were recorded and identified to species level, as several were rare only 114 species were used in the analysis. These represent 31 vascular plant families, from five clades. The 7714,864 sequence reads of soil fungi were filtered down to 606 species-level identifications. These were further filtered down to 483 species, representing 165 fungal families and seven Phyla.

3.1. *Model convergence and explanatory power*

Convergence of the MCMC was satisfactory for the HMSC models. On average the potential scale reduction factors for the variance partitioning (VP) and the species response to environmental variables (β-parameter) were close to 1. The VP had an average potential scale reduction factor of 1.05 (Upper confidence limit, CI 1.13) for the plant model and 1.02 (Upper CI 1.07) for the fungi model. While the β-parameter had an average of 1.04 (Upper CI 1.11) for the plant model and 1.00 (Upper CI 1.02) for the fungi model.

Model fits for both plants and fungi were good. For the plant model, the mean AUC was 0.97 ± 0.03 (Tjur R^2: 0.49 ± 0.2) for explanatory power and with an AUC of 0.87 ± 0.15 standard deviation (sd) (Tjur R^2:

0.32 ± 0.17 sd) for the predictive power. AUC for the fungi model was for explanatory power 0.91 ± 0.06 (sd) (Tjur R^2: 0.34 ± 0.17 sd) and for predictive power it was 0.80 ± 0.12 (sd) (Tjur R^2: 0.20 ± 0.14 sd). See Fig. S4 for the relationship between explanatory and predictive power of the respective models.

3.2. Relative importance of land use, local and biogeographical factors

To assess the relative importance of land use variables in comparison to soil, topography and climatic conditions, we partitioned the variance explained by the respective grouped variables. This revealed a particularly high importance of biogeographical and local variables for both vascular plant and soil fungi species, while variance explained by land use (land management (LM) and land use intensity (LUI)) was comparably low (Fig. 1). Climate and soil explained most of the variance of the three local and biogeographical categories for both taxon groups. Partitioning variance was more similar between topography and land use. For the vascular plant species, climate and local soil explained a similar proportion of partitioned variance, while local soil explained slightly more variance in occurrence patterns of fungi than climate (Fig. 1). A relatively high proportion of variance was captured by the random effects. For both taxon groups this was highest at the plot level (Fig. S5), particularly for soil fungi which had more variance explained by the plot level variable (median 35%) than for the land use or local and biogeographical variables.

Comparing the respective taxon groups, we found in general that species occurrence patterns for vascular plants were better explained by the soil, topography, climatic and land use variables than for soil fungi (Fig. 1). Variance explained by climate was three times more important in vascular plants than in soil fungi, and by soil was twice as important. Variance explained by topography and land use remained more comparable across the taxon groups. Although soil, topography, climatic and land use variables had similar relative importance across the taxonomic groups, they were more relevant to vascular plants than soil fungi. For soil fungi, a large proportion of variance in species occurrences was not explained by the fixed effects but attributed to random plot-level effects.

Considering the land use, local and biogeographical variables independently (i.e. not grouped per thematic category), the vascular plant model showed temperature and soil carbon concentration (PC1) to be the most important variables explaining species occurrences, followed by precipitation and soil pH and K (PC2) (Fig. 2). For the soil fungi, species occurrence was mainly related to the soil variables (e.g., soil carbon concentration (PC1), soil pH and K (PC2) concentration), while temperature explained slightly less variance in fungal occurrence, but twice as much as precipitation. The latter being comparable to the variance explained by LM, or the respective topography variables for soil fungi. For the vascular plants, LM and the topography variables also explained a comparably lower proportion of the variance in species occurrence than the other variables. In both models' LUI explained the least amount of variation.

3.3. Effect size and direction of species responses to the environment

The effect size and direction of the species response to the land use and soil, topography, and climatic variables showed a mixture of positive and negative responses across both taxon groups, analyzed for a posterior probability of at least 0.85 (Table 1). Responses were either dominated by a positive or negative probability of a significant association with a respective variable. The preference for respective conditions

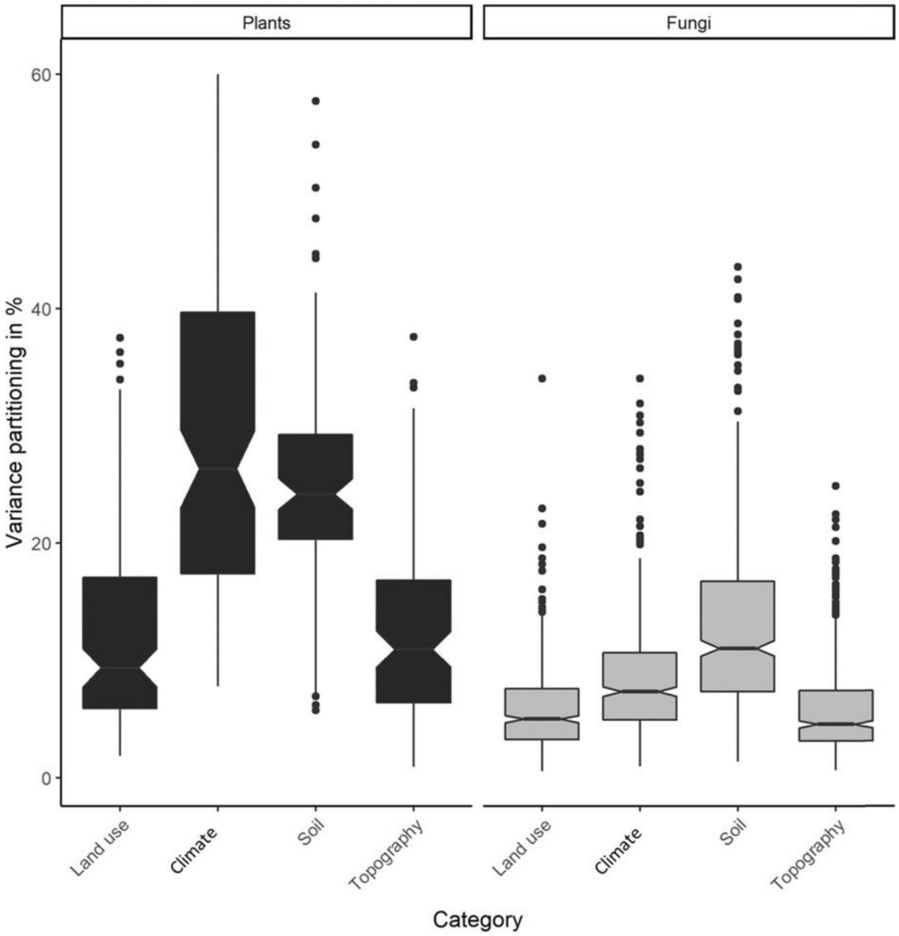

Fig. 1. Relative importance of land use and biogeographical variables in explaining variance in occurrence of plants and fungi species in semi- natural grasslands in central Germany. Random effects are accounted for, but not shown (see Fig. S4). The respective categories contain two variables each, land use = land management as pasture or meadow and standardized land use intensity; climate = mean annual precipitation and temperature; soil = first two PC loadings of a suit of soil variables (see main text), ecologically representing soil carbon concentration (TC and TOC) (PC1) and soil pH and plant available K concentration (PC2); and topography = topographic index and amount of hill shading.

across the species was 1.5 – 2 times as high in favor or not of respective variables, and only occasionally showed no clear trend. The majority of vascular plant species showed a positive response to warmer conditions with higher levels of precipitation and soil C (TC and TOC), seen by more positive responses especially for temperature and soil TC and TOC as represented by PC1 (Table 1). The vascular plant species generally had lower preference for areas with more shading and preferred lower lying areas (depression areas within the landscape), as seen by the predominantly negative responses to shading and tpi. Similarly, soil fungi species preferred warmer conditions and higher levels of soil C, as well as lower lying areas within the landscape, with three times more positive than negative responses to temperatures and a heavily dominated positive response to soil C, and a higher proportion of negative responses to tpi (Table 1). In contrast to vascular plants, several soil fungi species also showed a preference for shadier (and thus potentially cooler and moister) areas.

Our results showed clear LM and LUI effects for half or more of the vascular plant (ca. 49%) and soil fungal (52%) species (Table 1). Twice as many vascular plant species had a negative response to LM, meaning 33% of the species (38 species) are more likely to occur in meadows than pastures. Contrastingly, more soil fungi species generally had a positive response to LM, indicating that 31.5% of the species (152 species) preferred pasture management. Soil fungi species responded more prominently to LUI than vascular plants, with more than double the amount of species preferring higher LUI (139 species) rather than for lower LUI (63 species). The proportion of variance in species niches explained by the respective variables ranged from 1.6% to 15.7% for vascular plants, and was generally lower for soil fungi, between 1.6% and 4.8% (Table S4).

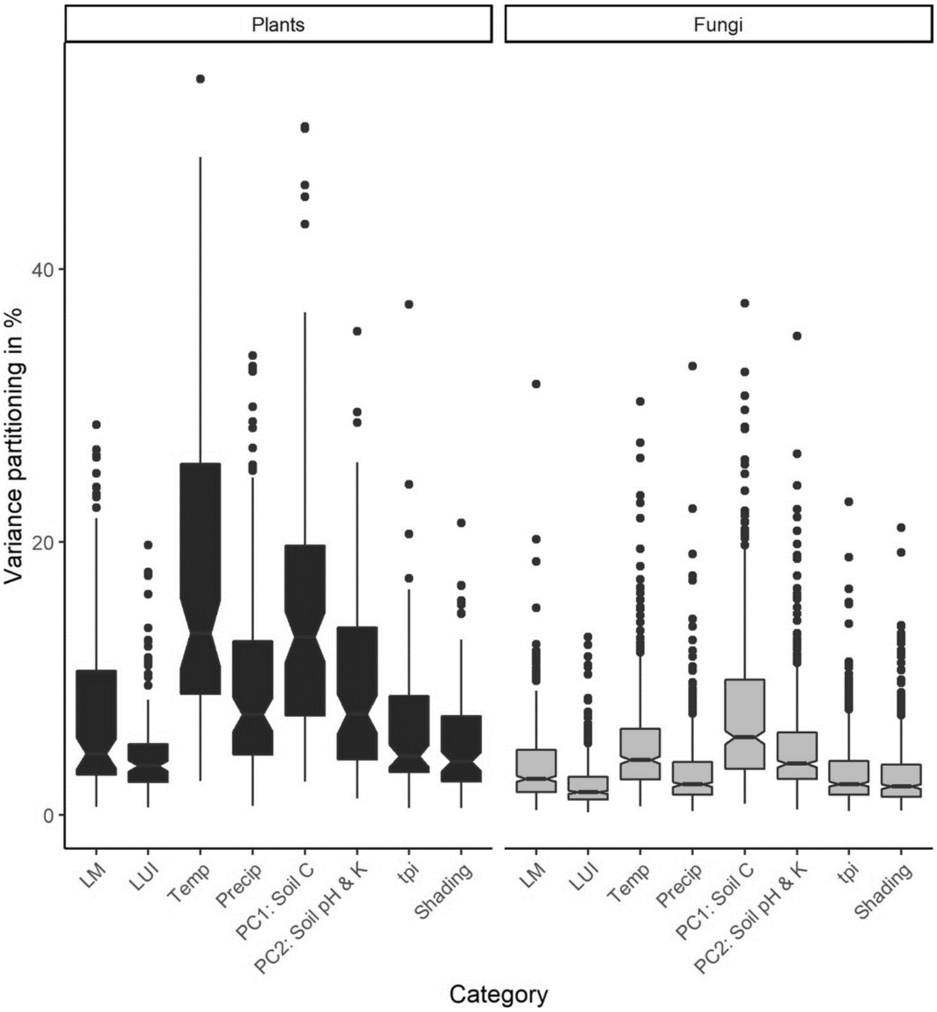

Fig. 2. Relative importance of the respective variables in explaining variation in species occurrence of plant and fungi species. These are the variables previously grouped into their respective land use and biogeographical categories in Fig. 1. LM = land management; LUI = land use intensity; Temp = average air temperature; Precip = average precipitation; tpi = topographic index, Shading = hill shading in the summer season.

Table 1
Percentage of species with a positive or negative response to the respective environmental variables within the HMSC models for plants and fungi respectively. Only responses with a posterior probability of at least 85% are reported. For land management (LM) meadows were used as reference. The overall (both positive and negative) response column reports the total percentage of species responding to the respective explanatory variable. Shaded blocks indicate which of the pair-wise comparisons had significantly (sign-test, $p < 0.05$) more positive (orange) or negative (blue) responses per variable.

Presence-absence model:		Plants			Fungi		
Category	Variable	% positive responses	% negative responses	Overall % responses	% positive responses	% negative responses	Overall % responses
Land use	LM*	15,8	33,3	49,1	31,5	20,5	52
	LUI*	27,2	21,1	48,2	28,8	13	41,8
Climate	Temperature	41,2	23,7	64,9	31,9	11,6	43,5
	Precipitation	36,8	20,2	57	17	21,5	38,5
Soil	Soil C (PC1)	43	21,9	64,9	51,6	1,4	53
	Soil pH (PC2)	28,9	23,7	52,6	22,6	17	39,5
Topology	tpi*	14	36,8	50,9	16,1	26,3	42,4
	Hill shading	16,7	30,7	47,4	47	4,8	51,8

3.4. *Responses of taxonomic groups*

Overall, the taxonomic classification of species into their respective clade (vascular plants) or phylum (soil fungi) level groupings explained only a moderate amount of variation in species occurrences. For vascular plants the more detailed taxa grouping explained 11% of the variation, and for soil fungi is was ca. 7%.

The species within both the vascular plant and soil fungi groups are dominantly from two or three clades or phyla, respectively. Vascular plants are mainly from the Asterids, Commelinids and Rosids. While soil fungi are dominated by the Ascomycota and Basidiomycota. Due to the dominance of the Ascomycota and Basidiomycota, the strong positive or negative species response to the respective environmental variables was each time dominated by these groups. These groups responses to the respective environmental variables were consistently similar (Fig. S7 and S8). For vascular plants there was more variance in which clades had a positive or negative response to, for example, LM, local climate or soil conditions. The positive and negative trends for LM was mainly due to a higher preference of a subset of Asterids, Commelinids and Rosids clades for one of the respective LM types. While the reminder of the Superasterids had a strong preference for pasture management (Fig. 3a). More Asterids and Rosids had a higher preference for warmer conditions and areas with higher soil C, while Commelinids and Superasterids preferred lower soil C and wetter regions (Fig. 3b-d). There were too few Ranunculids in the dataset for robust generalizations to be made.

3.5. *Residual species co-occurrence patterns*

The species to species matrices of model residuals, i.e. after controlling for environmental and random factors, showed low indication of biotic interactions with only 0.35% co-occurrences with a posterior probability of at least 0.85 for the vascular plant dataset (Fig. S9a). For soil fungi, the residual co-occurrence patterns showed more correlations (9.12%) with a posterior probability of 0.85 (Fig. S9b), especially positive associations (8.67%).

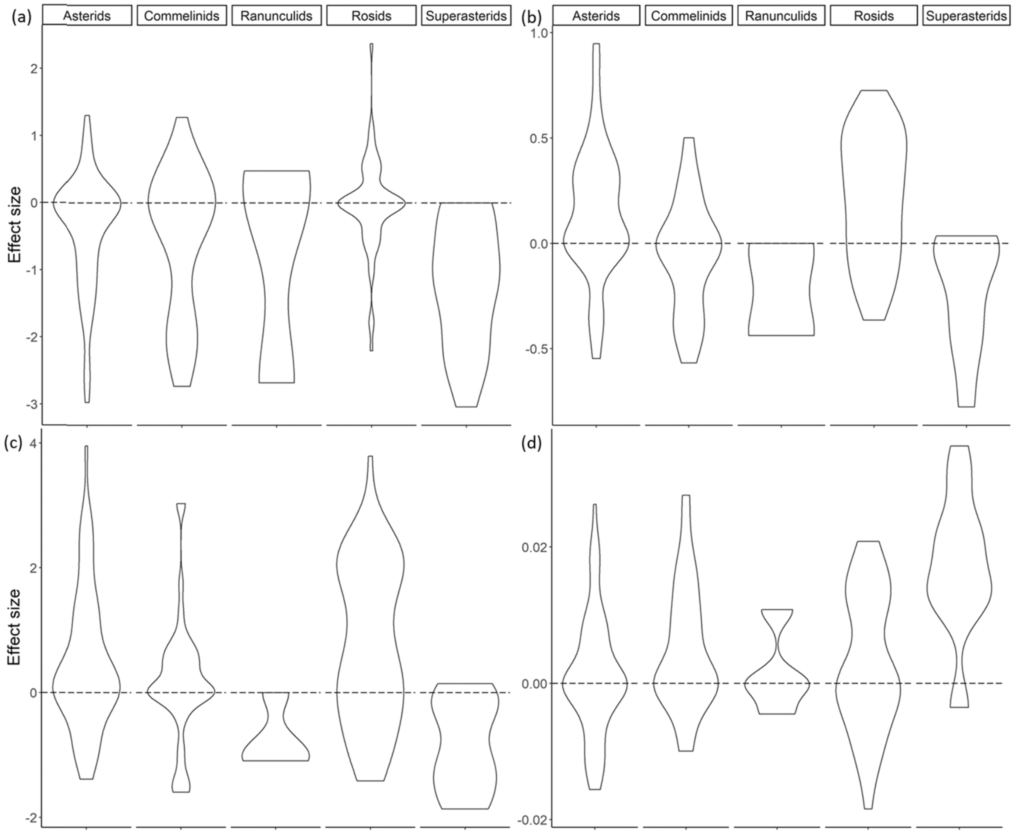

Fig. 3. Effect size and direction of plant clade responses to environmental variables (β parameter) (a) land management with meadows as reference (positive values indicate higher probability of species occurrence in pastures), (b) soil carbon (PC1) (positive values indicate higher probability of species occurrence with higher soil C levels), (c) average air temperature (positive values indicate higher probability of species occurrence under warmer temperatures) and (d) average precipitation (positive values indicate higher probability of species occurrence under wetter conditions). Only responses with a posterior probability of at least 85% are reported. The other environmental variables are presented in the supplements, Fig. S6.

4. Discussion

The importance of environmental filtering was more prominent than current land use and biotic interactions in explaining the (co-)occurrence of vascular plant and soil fungi species within semi-natural grasslands. Climate and local soil conditions were most important for vascular plants, while for soil fungi the soil variables played a more prominent role. These results contradict our expectation that LM and LUI would be more prominent in the community assembly of semi-natural habitats than the local and biogeographical context created by the soil, topography, and climatic conditions. Our findings partially support our expectation that these above- and belowground taxa groups have similar responses to land use variables, due to biotic filtering and the legacy effects of LM. However, these where less prominent than expected. Different combinations of variables explain the species occurrence patterns of these respective taxa groups, and we suggest that this is likely because these groups respond to their environment at different spatial grains.

4.1. Local and biogeographical context as main driver of community assembly

Our results indicate a strong effect of abiotic filtering by local and biogeographic conditions for vascular plant and soil fungi communities. For vascular plants, we observed hierarchical scale-dependency with larger-scale climatic conditions being most important followed by local-scale soil conditions and, using topography as a proxy, by microclimatic conditions. This is in line with expectations that large-scale biogeographic drivers such as climate define the regional species pool and the local communities are subsequently filtered by more local abiotic conditions and finally by biotic interactions (Carstensen et al., 2013). In contrast to the vascular plants, the belowground soil fungi communities were most strongly defined by local soil conditions, with larger-scale climate and small-scale microclimate being of lesser importance. This ‘reverse’ scale-dependency in abiotic filtering is not surprising, given the strong dependency of soil fungi communities on edaphic conditions even at global scales, although these might be in turn impacted by climate (Tedersoo et al., 2014).

The low impact of land use compared to biogeographical and local context is surprising considering the extensive research demonstrating strong effects of land use, and resulting legacy effects on local biodiversity (Gustavsson, Lennartsson and Emanuelsson, 2007; Soliveres et al., 2016), even in studies like ours that compare grazing versus mowing management (e.g., also see Cauwer and Reheul, 2009; Catorci et al., 2014; Rysiak et al., 2021). However, we note that our study considered a larger spatial grain of investigation compared most of these studies. Furthermore, the meta-analysis of Tälle et al. (2016) also found the overall effect size of grazing versus mowing to be relatively small, and that the direction of the effect was context specific (e.g., varied between continents or grassland types).

Although current LM practices and LUI of our semi-natural grasslands have been active for at least the last 10 years, the contrast of our findings to other studies may partially be due to overall lower levels of LUI at our sites. Our sites ranged from a low to moderate level of LUI, and did not include intensively managed grasslands, nor ones that have been artificially fertilized or re-seeded. In addition, our sampling design included sites that covered a high variation in both soil conditions and climate, which made it more likely to detect an effect of these factors. Our findings suggest that unless LM and LUI are very high, the environmental filter is most prominent in determining which species occur in semi-natural grasslands. Similarly, Ren and colleagues (2012) in their study of Inner Mongolian steppe grasslands also found seasonal variation in climate (early-growth season temperature and precipitation) rather than grazing intensity to be the main driver of grassland dynamics.

The impact of biotic interactions was limited, which might change if abundance data were considered. However, co-occurrence is assessed based on residual occurrence probabilities, which can be closely linked to abundances (Thuiller et al., 2014). Thus, we might expect only minor changes of the overall picture. The limited impact of biotic interactions indicates that within semi-natural grassland systems both vascular plant and soil fungi (co-)occurrences are dominantly shaped by abiotic filtering rather than residual species interactions. The plant-plant and fungi-fungi interactions that could be deducted from the residual variance in our analysis as co-occurrence patterns showed a higher proportion of positive co-occurrence patterns for soil fungi. This suggests either a more prominent role of inter-taxa facilitation in shaping the community (e.g., due to trophic relationships), or the influence of the local plant community (Lindahl, De Boer and Finlay, 2010). Dominance of positive interactions among fungi have also been shown by Abrego et al. (2020) in arctic plant roots confirming existence of positive co-occurrences of fungi in grassland ecosystems. In aboveground systems, biotic interactions change from competition under ’beneficial’ conditions to facilitation under stressful conditions (Callaway et al., 2002). Thus, our results showing limited evidence of biotic interactions for vascular plants could indicate that our conditions are somewhere in between.

Our analysis made a first attempt at considering the potential role of across taxa interactions, by analyzing the data pooled across taxa groups, but were limited by the high computational requirements and lack of convergence. However, since investigation of assembly processes in multi-taxa research is important, we suggest that future research might overcome the computational hurdles by analyzing common and rare species separately, or by pairing across taxa groups to obtain some insights of potential interactions across taxa. Furthermore, the model priors could be adapted to be more informative for respective data, and strategies can be implemented to improve model convergence and lower computational time (Bystrova et al., 2021).

4.2. Relative importance of local and climatic variables for vascular plants and soil fungi

In general, variation in vascular plant occurrence patterns was much more driven by climate conditions, whereas soil conditions, and unspecified (random) variation at plot level, was more relevant for the soil fungi. This is not surprising considering that vascular plants and soil fungi would be utilizing resources differently based on their inherent biological and ecological differences. Vascular plants have a much larger 'local' scale of resource use than soil fungi (Harrison et al., 2010), and are thus more impacted by variation in environmental conditions of larger magnitude than soil fungi, in this case climate conditions. Contrastingly, soil fungi are more directly impacted by biophysical and chemical properties within soil pores, and are less sensitive to larger scale differences in environmental conditions (Harrison et al., 2010, however, also see Tedersoo et al., 2014). Similarly, above- and belowground organisms vary in their temporal responses to environmental change due to their differences in life histories and other traits (Rudgers et al., 2020). Biotic interactions within and between taxa groups across the soil interface are known to operate at various spatial and temporal scales and to depend on local conditions (Slabbert et al., 2020; Jing et al., 2015), making it challenging to generalize the most important community assembly mechanisms. Our findings of high importance of the soil C for both vascular plant and soil fungi is not surprising, as carbon is the basis of all biomolecules these organisms need to build. Our results showed higher variation in soil fungi occurrence explained by soil C than for vascular plants, which could be an indicator of the more indirect link plants have to the soil conditions via microbial pathways of nutrient mineralization (e.g., breakdown of organic material into plant available nutrients) (Van der Heijden, Bardgett and van Straalen, 2008).

4.3. Relative importance of land management and land use intensity

The consistently lower proportion of variation explained by LUI in our study is in contrast to certain studies (e.g., Gossner et al., 2016), but also in support of others that have found other aspects related to land use to be more deterministic of above- and belowground dynamics than LUI (e.g., Scimone et al., 2007). The high proportion of variation captured by the plot level random variable for soil fungi occurrence suggest that we might have missed one or more important variables at finer spatial scales. For example, the type of livestock grazer, extent and seasonality of grazing, and amount of soil compaction are known to be important factors in pastures (Tóth et al., 2018). These likely vary across plots, and could be important for soil fungi considering the small-scale habitat heterogeneity created by grazers. More soil fungal species were positively related to pasture compared to meadow management, and this result is in line with another study that shows that pasture management can yield more diverse soil fungal communities in some site- and scale-dependent contexts (Slabbert et al., 2020). Our results also show that for soil fungi, grazing represents a stronger filter for particular species, possibly due to distinct local microclimates created by different grazers (Klimek et al., 2008) and the impact on plant community composition (Klimek et al., 2007; Socher et al., 2013; Allan et al., 2015) and plant metabolism (Brys et al., 2004). The higher preference for meadows for vascular plants was surprising, since pastures are usually more species rich than meadows (e.g. Klimek et al., 2007; Schlapfer et al., 1998), however we suspect this is due to the higher selectivity of grazing compared to mowing for certain plant species (Slabbert et al., 2020).

The lower impact of LM and LUI might also be a consequence of indirect abiotic effects, e.g. when farmers adapt their management to soil or climatic conditions (Talawar and Rhoades, 1998), or when the management impacts soil conditions (McLauchlan, 2006). However, this seems not to be the case in our study system, since we did not detect a systematic relationship between LM or LUI with the abiotic variables.

4.4. Broader taxonomic group responses to land use, local and biogeographical conditions

Only a moderate proportion of the variation in species occurrence could be explained by the higher taxa classifications that cluster species according to relatedness and indirectly link them in some cases to traits common for specific taxa groupings. Since we had to cluster soil fungi at much coarser taxa classification to get a comparable number of groups (clade for vascular plants and phylum′s for soil fungi), the classification was less informative than that of the vascular plants that were clustered at finer resolution. There were some clear preferences of certain vascular plant clades for specific environmental conditions, for example for higher soil carbon and warmer conditions, or vice versa. These group specific response, which might relate to phylogenetically constrained functional traits, could be further investigated to better understand the resulting ecosystem functions and ecosystem services (e.g., high fodder quality) that could be expected within certain environmental conditions.

5. Conclusion

We found that despite impacts of (low to moderate) land use practices on semi-natural grasslands, the local and biogeographical context as shaped by the soil, topography, and climatic conditions remains a more prominent driver of community assembly patterns for both vascular plants and soil fungi communities, while biotic interaction play a limited role. Large-scale variables were more relevant for explaining vascular plant occurrence patterns (i.e. climate), while soil fungi occurrence patterns were more explained by local-scale variables (i.e. soil conditions). Our results highlight the importance of the local and biogeographical context (soil, topography, climate) as driver for community assemblage, despite impact of current or past LM. These findings aid further research and policy recommendations for conserving multitrophic diversity within agroecosystems which are likely relevant to a broader set of taxonomic groups (e.g., insects, see Weiss et., 2013). For policy, our results suggest the need for policy instruments, such as the Common Agricultural Policy, to promote grassland management that are applicable to both local and biogeographical conditions instead of incentivizing ridged, homogenizing management practices which result in the loss of locally adapted management that is tailored to regional habitat heterogeneity (e.g., Dahlström et al., 2013). For researchers, our results highlighting the importance of controlling for soil and climate when investigating the impact of land use to ensure comparability and accurate research outcomes.

Authors′ contributions

A.K, C.B., H.A and C.R: designed the field study, **E.S, T.K, O.S, T.W, H.A and C.R** developed ideas; **A.K** collected the data; **E.S** conducted analyses and led the writing.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01960, as well as in the Appendix of this thesis.

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Chapter 4:

Large- and small-scale factors drive multi-trophic communities in agroecosystems

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Large- and small-scale factors drive multi-trophic communities in agroecosystems

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Abstract

1. *Context:* There is an increased interest in land management to promote multiple ecosystem functions and services within agricultural landscapes. Therefore, it is essential to understand the scale-specific drivers and interlinkages across multiple taxa that occur above and below the soil interface.
2. *Objectives:* We analyzed the impacts of large- and small-scale environmental drivers on the diversity and composition of multiple trophic groups within agroecosystems. We expected belowground (soil bacteria and fungi) communities to be more driven by local-scale variables, more mobile aboveground (wild bees, ground beetles) groups to be more driven by larger-scale processes, and vascular plants to respond to a combination of both.
3. *Method:* The study took place in summer 2018 at site- (16 km^2) and plot-level (within 1 m^2) across six sites in Central Germany, with sampling at 16 plots per site. Structural equation models were used to investigate drivers across the trophic groups.
4. *Results:* Landscape-level factors, e.g. amount of semi-natural habitat and weather conditions, were generally more prominent drivers for both above- and, unexpectedly, also belowground groups, while small-scale drivers (*e.g.* soil texture and pH) can also impact mobile aboveground groups. We found indirect and cascading effects of large-scale drivers *via* impacts on soil conditions or the interlinkages within and among the above- and belowground communities.
5. *Conclusions:* Our results highlight the importance of direct and indirect effects of multi-scale drivers on diversity, composition and connections among multiple trophic groups and further underscore the relevance of landscape-focused management that promotes semi-natural habitats, and thus supports multifunctionality within agroecosystems.

Key words:

above- and belowground communities, multifunctionality, agroecosystems, connectivity of multi-trophic communities, multi-scale drivers, cascading effects

Introduction

Anthropogenic demands on land are constantly increasing leading to considerable conflicts of interests, e.g. between utilizing provisioning services, such as food production, and sustaining regulating or cultural services (Newbold et al. 2015; IPBES 2019). Thus, there is an increased interest in maintaining multiple ecosystem functions and services particularly in agricultural landscapes (Soliveres et al. 2016a; Manning et al. 2018). Such multifunctionality can have beneficial impacts on both agricultural production and other important ecosystem functions, and can enhance ecosystem stability and service provision (Dainese et al. 2019; de Bello et al. 2021). Sustaining or even increasing multifunctionality is linked to the diversity of multiple taxonomic groups (Soliveres et al. 2016b; Wang et al. 2019) and the complexity of trophic interactions across the soil surface (Lefcheck et al. 2015; Soliveres et al. 2016b).

To counteract ongoing biodiversity declines in agroecosystems, several policy frameworks have been set up, such as the agri-environmental schemes within the EU Common Agricultural Policy (EC, 2017). However, such schemes are often aimed at specific taxa (e.g. establishing flower strips for pollinators) or ecosystem functions (e.g. cover crops to enhance in-field soil fertility), but usually do not consider multiple above- and belowground taxa and respective ecosystem functions. To address this gap, detailed studies analyzing multiple trophic groups that fill a broad range of functional roles within agroecosystems are essential (e.g. Billeter et al. 2008; Soliveres et al. 2016b). These range from those related to soil processes, e.g. soil microbes (Schimel and Bennett 2004); pollination and pest control, e.g. wild bees and ground beetles (Fusser et al. 2016; Senapathi et al. 2021); as well as taxa linking both aspects, e.g. plants (Hanisch et al. 2020). While some connections across trophic levels are already well-understood, e.g. plant-pollinator community relationships (Papanikolaou et al. 2017), other interactions and the impact of environmental drivers on multiple taxonomic groups still demand further research, e.g. linking plant species richness to soil biota (Liliensiek et al. 2012) or fungal to bacterial communities (Emmett et al. 2021).

Understanding the large- and local-scale factors that shape the diversity, composition and interconnectivity of multiple taxonomic groups is also relevant to set the efficiency of management options into a wider environmental context. Drivers known to affect the diversity in agricultural landscapes include large-scale climatic and weather conditions (Evers et al. 2021; Slabbert et al. 2022) and landscape-scale land use (Hedlund et al. 2004; Papanikolaou et al. 2016a), as well as local-scale microclimatic and soil conditions (Liliensiek et al. 2012; Vician et al. 2018). Climatic factors, such as mean annual temperature and precipitation, for example, are critical to physiological processes of both above- and belowground taxa, and important drivers across all groups (Tedersoo et al. 2014; Slabbert et al. 2022). Landscape-scale drivers have also been shown to affect both above-and belowground diversity, but the actual drivers differ (Sirami et al. 2019; Le Provost et al. 2020). Le Provost et al. (2020), for example, found aboveground taxa to benefit from land cover diversity, while permanence of land cover types has a positive impact on belowground diversity. In contrast, local-scale conditions, such as soil fertility, pH and plant composition, are especially relevant for soil microbes (Glassman et al. 2017).

Here, we investigated how the diversity and composition of taxa across multiple trophic levels are influenced by large- and small-scale abiotic drivers and landscape structure and expect above- and belowground taxa to be affected to a different extent (Slabbert et al. 2020). We focus on five taxonomic groups covering major functional roles across the soil interface, namely vascular plants, wild bees, ground beetles, and free-living soil bacteria and fungi. We relate their species richness, diversity and community composition to land use (proportion of semi-natural habitats and land cover diversity), large-scale weather conditions (mean annual temperature (MAT) and precipitation (MAP)), and local-scale variables describing microclimatic and soil conditions. We hypothesize that the belowground communities will be more driven by local-scale variables linked to soil properties and the micro-climatic conditions, while aboveground (more mobile) groups are most affected by larger-scale processes related to land cover and weather conditions. Furthermore, as plants straddle the above-belowground interface, we predict that a combination of small- and large-scale processes will be important drivers. We expect MAT and MAP to be important across all groups. We also considered feedback loops between certain taxa groups based on prior knowledge (e.g., between plant and soil microbial groups, and between soil bacteria and fungi). These relationships can be considered to be bi-directional as there is consistent evidence for strong feedback between plants and microbial communities (Liliensiek et al. 2012) as well as between soil fungi and bacteria (Landesman and Dighton 2017).

Methods

Study sites

Data for this study were collected as part of the Terrestrial Environmental (TERENO) Harz/Central German Lowland Observatory (Zacharias et al. 2011) managed by the Helmholtz Centre for Environmental Research - UFZ. The six study sites (ca 4 x 4 km) are located in Sachsen-Anhalt, central Germany, and represent a typical agricultural landscape within this region. The sites, located near Friedeburg (FBG), Schafstaedt (SST), Greifenhagen (GFH), Wanzleben (WAN) Harsleben (HAR) and Siptenfelde (SIP), cover 16 km2 and have varying configurations of land use and abiotic conditions (Table S1). Sampling within these landscapes took place at edge habitats including field margins and road verges. These linear elements provide valuable habitat to agrobiodiversity that is complementary to adjacent semi-natural vegetation (Suárez-Esteban et al., 2016).

Data collection

Wild bees and flying Carabidae

As part of the TERENO monitoring scheme, wild bees and carabids are sampled with insect traps which combine window and yellow pan traps (see Duelli et al. 1999 and Papanikolaou et al. 2016b for details). Sixteen insect traps are installed per site (total of 96 sampling points; exact trap locations are available on the UFZ TERENO website under Biodiversity Platforms > Investigation areas). Traps are operational during six weeks in spring-early summer and six weeks in late summer and emptied biweekly. Wild bees and flying carabids of 2018 were selected and identified to species level in the laboratory. Due to in-field conditions and accessibility restrictions during 2018 only 92 of the 96 sampling points could be sampled (Table S1).

Vascular plants

In summer 2018, a vegetation survey was done at the base of each insect trap covering 1 m^2 to determine vascular plant species richness and percentage cover based on the nine-grade Braun-Blanquet scale (Braun-Blanquet 1964). Recorded species names were cross checked against the Leipzig Catalogue of Vascular Plants (LCVP) using the *lcvplants* package (Freiberg et al. 2020) in *R* (R Core Team 2021), seedlings were omitted from the dataset, and species complexes were pooled to species level.

Free-living soil fungi and bacteria

Soil microbial communities of free-living soil fungi and bacteria were sampled using standard composite sampling. Five soil cores (*ca.* 6 cm diameter) were taken at each insect trap to a depth of 10 cm (after removal of the organic litter layer), pooled and sieved (2 mm) in-field. From the pooled sample ten grams were flash-frozen on dry-ice for microbial analysis. Amplicon sequence variants (ASVs) were identified with next-generation sequencing as outlined in Singavarapu et al. (2021) which were considerd to be the finest taxonomic units (i.e. species level). Only ASVs with a Phylum level identification were kept in the dataset, hereafter the data matrix was filtered using the *R phyloseq* package (McMurdie and Holmes 2019) to only keep ASVs that occurred more than 5 times in at least 1% of the dataset for further analysis. An additional 500 g soil sample was collected for standard soil analysis to determine soil moisture, soil texture and soil nutrients.

Biodiversity metrics

Three biodiversity metrics were used as response variables for the respective taxa groups, assessed at plot-level (i.e. local insect trap, floral survey plot and locations of soil core sampling): species richness, Shannon diversity index, and community composition.

To assess a change in community composition across plots we used the plot-level scores of a principal components analysis (PCA) per taxon group based on Hellinger transformed relative species abundances (Legendre and Gallagher, 2001; Schuldt et al*.* 2017). For vascular plants, cover categories were converted to percentage cover mid-points of the respective categories, with exponential transformation as recommended by Tichý et al. (2020). From the respective PCAs we used the 1st PCA axis, and additionally the 2nd axis when the proportion of explained variation was similar to the 1st axis.

Explanatory variables

To assess the importance of large- and small-scale processes on biodiversity metrics of multiple taxonomic groups, and their potential interaction with each other, we selected several predictor variables based on our hypothesis. These included four large-scale landscape predictors measured at site-level (16 km^2) and five small-scale predictors measured at plot-level (within 1 m^2).

Site-level predictors

Land cover of semi-natural habitat and landscape heterogeneity of land-use types were calculated at site-level (16 km^2) based on digitized habitat maps prepared from orthorectified aerial photos. Habitat classification followed the 2012 revised European Nature Information System (EUNIS; https://eunis.eea.europa.eu/habitats.jsp) to the third level. The EUNIS classifications were aggregated to more general habitat categories relevant for, e.g. wild bees based on Frenzel et al. (2016). These included a category for *arable land*, *managed grasslands*, *forest*, *semi-natural habitats*, and *urban*. Based on these classifications, we calculated the proportion of semi-natural habitat per site and the Shannon diversity as a proxy for landscape heterogeneity.

Weather data for the mean daily temperature and total daily precipitation was obtained for the six regions from weather stations managed by the UFZ (FBG, HAR, GFH and WAN) and the Deutscher Wetterdienst (DWD; SIP and SST) for the past 10 years (2009 -2018). From this we calculated mean annual temperature (MAT) and mean annual precipitation (MAP) per site for the past 10 years, the 12 months preceding field sampling (07.2017 - 06.2018) with potential impact on population growth and diversity in the following year, and seasonal weather conditions of the fortnight prior to sampling with a more direct impact on activity.

Plot-level predictors

Plot-level (1 m^2) variables sampled included soil related parameters as well as local topography. Soil parameters were determined from 500 g of the sieved soil collected in parallel to sampling soil microbes. The soil was under cooler storage in-field, and then stored at ca. 6 °C until standard soil parameters, soil moisture and soil acidity were measured following standard laboratory protocol (VDLUFA 1991). Soil parameters measured (as grams per 100 g of dry soil) included soil carbon (C), nitrogen (N) and the carbon-nitrogen ratio (using a Vario EL III Element Analyzer), and soil phosphorus (P) and potassium (K), as well as soil pH (KCl method). The proportion of soil moisture content was determined using a drying oven after the removal of coarse organic matter. Additionally, soil texture was determined and calculated as the percentage of silt, clay and sand within a 10 g sample. To capture more general microclimatic differences within and across sites we extracted local topography from digital elevation models with a resolution of 10 m, these included aspect (geographical direction), slope, elevation and hill shading (for summer months).

Statistical analysis

Initial variable selection was hypothesis driven. As we aimed to characterize the micro-habitats at the plot-level, we compressed the topography and soil-related measures per category (i.e. soil nutrients and soil texture) into a single variable by performing principle component analyses (PCA). We then used as standard only the first axis for further analysis, see Table 1 for details on proportion explained variation per axis and the main driver of variation. The soil variables for moisture and pH did not ecologically group well with the other soil variables, and thus were included in the analysis independently. As the remainder of the site- and plot-level variables were very different in their measurements, we standardized the data by scaling (mean-centering and unit variance).

Table 1. Proportion of explained variation per 1st axis for PCA's done for soil nutrients, soil texture and local topography *and* most prominent driver of variation.

Input variable	% explained variation on 1st PC axis	Most prominent driver of variation
Soil nutrients	44.58	proportion of soil nitrogen (N)
Soil texture	64.34	proportion of sand vs. silt particles
Local topography	33.46	variation in hill shading

All the predictor variables were checked for correlation using the Hmisc package (varclus function, spearman method) (Harrell, 2021). For variables that had a correlation of higher than 0.5 (transformed R2), we selected between them based on our assumption of higher ecological interest. This led to the exclusion of the seasonal weather variables and long-term climatic variables, as these were correlated to MAP and MAT, respectively, of the preceding 12 months. We decided to rather include MAP and MAT from the preceding 12 months as these conditions would have a more direct impact on population dynamics, while also accounting for seasonal activity. Additionally, soil pH was also correlated to MAT, however, to ensure predictors remain scale explicit, we retained both of these in the subsequent analysis while accounting for the direct link between predictors.

Using the final set of explanatory variables, we constructed three structural equation models (SEM), one per biodiversity metric using psem function from the piecewiseSEM package (Lefcheck 2016). The model structure was based on the hypotheses, and was initially set as linear mixed-effects models (lme4 package) with site as random factor. Since the model structure had singularity issues, due to several of the predictors being measured at site-level, we dropped the random factor which explained no or a negligible amount of variance. We evaluated the conditional independence claims arising from our model structure per response variable and added missing links between response and predictor variables that were statistically significant ($p<0.05$) and considered ecologically relevant. We optimized the models by performing step-wise backward selection based on Akaike Information Criterion (AIC) values. To capture variation in community composition, the 1st PC axis was selected for carabids, soil fungi and bacteria as these proportionally explained more variation (namely, 30%, 16 % and 24%, respectively) than the 2nd axes. For wild bees and vascular plants, both 1st and 2nd PC axes explained a comparable proportion of variation (wild bees: 14% and 12%; vascular plants: both 7%). To select only one PC axis per taxon group, we used a generalized linear model (gaussian distribution with identity link) to first model the relationship between soil bacterial and fungal community composition per plant PC axes, as a hypothesized connection. As plant PC1 explained most of the variation (lowest AIC) it was selected for further analyses. For wild bees we tested the SEM with the respective PC axes and, based on lowest AIC, proceeded with the 2nd PC axis. SEM models were visualized using the DiagrammR package (Iannone 2020). To visualize the shifts in community evenness and composition captured by the corresponding SEM, stacked bar graphs of the taxonomic grouping of the respective taxa groups were made using ggplot2 (Wickham, 2016). General data management, statistical analysis and visualizations were done using R 4.0.5 (R Core Team 2021).

Results

Data overview

We recorded 1033 specimens of 227 species of vascular plants, representing 142 genera; 28 830 wild bees specimens from 148 species and 15 genera; 5 830 specimens of ground beetles from 76 species and 32 genera. For the soil microbes, we recorded 1484 fungi ASVs from 327 genera, and 6121 bacteria ASVs from 464 genera (Table S2).

Structural equation model overview

The three biodiversity metrics, species richness, diversity (Shannon index) and community composition (PC axis), revealed complementary insights about the scale-specific drivers shaping the respective taxonomic groups (Fig. 1). All three final SEMs were robust (see Fischer’s C and p-values in Table 2). For all three biodiversity metrics, there was a low importance of most plot-level predictors with the exception of soil pH and high importance of several site-level variables. Only for the composition model was there a combination of small- and large-scale predictors that significantly explained the change in species composition across several of the taxa groups.

When comparing the proportion of explained variation per taxonomic group (R^2) for the respective models, we generally saw an upward trend of explained variation from richness to composition (Table 2). Comparing across taxonomic groups, explained variation was generally highest for soil microbes, followed by wild bees and vascular plants, while explanatory power was lowest for carabids irrespective of the response variable. Community composition as response was the most informative for soil bacteria, as well as for wild bees and soil fungi, while the explanatory power of the models did not differ much for vascular plants and carabids.

Species richness

Land-use related variables were of particular importance for species richness of aboveground groups and vascular plants, with consistent positive effects of semi-natural area, while land cover diversity had negative effects on wild bees and carabid beetles (Fig. 1a). Mean annual precipitation (MAP) was negatively related to the richness of aboveground groups, while vascular plant richness showed a positive relationship to mean annual temperature (MAT). Small-scale variables had little impact on both aboveground groups, except a small negative effect of proportion of sand in the soil on wild bees and a positive effect of hill shading on carabids.

Diversity

Results for diversity were similar to those of richness, however, a remarkable difference was found for wild bees (Fig. 1b). While wild bee richness was affected by MAP, land cover diversity, proportion of semi-natural habitat and soil texture, wild bee diversity was affected by none of the tested factors. Drivers of vascular plant diversity altered slightly in comparison to richness, but new drivers also occurred. Here, MAT no longer had a direct impact on vascular plant diversity, but acted indirectly via soil pH. Interestingly, we also found a direct effect of warmer conditions (MAT) reducing soil fungal diversity and a direct positive effect of MAP on soil bacterial diversity. Furthermore, we found an unexpected link between soil fungal diversity and carabid diversity, which creates a network of linkage across the large- and small-scale drivers and across multiple trophic groups. Soil fungal diversity was negatively associated with carabid diversity, while the former was impacted by soil pH which in turn was affected by MAT, MAP and soil texture.

Community composition

Bee composition was driven by similar large-scale predictors as found for richness. For carabids, the importance of site-level predictors related to the amount of semi-natural habitat and land cover diversity was reduced, while direct impacts of soil pH and indirect impacts of soil texture remained. Vascular plant composition was affected by land cover diversity rather than proportion of semi-natural area, and directly by MAP and MAT. Factors affecting soil fungal composition increased compared to species richness and diversity, with an additional site-level impact of land cover diversity and a plot-level impact of vascular plants. Via a link between fungal and bacterial communities, the impact of plants on fungi also transferred

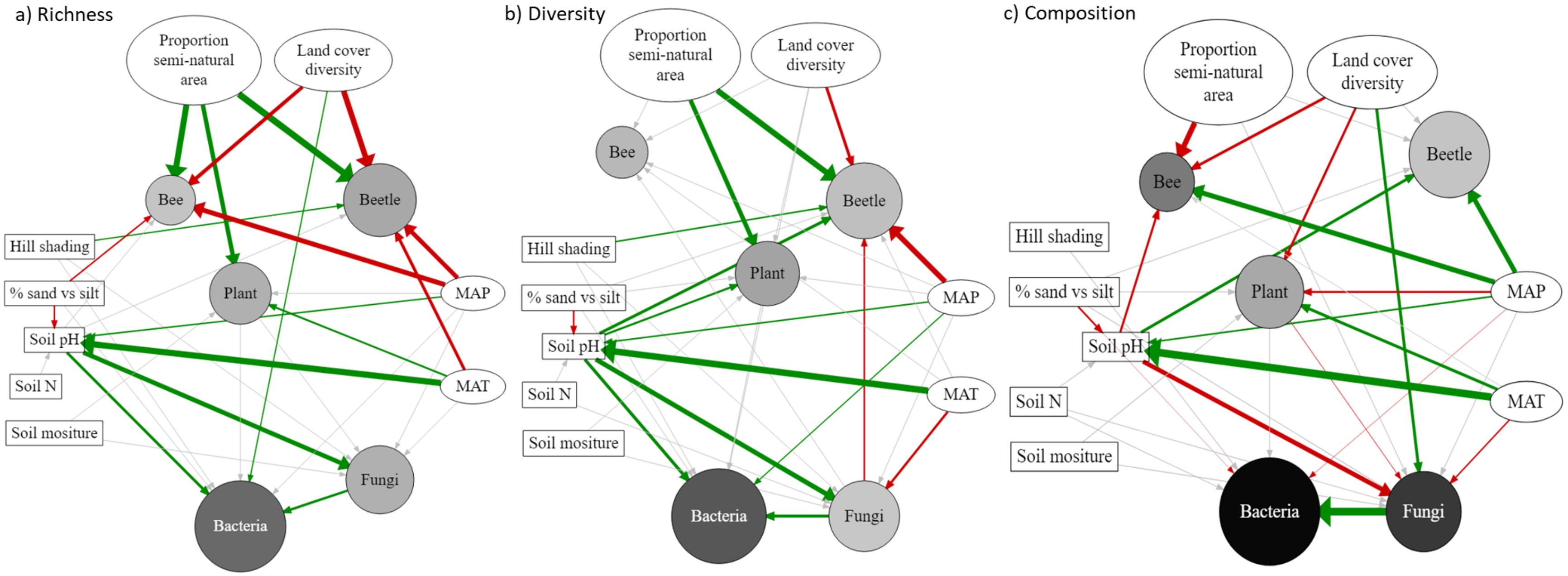

Fig 1. Structural equation models with species richness (a), diversity (b) and community composition (c) as response variable per taxonomic group (circles) and how these are impacted by site- and plot-level predictors (ellipse and rectangles; see methods for more details). Arrows indicate modelled connections between taxa and predictors, and between taxa groups. Green and red arrows denote a positive and negative effect, respectively, on richness or diversity, or a significant shift in community composition along the community PC axes. Arrow widths are adjusted to be proportional to the standardized effect size. Light grey lines are non-significant linkages. Taxa circles are shaded according to increasing proportion of explained variation (R^2). MAP, MAT: mean annual precipitation and temperature of the preceding year.

Table 2. Overview of the goodness-of-fit of the structural equation models per response variable, and the proportion of explained variation per taxonomic group (R^2).

Taxa	**Richness**	**Shannon diversity**	**Composition**
Vascular plant	0.32	0.38	0.34
Wild bees	0.25	0.25	0.55
Carabid beetles	0.37	0.32	0.27
Soil bacteria	0.63	0.72	0.97
Soil fungi	0.46	0.38	0.88
Soil pH	0.70	0.70	0.70
Model details:			
Goodness of fit (Fisher's C)	39.03	46.38	48.62
p-value	0.99	0.82	0.81
Degrees of freedom	62	56	58

to the bacteria. Thus, the soil microbial communities were also indirectly affected by the drivers shaping the vascular plant community.

Change in community composition under different drivers

When composition is visualized at the family level, wild bee communities shifted from domination by the family Andrenidae towards a more even composition of families as proportion of semi-natural habitat increased (esp. at FBG, with the exception of HAR) (Fig. 2). With increasing proportion of semi-natural habitat, the proportion of Halictidae (esp. *Lasioglossum* sp.), Megachilidae (dominantly *Osmia*, esp. at FBG) and Apidae (predominantly *Bombus* sp.; esp. at SIP) increased. At sites with more semi-natural habitat, Apidae were dominated by *Bombus* species (e.g. *ca.* 18 % at SIP), or a combination of several genera (e.g. at FBG).

For carabids, a change in community composition was driven by precipitation (MAP) where both drier and wetter sites had higher evenness across the dominant genera (*Trechus* and *Amara*; Fig. S 1b), while sites with intermediate levels of MAP had a higher dominance (up to 88 %) of *Trechus*. The drier sites, FBG and GFH, also had the highest proportion of the genus *Harpalus* (ca. 12% vs < 0.07% at other sites). The proportion of rarer genera also varied across the sites, ranging from ca. 5 % to 12 %, being lowest at high to intermediate MAP.

For the vascular plant community, a change in composition was driven by large-scale drivers of land use and weather. We found a high proportion of *Poales* genera (e.g. *Poa*, *Bromus, Dactylis*, *Arrhenatherum*, etc.) across all sites, but also a large portion of rare genera, with a relative abundance at genus level less than 5 %, that differed across sites with varying levels of land cover diversity (Fig. S2 c). At SIP, for example, the site with the highest land cover diversity, there was an increase in flowering genera from the orders *Apiales* and *Fabales*, all of which had a relative abundance of less than 5 %.

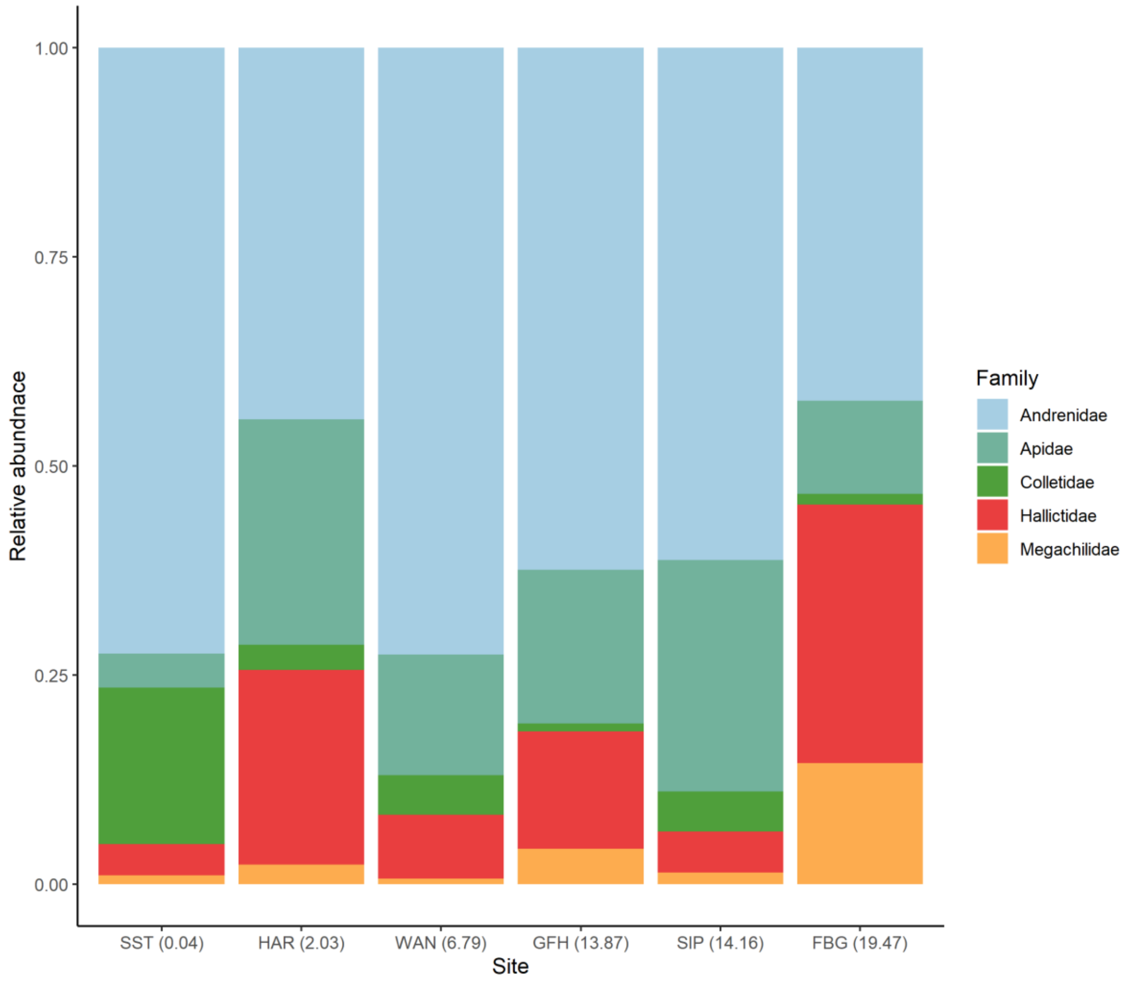

Fig 2. Relative abundance of wild bee families at sites with increasing proportion of semi-natural habitat (in parenthesis). See Fig. S1 for the full set of the taxa groups.

The strongest driver of soil fungal (direct) and bacterial composition (indirect *via* fungal composition) was soil pH, and indirectly MAT of the preceding year, however, the proportions of more common soil fungi and bacteria orders were comparable across the sites irrespective of differences in MAT (results not shown). However, when focusing in on only the top ten most abundant families, we could see a change in community composition of both soil microbial communities already at the order-level (Fig. S 1d & e). Furthermore, there was also a prominent shift in proportion of rarer orders across sites, where the proportion of rare orders (with a relative abundance at order level less than 5 %) was particularly high for soil bacteria increasing with an increase in MAT (results not shown).

Discussion

Our results revealed clear shifts in species richness, diversity and species composition of all taxonomic groups under specific environmental conditions that are especially linked to landscape-level drivers, with climatic drivers often mediated via impacts on soil pH to soil microbes. These results support our hypothesis for the cross-cutting importance of annual climatic conditions for all groups and our expectation that more mobile aboveground groups (wild bees and flying carabids) would be predominantly impacted by larger-scale drivers. However, the importance of small-scale factors was lower than expected (except of soil pH) for vascular plants, as well as soil microbes. We were surprised to find that higher diversity of land cover types has a positive effect on soil microbial richness (via soil bacterial richness), as well as the composition of both microbe groups (directly on soil fungi, indirectly via vascular plants). Likewise, we were surprised to find that soil texture, soil pH and the proportion of hill shading influenced biodiversity metrics of wild bees and carabids, as well as the effect of soil fungi and soil pH on carabid diversity.

Importance of landscape-level factors in shaping biotic communities

Landscape structure variables were more prominent drivers for aboveground taxonomic groups (both insect groups and vascular plants) than for soil microbes. Wild bee and carabid communities were supported by higher proportions of semi-natural habitat, but were negatively affected by an increase of other land use types (e.g. forested area or managed grasslands). For carabids, this negative effect could be due to specific habitat requirements. Predominantly flying carabids, as captured in our flight traps, are usually adapted to open land, and higher proportions of, e.g. forested or urban areas can create an obstacle for their dispersal (Kotze et al. 2011). In contrast to richness and diversity, carabid community composition was mainly driven by precipitation and an indirect impact of temperature by altered soil acidity. This can be expected as carabids vary greatly in their adaptations to thermal and moisture tolerances (Kotze et al. 2011), as well as soil pH (Sadej et al. 2012). These contrasting results highlight the different roles environmental drivers can play in shaping either community composition or patterns of species richness and abundance distributions.

In contrast to carabids, weather and landscape conditions impacted both community composition and species richness but not diversity of wild bees. The strong impact of landscape structure is likely related to the abundance of floral resources (Papanikolaou et al. 2017), and shelter and nesting sites (Harmon-Threatt 2020). This impact is even reflected by community changes at the family level where a high proportion of agricultural fields (e.g. in SST) lowers the proportion of above-ground nesting families (e.g. Halictidae and Megachilidae) and promotes the dominance of ground nesting ones (e.g. Andrenidae). The negative impact of land cover diversity on wild bee species richness might be a sampling artifact, as within agricultural dominated landscapes with lower flower resource availability, the traps may have been more attractive to the pollinating insects that are present than otherwise expected (Baum and Wallen 2011).

We also found landscape-level conditions to be of importance in shaping local soil microbial communities. This is surprising since soil microbial communities are usually thought to be primarily impacted by soil conditions at very small scales (Herold et al. 2014; Glassman et al. 2017). However, there is also a growing body of literature reporting that global and local soil microbial communities are strongly driven by large-scale factors such as climate (Větrovský et al. 2019) which has an influence on decomposition conditions. Our results are thus in line with studies that have also used coarse-grained sampling for investigating the drivers shaping microbial communities (Tedersoo et al. 2014; Větrovský et al. 2019). However, our study is one of the first to also find these patterns to be present not only at global and continental scales, but also at landscape scales.

Our results show that the impact of landscape structure can also be indirect, e.g. when the diversity of land cover defines the diversity of local plant communities, which in turn impact soil fungal and (indirectly) soil bacterial diversity. But we also found direct impacts of land cover diversity on soil bacterial richness, which is likely related to variation in the availability and diversity of suitable habitat niches and source pools spores can disperse from (Amarasekare 2003).

Importance of local-scale variation in shaping biotic communities

Overall, small-scale drivers were less important than larger-scale drivers at influencing biodiversity of above- and belowground taxa. Only soil pH had a prominent influence across all three biodiversity metrics, however it was strongly driven by the impact of temperature, and to a lesser extent precipitation. Thus, these large-scale drivers had a strong impact at a local-scale via soil pH. This prominent link is in support of studies reporting climate, along with basal geology, to be dominant drivers of soil pH, mainly due to long-term impacts on weathering processes and influences on accumulation and decomposition of organic material (Reuter et al. 2008).

The lower significance of other soil variables and topography for soil microbes was unexpected as they are in contrast with other studies showing edaphic variables to be prominent in shaping microbial communities (Herold et al. 2014; Glassman et al. 2017). This could be due to small-scale heterogeneity being a more primary driver (Herold et al. 2014; Kaiser et al. 2016) which our sampling grain does not capture well. Cordero and Datta (2016), for instance, suggest a scale of investigation between 10-10^3 um for determining local drivers and biological interactions of soil microbes. Alternatively, there might be a lagged microbial response to aboveground disturbances (e.g. from agricultural practices and road verge management) (Berga et al. 2012) or one missed due to fast turn over times occurring at much shorter time intervals than sampling accounts for (e.g. an hourly-scale; Landesman and Dighton, 2017). Furthermore, the strong importance of soil pH may have proportionally outweighed the contribution of the other edaphic factors. The latter, would confirm the growing body of literature suggesting soil pH to play a central role in all soil mediated processes (Glassman et al. 2017).

Several small-scale factors were of higher importance for the insect groups than predicted, suggesting they are representative of a larger spatial scale covering wild bee or carabid movement. More fine textured soils, for example, had a negative impact on wild bee richness, as most ground nesting bees prefer sandy or sandy-loamy soils (Harmon-Threatt 2020). It is possible that finer textured soil could lead to wetter nesting conditions which would increase the risk of pathogens (e.g. pathogenetic fungi, bacteria or protists) and could hinder larval development due to lowered soil temperature (Harmon-Threatt 2020). Soil texture also indirectly had an impact on carabid community composition via soil pH, which is a more obvious link for ground-dwelling organisms. Their larvae and imagos are largely affected by microclimatic conditions that are mediated by soil composition in interaction with climate (Thiele 1977). Carabid richness and diversity were also positively affected by hill shading, as is expected as many carabid species have a high preference for well sheltered habitats (Bennewicz and Barczak 2020; Guseva and Koval 2021). Amara species assemblages, for example, are known to be very sensitive to shading (Guseva and Koval 2021), corresponding with our results of higher species richness and diversity in shadier habitats, and supporting the interpretation of positive effects semi-natural habitats have on carabid diversity. Small-scale soil pH and texture further had an indirect impact on carabid diversity as mediated through the impact of soil fungi, as one might have expected since fungal infections of carabids are closely associated with host habitats and microhabitat conditions (Sugiura et al. 2010). Our results of soil fungal diversity being favored by basic soils under warmer temperatures and having a negative impact on carabid diversity could be due to these conditions favoring pathogenic or ectoparasitic fungi (Delgado-Baquerizo et al. 2020). This seems likely, considering that a large proportion of the top 10 most abundant soil fungi families in our sites were pathotrophic.

Connectivity across trophic groups

We found a strong link between the soil fungi and bacteria as expected, while the link between plants and soil microbes was weaker than predicted. This could be because we have analyzed the plants and soil microbes at species level rather than functional group level. Gastine et al. (2003), for example, found that the functional role of species is more informative for understanding the relationship between plants and soil microbial communities than species richness and identity. Alternatively, it might be an issue of scale-mismatching (De Deyn and Van der Putten 2005; Cordero and Datta 2016), since finding a suitable survey scale for studying aboveground–belowground diversity relationships is challenging (De Deyn and Van der Putten 2005).

However, identified links among trophic groups allow the identification of indirect effects of environmental drivers, e.g. when landscape- and small-scale conditions define plant or fungal communities, which in turn modify bacterial communities in addition to direct environmental effects. Here, we show that there are complex networks of connectivity across multiple trophic groups and their environmental drivers across the soil interface. Specifically, we found a cascading impact of large-scale drivers (MAT and MAP) to small-scale conditions (soil pH) that then affected belowground (soil fungi) and aboveground taxa (carabids). This highlights the importance of considering the entire system with both direct and indirect effects of environmental drivers and the interlinkages among trophic groups for the maintenance of multifunctionality of ecosystems (Manning et al. 2018; Felipe-Lucia et al. 2020).

Maintaining multifunctionality within agroecosystems

Our work shows that the beneficial effects of semi-natural areas in the landscape do not only affect local aboveground and plant communities, but also lead to knock-on effects, either direct or indirect, on soil microbial community composition and diversity. With this, managing semi-natural areas provides great potential to improve multifunctionality across multiple trophic levels in the agricultural landscape. Beneficial impacts on the diversity of wild bees, for example, can increase the stability of pollination services for crops (Dainese et al. 2019; Senapathi et al. 2021) and wild plants (Potts et al. 2010). We also observed shifts in the diversity and composition of wild bees, already visible at the family level, indicating impacts on the functional structure and likely the provisioning of pollination services. Bumblebees, for example, are good pollinators of crops (Fussell and Corbet 1992) and their proportions increased with semi-natural area, suggesting that pollination quality can be affected by the amount of semi-natural habitat. In the same way, supporting a higher diversity of carabids which serve as important natural enemies (Fusser et al. 2016) or weed control agents (Bohan et al. 2011), will increase and stabilize biocontrol services provided for agricultural production (Blubaugh and Kaplan 2016; Snyder 2019). Improving the diversity of plants (including rare genera) will also increase functional trait diversity (Finney and Kaye 2017), which in turn can increase ecosystem services linked to these traits (Hanisch et al. 2020).

Our results also indicate the importance of considering not only species richness or community composition but also differential impacts of environmental drivers on abundance distributions and therewith aspects of rarity. In the plant kingdom, different functional contributions are made by common and rare species to ecosystem multifunctionality (Soliveres et al. 2016b). This is also the case for other aboveground (Senapathi et al. 2021) and likely also for belowground communities (Ramirez et al. 2018). The diversity of rare soil fungi and bacteria orders, for example, is especially important for belowground processes such as leaf litter decomposition, nutrient cycling, carbon sequestration and bioremediation (Wakelin et al. 2009; Burns et al. 2013).

The strong impacts of weather conditions observed are particularly relevant for potential land-based mitigation actions against climate change. It has been shown that the amount and diversity of semi-natural habitats can buffer the effects of climate change and weather extremes on pollinators (Oliver et al. 2015; Papanikolaou et al. 2016b). Given the beneficial effects of semi-natural habitats on multiple taxonomic groups and the interlinkages across the soil interface, such buffering effects might also stabilize the entire multifunctionality within agroecosystems.

Conclusions

Identifying the spatial scale of relevant drivers and the interconnections among taxa of different trophic levels has important implications for policy frameworks, which also act at multiple spatial scales and target different taxonomic groups. Our results emphasize the importance of landscape-level drivers, and highlight the need for policy instruments to focus on this coarser scale for ensuring multifunctionality of agroecosystems. We found, for example, that more species rich and diverse biotic communities across the soil surface are promoted by higher proportions of semi-natural habitats. More heterogeneity at the landscape-level supports higher biodiversity and promotes the abundance of common service providers and occurrence of specialists, which enhances the multifunctionality and stability of agroecosystems (Soliveres et al. 2016b).

In conclusion, our results emphasize the importance of management of agroecosystems to promote multifunctionality across multiple trophic groups, and especially highlights the necessity of landscape focused planning that promotes semi-natural habitats. By maintaining more heterogeneity at a landscape-scale there will be higher stability of the biotic communities and the ecosystem services they provide.

Authors' contributions

E.S, T.K, T.W, H.V and O.S conceptualized and developed ideas. M.F, O.S and E.S designed the field study. M.F, E.S and B.S collected and processes data; E.S conducted analyses and led the writing, with contributions from all authors for results interpretation and finalization of the manuscript.

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Chapter 5: Synthesis

It has become increasingly vital to understand how land use and land use intensity, for example within agricultural systems, have an effect on multiple scales and across multiple trophic levels on ecological functions and process. This level of understanding of the scale sensitivity of different taxonomic groups, ecological mechanisms and drivers of change is required for developing scale-relevant policies for effective conservation and sustainable management of ecosystems. Through my research I address these issues. Here I synthesize the respective research chapters, summarizing the main findings and highlighting their relevance to advancing scientific knowledge of the complexity of above- and belowground biodiversity patterns and responses to land use and their relevance for policy development toward promoting ecosystem multifunctionality. Furthermore, I discuss research limitations and opportunities for future research.

Main findings

In my thesis, I addressed the importance of considering multiple spatial scales and trophic groups when investigating the impact of land use on biodiversity and underlying community assembly processes. My research findings highlight that scale-dependent responses of above- (vascular plants) and belowground (soil fungi and bacteria) biodiversity to land use are the norm, rather than the exception (**Chapter 2**, Slabbert et al. 2020). Furthermore, my work found that both landscape- and local-scale drivers impact the diversity and composition of above- and belowground biodiversity within agroecosystems (**Chapters 3 and 4**, Slabbert et al. 2022). However, abiotic factors remained more important in comparison to land use [land management (LM) and land use intensity (LUI)] (**Chapter 3**, Slabbert et al. 2022) especially at larger spatial scales (**Chapter 4**).

The scale-dependent response to management as pastures (livestock grazing) or meadows (hay production), were highly context-dependent and less consistent across ecologically linked taxonomic groups than expected (**Chapter 2**). These findings indicate that scale-dependent responses to land use cannot easily be generalized across the soil surface, across taxonomic groups or between sites with different land use histories and management practices. Furthermore, my findings underscore that in order to more holistically understand LM impacts on above- and belowground biodiversity it is necessary to consider multiple biodiversity metrics (e.g. changes to density (abundance), evenness and spatial aggregation, not only species richness) (**Chapter 2**) and to control for abiotic factors such as climatic and soil conditions (**Chapters 2** and **3**).

To better understand the drivers of agrobiodiversity, I further investigated the relative importance of land use in comparison to biotic and abiotic drivers on above- and belowground components of biodiversity within managed semi-natural grasslands (**Chapters 2** and **Chapter 3**). Here I specifically studied the relative contribution of biotic and abiotic parameters in explaining vascular plant species and soil microbes (only soil fungi, **Chapter 3**; or soil fungi and bacteria, **Chapter 4**) occurrence patterns within semi-natural grasslands. In **Chapter 3**, I found that abiotic variables (soil, topography, and climate) were notably more important for shaping both vascular plant and soil fungal communities in comparison to land use (LM and LUI) and biotic interactions. Furthermore, while the relative importance of these explanatory variables was similar across both taxon groups, climate conditions were more important for vascular plant communities, while soil variables (e.g. soil acidity and fertility, including soil carbon and potassium content) were more important for soil fungal communities (**Chapter 3**). Species-specific responses to the various factors showed some commonality across taxon groupings, but not as much as one might expect given the extensive history of previous LM and ecological links across taxonomic groups (**Chapters 2** and **3**). When investigating the impact of large- and small-scale drivers on multiple taxonomic groups I found that large-scale drivers were especially important for shaping the species richness, diversity and composition of above- and belowground groups (**Chapter 4**), however, there were also linkages across drivers of different scales and between trophic groups. For example, I found that climate drivers (mean annual precipitation and temperature) have a strong impact on belowground groups as mediated via its impact on soil acidity (soil pH). While more mobile aboveground groups (wild bees and carabid beetles) were predominantly affected by large-scale drivers, but small-scale drivers can also have a significant effect on species richness and diversity. Here specifically, I found soil texture as mediated via its effect on soil pH, to have an effect on the composition of wild bees and carabids (**Chapter 4**).

With respect to the LM comparisons of pasture versus meadow management of semi-natural grasslands, I found that biotic communities within both these managed systems can harbor high diversity and are, in part, distinctly different while also having high species overlap (**Chapters 2** and **3**). For example, I found that about half of the plant and soil fungal species exhibited distinct LM preferences and responses to LUI (**Chapter 3**). The taxa had opposite LM preferences, with more vascular plant species favoring pasture management than meadow management, whilst the opposite was found for soil fungal species.

Relevance

Through my research findings I specifically provide further insights into scale-dependent responses of multiple trophic groups, the importance of multiple scale-specific drivers and the connectivity across drivers and trophic groups. These insights could be applied towards informing further multi-scale and multi-taxa research and development of more spatially explicit policy instruments aimed at promoting multifunctional within agroecosystems.

Relevance for advancing scientific knowledge and guiding future research

The scale of investigation of ecological systems relates a scale-dependent story, and so too when trying to understand the impact that anthropogenic disturbances and management have on (agro)ecosystems. My work highlights the commonality of scale-dependent responses (**Chapter 2**), the role of multi-scale drivers (**Chapters 3** and **4**) and how biodiversity patterns cannot easily be generalized even where close ecological links or land use legacy effects may be expected (**Chapter 2**). In **Chapter 2**, my results especially pointed to the higher complexity of scale-dependent responses of belowground groups (soil microbes) than vascular plants to environmental factors and advocates for more scale-explicit investigation of soil microbial communities. Furthermore, my work underscores the added insight that can be gained by investigating biodiversity responses and drivers using several complementary biodiversity metrics (**Chapters 3** and **4**). Here specifically my research points to the necessity of studying biodiversity patterns not only by assessing species richness but also its underlying components related to the change in density, evenness and spatial aggregation (**Chapter 2**). When wanting to understand the interconnectivity of impacts across the soil surface I found investigating changes to community composition to be more informative than only considering changes to richness or diversity (**Chapter 4**).

Furthermore, my findings (**Chapter 3**), emphasize the necessity of accounting for soil and climate when investigating the influence of land use, as well as considering the environmental context at both small and large spatial scales when making LM and biodiversity conservation decisions. By being more explicit in these aspects, land use research findings could become more consistent in informing management. As well as support the development of policy instruments that promote management that is most suitable for the specific environmental context.

Relevance for advancing the multifunctionality of agroecosystems

My research confirms the potential agriculture dominated landscapes hold as multifunctional ecosystems. For example, I found that semi-natural grasslands and linear elements in the agroecosystem can have a high diversity of both common and rare species (**Chapters 2** and **4**) that fulfill a range of functional roles emphasizes the multifunctional potential of agroecosystems. Rare species especially have been found by previous research to be highly relevant to promoting ecosystem multifunctionality as they have less ecosystem service trade-offs (i.e. where the contribution of one service provider cancels out that of another) and lower trait redundancy than common species. Ecological functions provided by these trophic rich systems have a direct positive effect on agricultural production (Wagg et al. 2014; Bender et al. 2015; Dainese et al. 2019), resulting in a win-win effect for both ecological systems and societal benefits. Moreover, my findings that managed grasslands, or remnant elements of semi-natural habitat are still predominantly driven by abiotic factors rather than only anthropogenic related factors (**Chapters 2**, **3** and **4**) suggest that these areas within agroecosystems have high value for nature preservation. This is in support of other findings that have stressed the conservation value of semi-natural grasslands, as studied in **Chapters 2** and **3**, under pasture and meadow management (Tälle et al. 2016). While field margins and road verges, as studied in **Chapter 4**, provide complementary habitat to agrobiodiversity and promote movement of beneficial fauna and flora within agroecosystems (Phillips et al. 2019). Furthermore, these semi-natural areas within agroecosystems could provide a multitude of other ecosystem functions (Soliveres et al. 2016b; Phillips et al. 2019), while still producing biomass equivalent to commercially managed areas (Weisser et al. 2017).

Relevance for land management of semi-natural grasslands

Currently, there is high variation across studies in the effects of grassland LM on biodiversity (Tälle et al. 2016). Based on current research, it is not possible to reach a sound verdict as to whether policy should advance pasture or meadow management. Findings from my second chapter (**Chapter 2**) regarding the commonality of scale-dependent effects of land use on multiple taxa and biodiversity metrics add new insights to why there may be so much variation across different studies regarding this issue. The debate around how to best balance the advantages and disadvantages of the respective management directions could be moved forward with more scale-explicit studies that ideally also investigate the impacts of grassland management across multiple taxonomic groups. Furthermore, my findings suggest that the management decision of semi-natural grasslands, as either pasture or meadow, should not be seen as a clear dichotomy, but rather a complex continuum (**Chapter 2**). My results showed that both management approaches could harbor species rich biotic communities, however, I did find clear LM impacts (**Chapter 3**). This was specifically in the form of taxonomic preferences to specific grassland management practices, showing that not all taxonomic groups or trophic levels are benefited by the same management. While too high or too low LUI was detrimental to maintaining a species rich community of different trophic groups (**Chapter 2**). My findings suggest that different species and trophic groups would be promoted by different management approaches. Thereby advocating that for promoting diversity and multifunctionality at a landscape level it would be advantageous for a heterogeneity of LM approaches at low to moderate levels of LUI (Slabbert et al. 2020; 2022). Increasing heterogeneity in management, as well as lowering LUI as recommended by Gossner et al. (2016), would be beneficial for conservation of these species-rich habitats (Dahlström et al. 2013), while also advancing the overall multifunctional value of agroecosystems (Grass et al. 2020).

Relevance for policy development

It has become increasingly evident that the EU Common Agricultural policy requires a strategic restructuring for increased environmental and economic sustainability (Pe'er et al. 2020). Studies, such as that of Arponen et al. (2013), among others, highlight the need for policy instruments to not only be targeting conservation at a small-scale of farm-level, but to have more of a landscape-level approach so as to enhance ecological processes through higher connectivity across farm land regions. My research also advocates for policy and management strategies to take on a multi-scale, as well as a multi-taxa approach to promote biodiversity and multifunctionality of (agro)ecosystems (**Chapters 2**, **3** and **4**). This arose as an overarching theme of my research as investigating agroecosystems across multi-scale and multi-taxa groups each time added valuable insight that would otherwise not have been evident. For example, **Chapter 3** highlights the importance of large- and small-scale drivers shaping above- and belowground communities in agroecosystems. Landscape-level drivers, related to land use and climate were especially important in shaping these biotic communities and maintaining a high level of biodiversity. These results add further insight into the relevance of scale-dependent processes, as well as the high context-specificity of land use impacts, as discussed in **Chapter 2**.

The research findings presented in this thesis highlight the need for policy structures to incorporate more context specificity to ensure management is sustainable for the local ecological and socio-economic context. Furthermore, my work supports the growing body of scientific evidence advocating that to address the biodiversity crisis LM practices (including policy driven ones such as the implementation of agri-environmental schemes) should increase landscape heterogeneity and habitat complexity within agroecosystems at both the local and landscape scale (e.g. Caro et al. 2016; Loos et al. 2021; Marja et al. 2022). These recommendations are in support of the call for policy structures to adapt a new approach in how environmental issues are addressed (Paloniemi et al. 2012; Henle et al. 2014; Tscharntke et al. 2021).

Caveats and future directions

Research across the soil surface is challenging due to several factors, yet it is essential for understanding ecosystem functioning more holistically as well as the impact anthropogenic disturbances have. These should ideally consider multiple scales and trophic groups. Study limitations have been discussed within each research chapter, but more general ones are discussed here as aspects future research could take into consideration.

Wider range of trophic groups and consideration of functional diversity

Future studies could include a wider range of taxonomic groups that fulfill a broader range of functional roles. At the moment the selected taxa groups are limited to 2 – 5 groups only, fulfilling a narrower range of ecosystems functions. Other taxonomic groups that could be included are, for example, arachnids (Hambäck et al. 2021), Collembola and nematodes (Deyn et al. 2004), birds (Frenzel et al. 2016) and a range of other wild insect pollinators (Senapathi et al. 2021).

Research specifically relating biodiversity to ecosystem functioning within terrestrial systems is still limited (Eisenhauer et al. 2019), and even more so within agroecosystems. Thus, it is recommended that future studies also more explicitly take into consideration functional roles of the studied taxonomic groups. Gastine et al. (2003), for example, found that biodiversity patterns across trophic groups was less related to the identity of the species in the community and more by the functional role the respective species fulfilled. Furthermore, functional responses to disturbance have been found to be faster than changes in community composition for soil bacteria (Berga et al. 2012). By additionally investigating the impact of land use on functional-trait diversity could add valuable insight as to how land use is impacting ecosystem functioning and stability across multiple trophic levels (de Bello et al. 2021). To include this aspect, however, may limit the selection of taxonomic groups included in studies to those for which there are reliable, context relevant databases available or where functional traits can easily be measured under field or experimental conditions. Furthermore, it introduces additional computational constraints on analysis when working with large datasets (e.g. DNA sequenced data). See **Chapter 3**'s discussion for suggestions how computational challenges could be addressed.

Spatially explicit sampling campaigns

Multi-trophic studies could also improve by increasing the ability to accurately capture biodiversity patterns and interactions by reassessing how sampling campaigns are designed. For example, my work suggested that it may be necessary to tailor sampling more to the ecological habitat range of the respective taxa groups and the scale at which ecological processes take place, e.g. intra-specific interactions, than just using a standard sampling grain across all taxa. For example, it has been suggested that to detect ecological interconnections of microbial communities, as sampling scale of 10 - 10^3 µm should be used, a spatial gradient several magnitudes finer than the one more commonly used by field studies (Cordero and Datta 2016). Considering this, sampling smaller organisms should be done at finer scales, rather than using a pooling approach to try and match the 1 m^2 sampling size set for larger taxa, e.g. plants. Furthermore, research initiatives monitoring several taxonomic groups independently should in advance also take into consideration the spatial compatibility of the individual sampling campaigns to ensure that the independently studied groups can also be synergized without issues of mismatched spatial coverage or excessive overlap.

Broader spatial and temporal coverage

Although my research is conducted in agricultural landscapes similar to the broader European context, future studies could be done over a larger spatial extent, covering a wider range of biogeographical contexts, LM combinations and LUI gradient. It would, for example, be interesting to conduct a similar study as in **Chapters 2** and **3** on grasslands across a wider range of LUI. The grasslands considered in these chapters have generally lower LUI than other parts of Germany and Europe. It is also more common for grasslands to be fertilized and artificially reseeded, management practices the grasslands I studied were not subjected to. Furthermore, many of my results considered a single temporal grain of investigation. Studying temporal scale-dependence of multiple-trophic groups simultaneously could further enhance our understanding of the complexity of ecological networks. The recent multi-taxa study by Schwarz et al. (2020) has already contributed valuable insights regarding the temporal scale-dependence of plant-pollinator networks. Schwarz et al. (2020) show that adding this dimension at either a broad temporal scale or narrower one could provide important insights to the underlying mechanisms and temporal dynamics shaping biotic communities. Moreover, the recent global synthesis by Senapathi et al. (2021) further emphasize the role a diverse pollinator community has for ensuring temporal stability in crop pollination.

Increased policy focus

Another area for more detailed research would be multi-scale studies that consider the impact of policy measures more explicitly. Although, I have been able to make some policy relevant recommendations based on my research findings, my work does not directly consider the impact of specific policy instruments on agrobiodiversity across multiple tropic groups and scales. This would be an additional avenue of research that would be important to pursue to assess the effectiveness of current policy and make science-based recommendations for improvement (e.g. Marja et al. 2019, 2022). Conducting more policy specific studies with a multi-scale and multi-trophic coverage could, for example, add valuable insights to the scale-dependent effects of current policy instruments. The recent study by (Nilsson et al. 2021) is a good example of how the impact of specific policy measures could be investigated for multiple taxa groups.

Conclusion

Placing my research findings within the context of a social-ecological perspective of a land manager or a project manager, my findings offer a glimmer of hope that highly transformed and managed landscapes, dominated by agricultural production activities, can again be restored to healthier, more biodiversity-rich systems of high ecosystem multifunctionality. My results suggest that moving towards multifunctional agroecosystems would not be limited by abiotic factors. Moreover, my work suggests that when studying land use impacts or making LM decisions it is important to control for the soil and climatic conditions to more accurately account for and prioritize ecological processes within agroecosystems. Thus, based on my research I recommend policies and LM approaches to be tailored according to the environmental context and scales of ecological importance rather than only administrative- or farm-level boundaries. This could help resolve the mismatch my collaborative work with EU and USE colleagues identified between agri-environmental subsidies allocation and environmental need, including areas experiencing high levels of biodiversity loss and habitat degradation (Biffi et al. 2021).

The explorative research by Vervoort et al. (2012) on the different perspectives of project or organization managers within social-ecological systems, also identified social dimensions or constructs to be the main challenge faced when trying to bring about positive change toward sustainability, and not biogeographical aspects. This suggests that challenges that hinder a paradigm shift toward more multifunctional agroecosystems are more likely to be due to societal constructs, for example, related to global markets, respective policy incentives and their implementation, than the environmental context. Thus, if societal (e.g. administrative, political and economic) limitations and challenges are more constructively addressed and interactively solved across disciplines, there is the possibility of bringing about a system change that also will promote healthier social-ecological agroecosystems.

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Appendix

Chapter 2: Supplementary material

Table S1. Average soil chemical properties of the grasslands managed as meadows or pastures at the respective Terrestrial Environmental Observatories (TERENO) sites. Properties listed include the pH value (pH), organic carbon to total nitrogen ratio (C:N), total organic carbon (TOC), total nitrogen (N), calcium carbonate ($CaCO_3$), potassium (K) and phosphorus (P). Nutrients are measured as mg/100g soil, with P and K as the plant available concentrations. Site names refer to the nearest large village. Asterisks' indicate significance differences ('*', $p < 0.05$; '**', $p < 0.01$; '***', $p < 0.001$) between management types based on a Welch t-test. See Table 1 for more site detail.

Study site	Soil parameters	Meadow		Pasture		t-value	p-value
		Mean	Standard error	Mean	Standard error		
Harsleben	pH	7.24	0.11	6.91	0.11	3.04	**
	C:N	8.36	0.13	9.59	0.13	-9.60	***
	TOC	17.06	0.63	21.84	0.63	-7.60	***
	TN	2.04	0.07	2.28	0.07	-3.58	***
	$CaCO_3$	35.05	4.34	23.94	4.34	2.56	*
	K	36.65	3.00	30.06	3.00	2.20	*
	P	5.97	1.16	5.97	1.16	0.00	ns
Siptenfelde	pH	5.54	0.18	6.34	0.18	-4.41	***
	C:N	9.10	0.25	9.26	0.25	-0.65	ns
	TOC	25.11	1.86	37.02	1.86	-6.41	***
	TN	2.69	0.13	4.00	0.13	-9.88	***
	$CaCO_3$	15.88	1.51	20.34	1.51	-2.94	**
	K	8.96	3.68	23.46	3.68	-3.94	***
	P	1.85	0.45	3.81	0.45	-4.37	***
Friedeburg	pH	7.59	0.03	7.39	0.03	5.83	***
	C:N	10.52	0.20	9.98	0.20	2.74	*
	TOC	25.04	1.62	22.44	1.62	1.61	ns
	TN	2.42	0.17	2.25	0.17	1.00	ns
	$CaCO_3$	71.58	4.19	44.59	4.19	6.44	***
	K	30.36	3.54	29.05	3.54	0.37	ns
	P	18.87	4.19	13.87	4.19	1.19	ns
Wanzleben	pH	7.41	0.03	7.31	0.03	3.63	***
	C:N	10.97	0.22	10.32	0.22	3.01	**
	TOC	47.02	2.69	49.39	2.69	-0.88	ns
	TN	4.43	0.30	4.79	0.30	-1.18	***
	$CaCO_3$	109.60	8.70	97.70	8.70	1.37	ns
	K	11.44	1.67	15.25	1.67	-2.29	*
	P	1.08	0.30	2.02	0.30	-3.16	**

(Table S1 continues)

(Table S1 continued)

Study site	Soil parameters	Meadow		Pasture		t-value	p-value
		Mean	Standard error	Mean	Standard error		
Greifenhagen	pH	5.67	0.12	6.49	0.12	-6.66	***
	C:N	7.41	0.10	8.27	0.10	-8.46	***
	TOC	15.05	0.77	22.90	0.77	-10.26	***
	TN	2.04	0.09	2.76	0.09	-8.49	***
	$CaCO_3$	18.02	1.07	16.48	1.07	1.44	ns
	K	6.65	2.88	29.63	2.88	-7.99	***
	P	0.51	0.57	5.41	0.57	-8.52	***

Table S2. Analysis of Deviance for linear mixed effects models (random intercept for site) performed on the (a) soil properties and (b) landscape features across land management (LM) types (meadow versus pasture) and within sites, including the interaction of LM and site. Soil parameters tested include the, pH values (pH), calcium carbonate ($CaCO_3$), phosphorus (P) and potassium (K). Landscape features tested include the grasslands altitude, slope and coefficient of variation in slope (Slope cv) and aspect and coefficient of variation thereof (Aspect cv). Results report type III Wald chi-square test results including the Chi^2 value, degrees of freedom (Df) and the p-value of the Chi^2 test (p-chi^2). Asterisks' indicate significance differences: 0, '***'; 0.001, '**'; 0.01, '*'; 0.05, '.'). For more detail on the sites, see Table 1.

a)

Response variable:	pH				$CaCO^3$				P				K		
	Chi^2	Df	p-chi^2		Chi^2	Df	p-chi^2		Chi^2	Df	p-chi^2		Chi^2	Df	p-chi^2
Intercept	550.65	1	2E-16	***	24.71	1	7E-07	***	3.57	1	0.06	.	0.58	1	0.45
Between land management (LM)	0.28	1	6E-01		2.17	1	1E-01		0.49	1	0.49		0.02	1	0.90
Within groups (Site)	31.38	4	0E+00	***	26.95	4	2E-05	***	5.07	4	0.28		6.49	4	0.17
LM:Site	6.91	4	1E-01		1.47	4	8E-01		0.80	4	0.94		3.96	4	0.41

b)

Response variable:	Altitude				Slope				Slope cv				Aspect				Aspect cv			
	Chi^2	Df	p-chi^2		Chi^2	Df	p-chi^2		Chi^2	Df	p-chi^2		Chi^2	Df	p-chi^2		Chi^2	Df	p-chi^2	
Intercept	0.26	1	0.61		2.46	1	0.12		0.63	1	0.43		67.41	1	2E-16	***	0.72	1	0.40	
Between land management (LM)	103.69	1	<2e-16	***	56.45	1	0.00	***	12.04	1	0.00	***	15.75	1	7E-05	***	0.00	1	0.96	
Within groups (Site)	1.97	4	0.74		1.17	4	0.88		20.16	4	0.00	***	1.32	4	9E-01		2.48	4	0.65	
LM:Site	320.19	4	<2e-16	***	41.79	4	0.00	***	123.14	4	0.00	***	12.23	4	2E-02	*	19.11	4	0.00	***

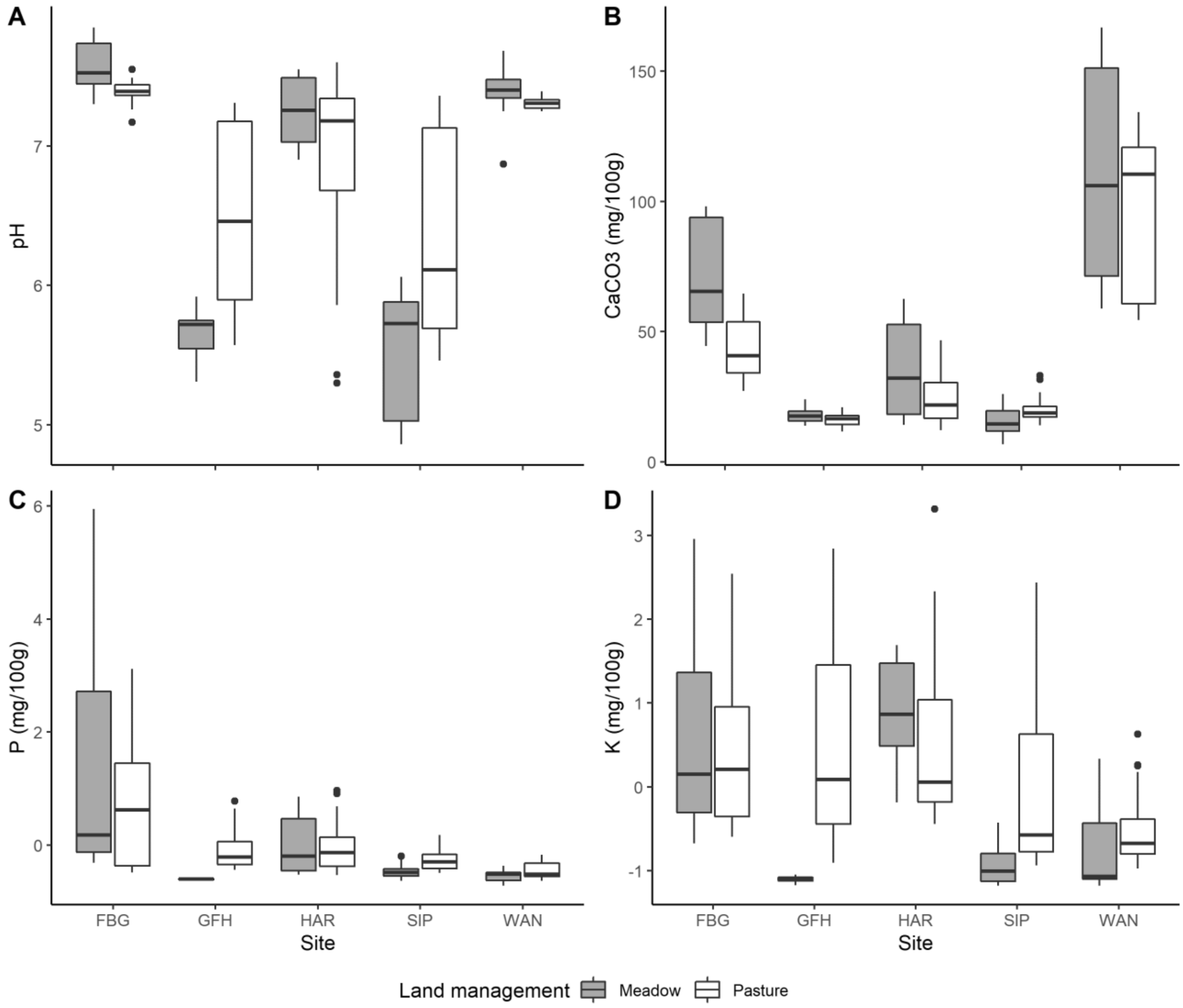

Figure S1. Boxplots of soil properties across grassland land management (LM) types within and across study sites [Friedeburg (FBG), Greifenhagen (GHF), Harsleben (HAR), Siptenfelde (SIP) and Wanzleben (WAN)]. Site names refer to the closest large village, see Table 1 for further details. Soil parameters tested include the, pH value (pH), calcium carbonate ($CaCO_3$), phosphorus (P) and potassium (K). P and K were measured at plant available concentrations. The analyses per soil variable were performed as mixed effect models with interaction effect between LM types (meadow versus pasture) and site location. See Table S5 for further details and ANOVA results.

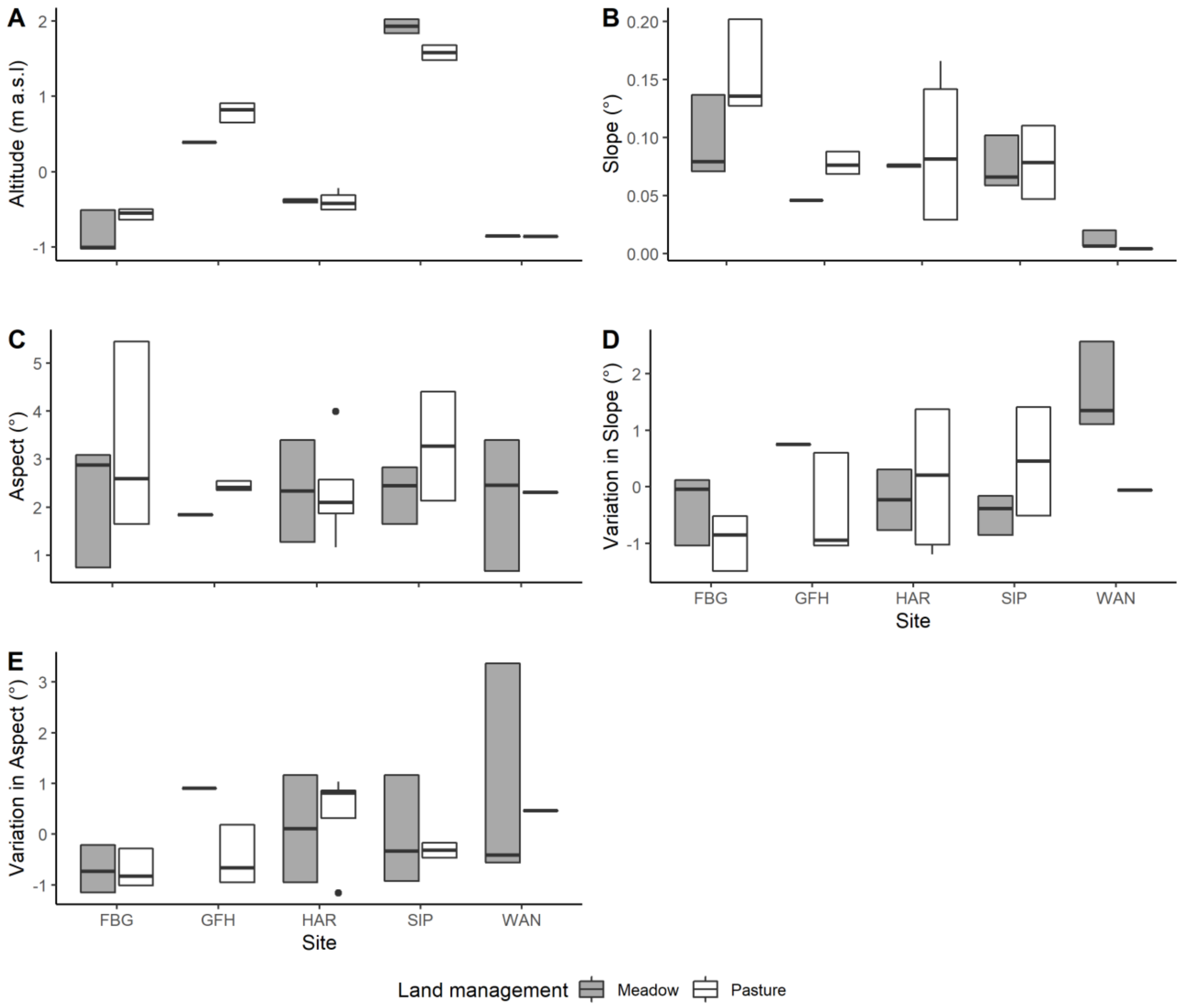

Figure S2. Boxplots of landscape features across grassland land management (LM) types within and across study sites [Friedeburg (FBG), Greifenhagen (GHF), Harsleben (HAR), Siptenfelde (SIP) and Wanzleben (WAN)]. Site names refer to the closest large village, see Table 1 for further details. The analyses per landscape feature were performed as mixed effect models with interaction effect between LM types (meadow versus pasture) and site location, followed by a type III ANOVA. See Table S5 for further details and ANOVA results.

Table S3. Overview of the most abundant species per taxonomic group (plants, fungi and bacteria) across the Terrestrial Environmental Observatories (TERENO) sites. The top five rank abundant species are listed per site-land management combination, with the top five indicated in bold. (a) Plant species are reported as proportional percentage cover and sum of percentage cover of the top ranked species. (b) Fungi and (c) bacteria were recorded to operational taxonomic units (OTU; for bacteria these are used as species equivalent, while for fungi these could be associated with specific species. These are reported as proportional and total OTU reads (used as a proxy for abundance) for the top ranked species per taxa. Site names refer to the nearest large village.

a)

Sites	Friedeburg				Greifenhagen				Harsleben				Siptenfelde				Wanzleben			
Land management	Meadow		Pasture		Meadow		Pasture		Meadow		Pasture		Meadow		Pasture		Meadow		Pasture	
Top rank abundant species	Proportional % cover	Sum of % cover	Proportional % cover	Sum of % cover	Proportional % cover	Sum of % cover	Proportional % cover	Sum of % cover	Proportional % cover	Sum of % cover	Proportional % cover	Sum of % cover	Proportional % cover	Sum of % cover	Proportional % cover	Sum of % cover	Proportional % cover	Sum of % cover	Proportional % cover	Sum of % cover
Achillea millefolium	3	125	4	228	0	3			**7**	**178**	2	103	5	217	4	97				
Agrimonia eupatoria	1	48	**7**	**382**					5	120	**13**	**746**								
Agrostis capillaris									1	33	2	84	**6**	**261**	1	35	1	29		
Agrostis stolonifera									3	74					1	20	**25**	**814**	**13**	**525**
Apera spica-venti	**15**	**696**																		
Arrhenatherum elatius	**9**	**410**	4	231	0	1			6	155	**10**	**586**	**5**	**240**	5	118	0	14	1	50
Brachypodium pinnatum									2	42	**13**	**717**								
Carduus acanthoides	**6**	**261**																		
Carex hirta															1	13	1	19	**21**	**887**
Centaurea jacea			2	85					**20**	**491**										
Crepis biennis	0	7	1	37	1	7	1	22	0	7			**9**	**427**	**12**	**310**				
Dactylis glomerata	**12**	**546**	4	233	**12**	**153**	4	132	2	45	1	76	**11**	**498**	**11**	**283**	1	31		
Elymus repens	3	149	0	16	2	20	**12**	**434**	0	6	0	8	1	27	**9**	**223**	2	61	2	79
Festuca rubra	0	21	**12**	**648**					**11**	**272**	**10**	**571**	**15**	**674**	1	24				
Festuca rupicola	0	9	**8**	**421**							**9**	**499**								
Festuca arvensis	1	30	0	20	**9**	**118**							1	41	5	136	**9**	**292**	5	206
Galium album			**7**	**368**			1	35	3	69	1	44								
Juncus compressus																	**17**	**566**		
Lolium perenne	1	38	0	24	2	21	**37**	**1329**	0	7			0	2	0	7			2	88
Phleum pratense			0	2	**12**	**151**	2	56	0	8			2	74	1	26	4	125	0	13
Poa pratensis	3	117	2	91	**8**	**103**	**9**	**305**	**9**	**209**	2	84	2	76	**6**	**146**	**16**	**518**	**21**	**856**
Poa trivialis			2	88					0	1	0	12	0	8	0	2			**6**	**241**
Ranunculus repens	0	12			**8**	**104**	0	11							3	72	0	10	**10**	**414**
Scirpus sylvaticus																	**15**	**487**		
Taraxacum sect. Ruderalia	3	123	2	122	7	84	**14**	**486**	0	9	0	9	5	213	**6**	**161**	1	18	0	10
Trifolium campestre	0	2	**4**	**234**					0	4	1	74								
Trifolium repens	2	102	3	163	2	28	**10**	**348**			0	1	2	94	3	86			4	172
Tripleurospermum inodorum	**5**	**254**																		
Trisetum flavescens	0	1	3	168					**7**	**158**	3	187	0	12	1	34				
Total of current subset	**63**	**2951**	**64**	**3561**	**63**	**793**	**88**	**3158**	**77**	**1888**	**67**	**3801**	**63**	**2864**	**70**	**1793**	**90**	**2984**	**85**	**3541**
Grand Total of full dataset	100	4692	99	5534	100	1250	100	3602	100	2442	100	5660	100	4563	100	2557	100	3327	99	4185

(Table S3 continues)

(Table S3 continued)
b)

	Sites	Friedeburg				Greifenhagen				Harsleben				Siptenfelde				Wanzleben			
	Land management	Meadow		Pasture		Meadow		Pasture		Meadow		Pasture		Meadow		Pasture		Meadow		Pasture	
Species	**Phylum**	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum
Mortierella minutissima	Zygomycota	**6**	**27143**	**4**	**16576**	**9**	**12433**	**5**	**21431**	**7**	**19559**	1	4117	**4**	**18425**	**9**	**25445**	**6**	**24819**	**8**	**32328**
Exophiala equina	Ascomycota	**3**	**13752**	**2**	**9162**	**2**	3395	**7**	**30773**	**4**	**10202**	**3**	**14634**	1	2675	2	4208	1	5150	0	494
Cryptococcus terreus	Basidiomycota	2	8452	**2**	**8422**	3	4862	**6**	**25307**	**6**	**18167**	2	12460	1	4520	1	3722	0	44		
Cryptococcus terricola	Basidiomycota	0	50			**4**	**5783**	2	6557	0	62	0	1901	**3**	**13778**	**3**	**7891**	0	1	0	2
Preussia flanaganii	Ascomycota	1	2142	2	6994	0	434	**4**	**15498**	**6**	**16843**	1	6827	0	738	**2**	**6957**	0	921	2	6461
Mortierella alpina	Zygomycota	**2**	**9454**	1	2917	1	753	2	7364	1	1386	1	3172	1	4764	**2**	**6958**	0	35	0	17
Mortierella exigua	Zygomycota	1	2629	1	4545	**4**	**5196**	1	4391	1	3433	0	1992	0	840	1	3131	2	9072	**3**	**13184**
Mortierella elongata	Zygomycota	**4**	**17943**	2	6886	0	41	2	9325	2	6740	0	930	0	9	0	382				
Camarophyllopsis hymenocephala	Basidiomycota			0	25			0	2	0	2	**5**	**30826**								
Agaricales spp.	Basidiomycota																	**6**	**24277**	**3**	**11947**
Ascomycota spp.	Ascomycota																	**8**	**34487**		
Cryptococcus spp.	Basidiomycota	0	2			4	**5551**	0	1097	0	3	0	316	2	7197	1	3622	0	1	0	1
Agaricales spp.	Basidiomycota											**4**	**24405**								
Inocybe griseovelata	Basidiomycota	**7**	**29127**	0	3			0	1									0	9		
Ascomycota spp.	Ascomycota			0	640			0	233	**4**	**10933**	2	10649								
Clavariaceae spp.	Basidiomycota	0	1	0	4	1	929	0	1954	0	312	0	1903	**4**	**16028**	0	375	1	2747		
Clavaria spp.	Basidiomycota													**4**	**16094**	0	89				
Hygrocybe nigrescens	Basidiomycota							0	1			**3**	**15169**	2	8819						
Unclassified fungi	Unclassified fungi	0	217	**2**	**8224**					0	1	2	13759								
Mortierella spp.	Zygomycota	0	1	0	1	**9**	**12990**					0	82	1	2444	0	330				
Cuphophyllus spp.	Basidiomycota											**3**	**18430**								
Ascomycota spp.	Ascomycota			**3**	**14266**					0	256	0	802								
Funneliformis geosporum	Glomeromycota	0	17	0	102			0	36	0	264	0	4	0	9	0	487	1	3419	**3**	**13786**
Ascomycota spp.	Ascomycota																	**4**	**16618**	0	141
Agaricales spp.	Basidiomycota							0	14			0	4	**4**	**17682**	0	1				
Mortierella spp.	Zygomycota							0	17							0	56	0	269	**3**	**12465**
Agaricus campestris	Basidiomycota					0	6	**2**	**10095**							0	9				
Phoma herbarum	Ascomycota																	**2**	**10614**	0	1
Geoglossales spp.	Ascomycota															**3**	**8385**				
	Total of current subset	**25**	**110930**	**18**	**78767**	**36**	**52373**	**30**	**134096**	**30**	**88163**	**28**	**162382**	**27**	**114022**	**25**	**72048**	**30**	**132483**	**22**	**90827**
	Grand Total of filtered dataset	90	437258	91	427315	93	144550	92	444239	92	292648	92	573047	91	426929	89	284368	93	442542	93	412859

(Table S3 continues)

(Table S3 continued)
c)

Sites	Friedeburg				Greifenhagen				Harsleben				Siptenfelde				Wanzleben			
Land management	Meadow		Pasture		Meadow		Pasture		Meadow		Pasture		Meadow		Pasture		Meadow		Pasture	
Top rank abundant OTUs	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum	Proportion	Sum
Otu0000002			**1**	**9495**																
Otu0000004			**2**	**23430**																
Otu0000006			**2**	**19764**																
Otu0000008			**1**	**11627**																
Otu000001	**6**	**27143**			**9**	**12433**	**5**	**21431**	**7**	**19559**	1	4117	**4**	**18425**	**9**	**25445**	**6**	**24819**	**8**	**32328**
Otu0000010			**2**	**17852**																
Otu000002	**3**	**13752**			2	3395	**7**	**30773**	**4**	**10202**	**3**	**14634**	1	2675	2	4208	1	5150	0	494
Otu000003	2	8452			3	4862	**6**	**25307**	**6**	**18167**	2	12460	1	4520	1	3722	0	44		
Otu000004	0	50			**4**	**5783**	2	6557	0	62	0	1901	**3**	**13778**	**3**	**7891**	0	1	0	2
Otu000005	1	2142			0	434	**4**	**15498**	**6**	**16843**	1	6827	0	738	**2**	**6957**	0	921	2	6461
Otu000006	**2**	**9454**			1	753	2	7364	1	1386	1	3172	1	4764	**2**	**6958**	0	35	0	17
Otu000010	1	2629			**4**	**5196**	1	4391	1	3433	0	1992	0	840	1	3131	2	9072	**3**	**13184**
Otu000012	**4**	**17943**			0	41	2	9325	2	6740	0	930	0	9	0	382				
Otu000015							0	2	0	2	**5**	**30826**								
Otu000016																	**6**	**24277**	**3**	**11947**
Otu000017																	**8**	**34487**		
Otu000019	0	2			**4**	**5551**	0	1097	0	3	0	316	2	7197	1	3622	0	1	0	1
Otu000025											**4**	**24405**								
Otu000028	**7**	**29127**					0	1									0	9		
Otu000036							0	233	**4**	**10933**	2	10649								
Otu000039	0	1			1	929	0	1954	0	312	0	1903	**4**	**16028**	0	375	1	2747		
Otu000043													**4**	**16094**	0	89				
Otu000044							0	1			**3**	**15169**	2	8819						
Otu000051	0	1			**9**	**12990**					0	82	1	2444	0	330				
Otu000052											**3**	**18430**								
Otu000064	0	17					0	36	0	264	0	4	0	9	0	487	1	3419	**3**	**13786**
Otu000070																	**4**	**16618**	0	141
Otu000087							0	14			0	4	**4**	**17682**	0	1				
Otu000097							0	17							0	56	0	269	**3**	**12465**
Otu000100					0	6	**2**	**10095**							0	9				
Otu000101																	**2**	**10614**	0	1
Otu000134															**3**	**8385**				
Total of current subset	**25**	**110713**	**7**	**82168**	**36**	**52373**	**30**	**134096**	**30**	**87906**	**26**	**147821**	**27**	**114022**	**25**	**72048**	**30**	**132483**	**22**	**90827**
Grand Total of filtered dataset	90.1	437258	71.4	1120585	93	144550	91.6	444239	91.8	292648	91.6	573047	90.8	426929	89.3	284368	93.1	442542	93.1	412859

Table S4. Biodiversity metrics used to investigate scale-dependency of land management (pasture versus meadow) responses in semi-natural grasslands. Table adapted from Chase *et al*. (2018).

Metric	**Definition**	**Interpretation**
N	Total number of individuals	Measure of density of individuals. N scales roughly linearly with area.
α-S, γ-S	Observed richness of species from α-scale (average of observations at subplot-level per LM) and from γ-scale (sum across all observations per LM)	Number of species at local scale (= α-diversity) and large scale (= γ-diversity)
α-S_n, γ-S_n	The expected richness for *n* randomly sampled individuals (Hurlbert, 1971). Can be calculated from α- or γ-scale	Estimate of richness at α- or γ-scale after controlling for differences due to aggregation and number of individuals [i.e. only reflects species abundance distribution (SAD)]
α-PIE, γ-PIE	Probability of interspecific encounter ($S_{n=2}$ - $S_{n=1}$; Hurbert, 1971; Olszweski 2004). Can be calculated from α- and γ-scale.	Measure of evenness at α- or γ-scale that is quantified by the slope at the base of the rarefaction curve; sensitive to common species.
α-S_{PIE}, γ-S_{PIE}	Equally abundant species needed to yield a probability of encounter (PIE) at α-or γ-scale (Jost 2006) (= 1/(1 - PIE)).	Effective number of species of PIE (= 1 - Simpson diversity index); measured at α- or γ-scale
β-S	Ratio of total treatment γ-S and average plot α-S (Whittaker 1960)	More species turnover results in larger β-S due to increases in spatial aggregation, N, and/or unevenness of the SAD
β-S_n	Ratio of the total treatment γ-S_n and α-S_n	Like β-S but emphasizes aggregation due to common and rare species
β-S_{PIE}	Ratio of total treatment γ-S_{PIE} and α-S_{PIE} (Jost, 2007)	Like β-S but emphasizes aggregation due to common species only

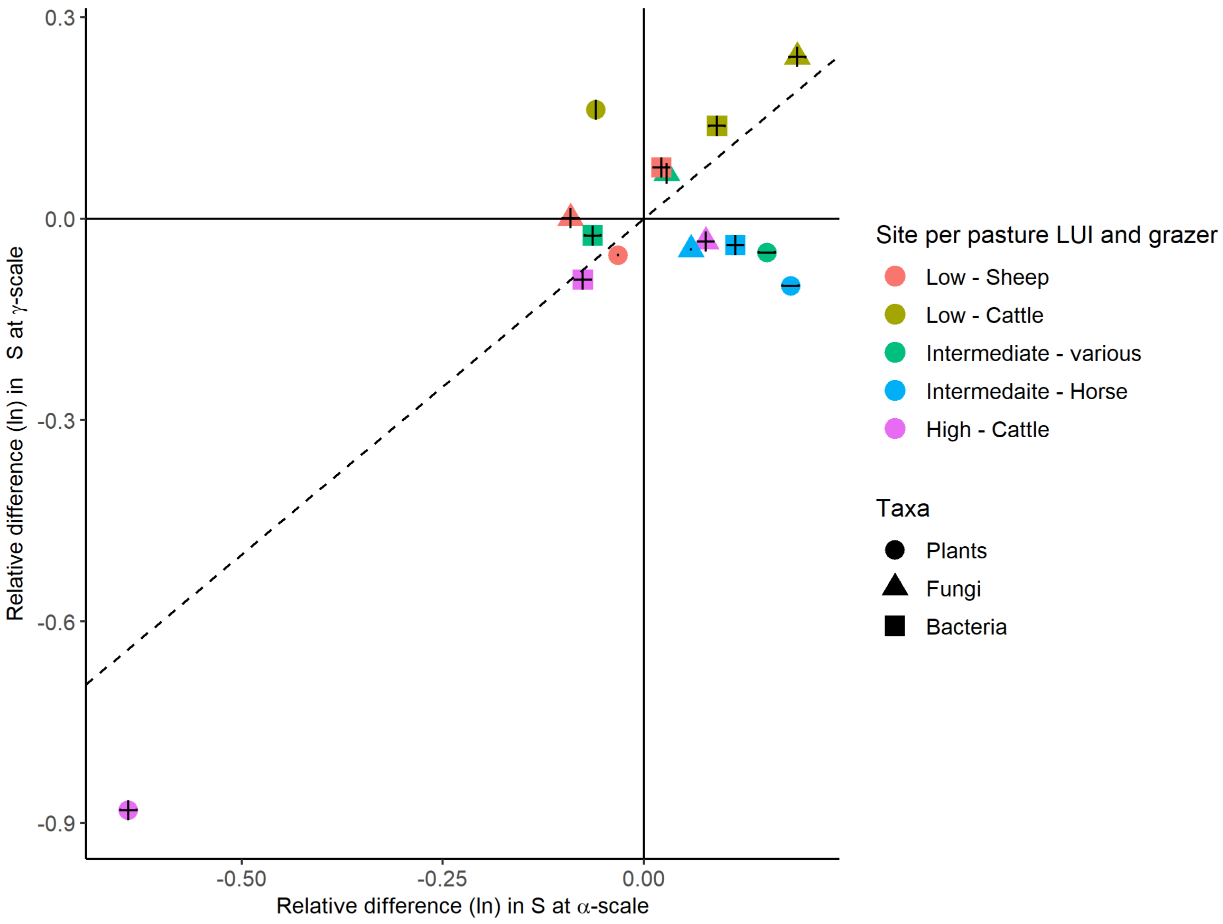

Figure S3. Scale-dependent impact of land management (pasture versus meadow) observed as a change in the log response ratio [Relative difference (ln)] in species richness (S) at the α- (subplot-) and γ-scale (site-level) for above- (i.e. plants circles) and belowground taxa (i.e. soil fungi and bacteria, triangles and squares, respectively). The log response ratios between management types were calculated with meadows as reference, thus positive values indicated that S is higher in pasture management. Horizontal and vertical bars plotted with each response indicate where there was a significant difference ($p < 0.05$) in S between LM types based on the ANOVA and permutation tests, for α- and γ-scales respectively. The dashed 1:1 line indicates no scale-dependence. Sites are color coded according to pasture land use intensity (LUI) calculated as livestock units per hectare per annum, see Table 1 for more details.

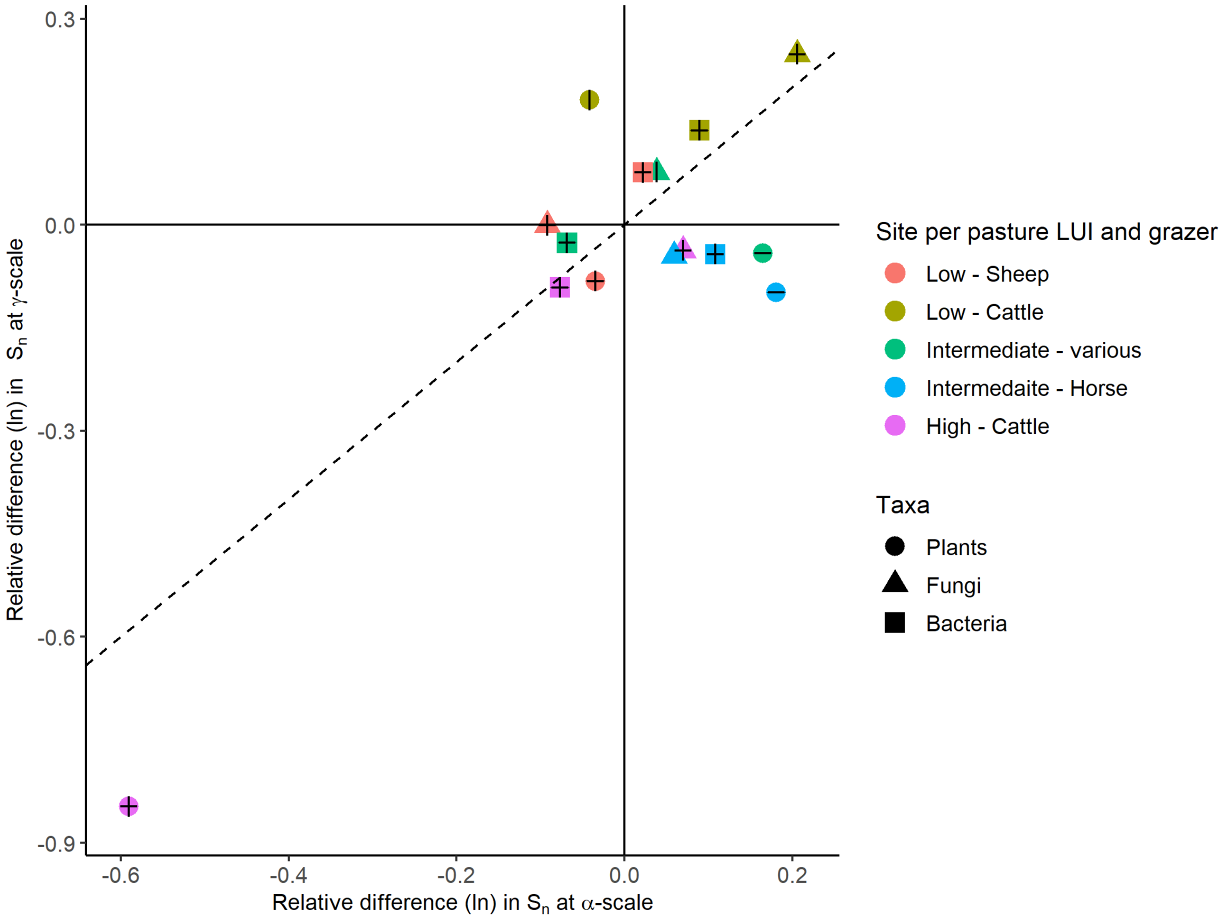

Figure S4. Scale-dependent impact of land management (pasture versus meadow) observed as a change in the log response ratio [Relative difference (ln)] in rarefied species richness (S_n) at the α- (subplot-) and γ-scale (site-level) for above- (i.e. plants, circles) and belowground taxa (i.e. soil fungi and bacteria, triangles and squares, respectively). The log response ratios between management types were calculated with meadows as reference, thus positive values indicated that S_n is higher in pasture management. Horizontal and vertical bars plotted with each response indicate where there was a significant difference ($p < 0.05$) in S_n between LM types based on the ANOVA and permutation tests, for α- and γ-scales respectively. The dashed 1:1 line indicates no scale-dependence. Sites are color coded according to pasture land use intensity (LUI) calculated as livestock units per hectare per annum, see Table 1 for more details.

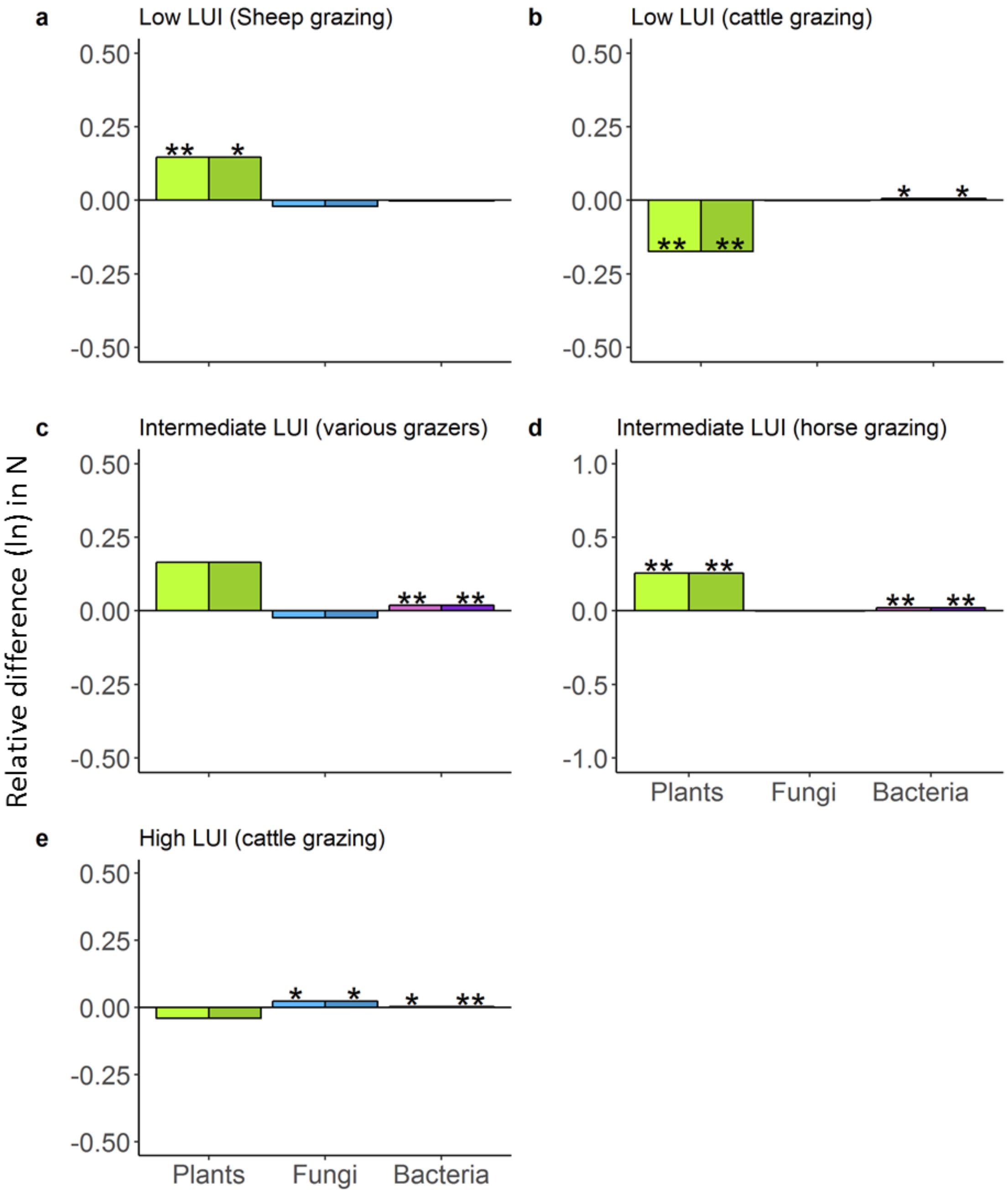

Figure S5. Scale-dependent impact of land management (pasture versus meadow) on the log response ratio [Relative difference (ln)] in density of individuals (N) for above- (i.e. plants green) and belowground taxa (i.e. soil fungi and bacteria blue and purple, respectively). The log response ratios between management types were calculated with meadows as reference at α- (subplot-, lighter hue) and γ-scale (site-level, darker hue) per taxa. Asterisks indicate significance differences (‘*’, $p < 0.05$; ‘**’, $p < 0.01$; ‘***’, $p < 0.001$) between management types based on ANOVA and permutation tests, for α- and γ-scales respectively. Sites are labeled according to pasture land use intensity (LUI) calculated as livestock units per hectare per annum, see Table 1 for more details.

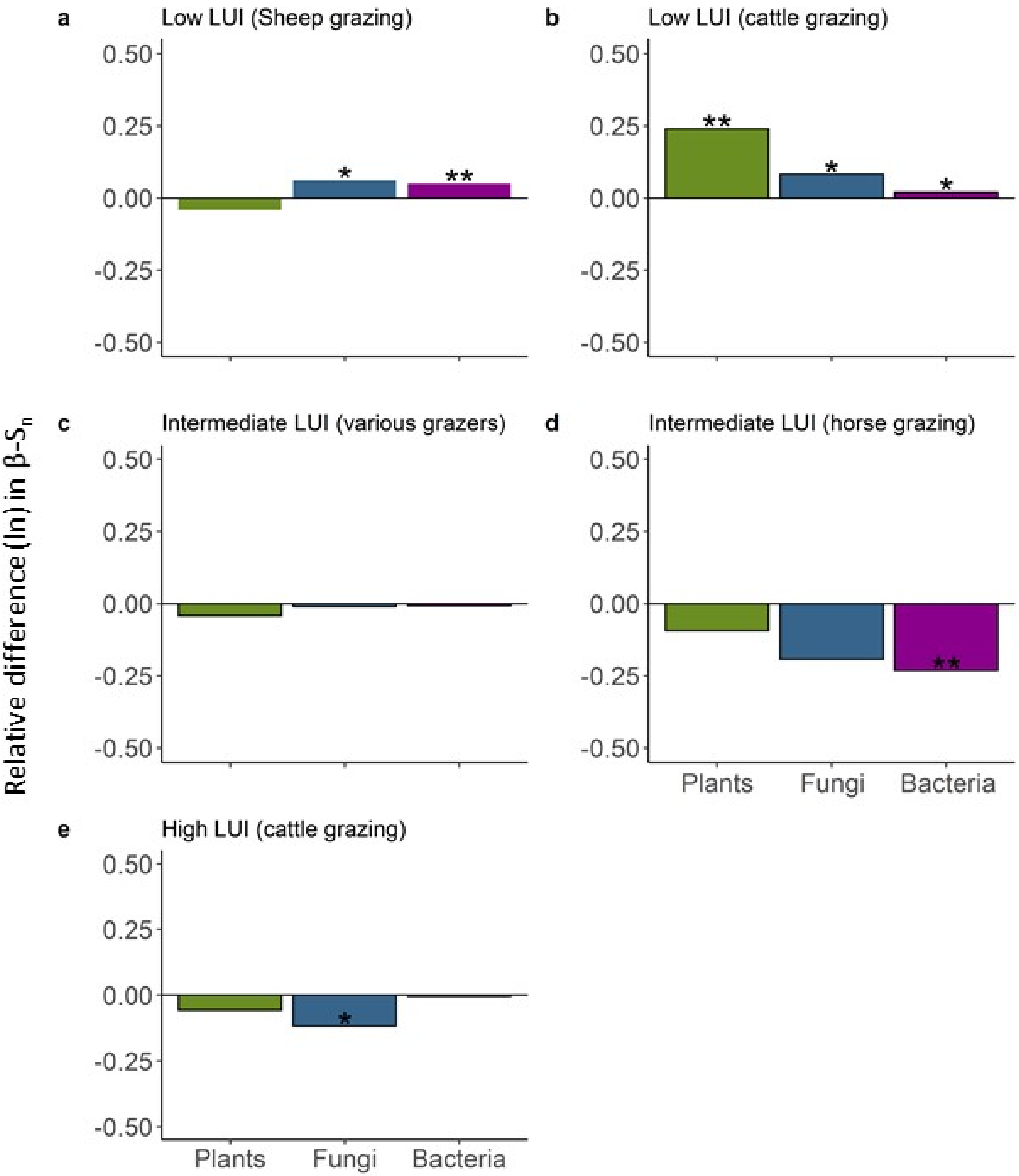

Figure S6. Scale-dependent impact of land management (pasture versus meadow) on the log response ratio (Relative difference (ln)) in turnover of rare species (β-Sn) for above- (i.e. plants green) and belowground taxa (i.e. soil fungi and bacteria blue and purple, respectively). The log response ratios between management types were calculated with meadows as reference, thus positive values indicate higher spatial aggregation in pastures. Asterisks indicated significant differences (‘*’, $p < 0.05$; ‘**’, $p < 0.01$; ‘***’, $p < 0.001$) across management types based on permutation tests. Sites are labeled according to pastoral land use intensity (LUI) calculated as livestock units per hectare per annum. See Table 1 for more details on LUI per site.

Table S5. Absolute difference between land management (pasture versus meadow) in the density of individuals (N), species richness (S), rarefied species richness (S_n) and evenness (S_{PIE}) between management types. Differences were calculated with meadows as reference and are presented with p-values derived from ANOVA and permutation tests for the respective scales. Significant values ($p < 0.05$) are marked in bold. Site names refer to the nearest large village along with pasture land use intensity (LUI) calculated as livestock units per hectare per annum, see Table 1 for more details.

a) Alpha diversity

Site	Index	Plants		Fungi		Bacteria	
		Difference (D-bar)	p-value	Difference (D-bar)	p-value	Difference (D-bar)	p-value
HAR	N	**19.40**	**0.01**	-306.23	0.16	-61.80	0.31
	S	-0.57	0.13	**-36.50**	**0.02**	**60.65**	**0.02**
	S_n	**-0.56**	**0.03**	**-35.70**	**0.02**	**61.48**	**0.02**
	S_{PIE}	-0.27	0.69	**-11.98**	**0.01**	2.66	0.68
SIP	N	**-24.25**	**0.01**	-12.57	0.42	**234.45**	**0.01**
	S	-0.97	0.35	**85.85**	**0.01**	**270.20**	**0.01**
	S_n	-0.64	0.45	**85.97**	**0.01**	**264.32**	**0.01**
	S_{PIE}	-0.88	0.27	**20.02**	**0.01**	**94.63**	**0.01**
FBG	N	28.07	0.14	-331.43	0.42	**690.47**	**0.01**
	S	**2.30**	**0.03**	11.00	0.34	**-183.83**	**0.01**
	S_n	**2.31**	**0.01**	**13.00**	**0.20**	**-195.88**	**0.01**
	S_{PIE}	**2.79**	**0.01**	**11.80**	**0.02**	**-55.24**	**0.01**
WAN	N	**34.03**	**0.01**	-2.43	0.61	**829.57**	**0.01**
	S	**1.87**	**0.01**	15.67	0.43	**319.67**	**0.01**
	S_n	**1.65**	**0.01**	15.81	0.44	**297.29**	**0.01**
	S_{PIE}	**2.55**	**0.01**	4.43	0.33	26.70	0.19
GFH	N	-4.93	0.51	**352.97**	**0.01**	**132.40**	**0.01**
	S	**-7.33**	**0.01**	**30.93**	**0.03**	**-216.73**	**0.01**
	S_n	**-6.47**	**0.01**	**27.54**	**0.03**	**-218.78**	**0.01**
	S_{PIE}	**-4.10**	**0.01**	**2.78**	**0.05**	**-125.99**	**0.01**

b) Gamma diversity

Site	Index	Plants		Fungi		Bacteria	
		Difference (D-bar)	p-value	Difference (D-bar)	p-value	Difference (D-bar)	p-value
HAR	N	**388.00**	**0.01**	-6124.50	0.22	-1236.00	0.28
	S	-3.33	0.17	**0.83**	**0.02**	**409.33**	**0.01**
	S_n	**-4.75**	**0.04**	**-0.98**	**0.03**	**409.90**	**0.01**
	S_{PIE}	-2.64	0.10	-3.30	0.11	**27.29**	**0.01**

(Table S3 continues)

(Table S3 continued)

SIP	N	**-485.00**	**0.01**	-251.33	0.38	**4689.00**	**0.01**
	S	**7.33**	**0.04**	**357.33**	**0.01**	**794.00**	**0.01**
	S_n	**8.04**	**0.01**	**358.39**	**0.01**	**791.31**	**0.01**
	S_{PIE}	**3.41**	**0.03**	4.77	0.72	**187.90**	**0.01**
FBG	N	842.00	0.09	-9943.00	0.37	**20714.00**	**0.01**
	S	-3.00	0.53	**101.00**	**0.01**	**-129.00**	**0.01**
	S_n	-2.36	0.49	**110.06**	**0.01**	**-133.73**	**0.01**
	S_{PIE}	5.07	0.19	**50.24**	**0.01**	**-101.64**	**0.01**
WAN	N	**1021.00**	**0.01**	-73.00	0.61	**24887.00**	**0.01**
	S	-4.00	0.50	-51.00	0.14	**-218.00**	**0.01**
	S_n	-3.72	0.50	-49.89	0.14	**-234.27**	**0.01**
	S_{PIE}	0.54	0.54	9.34	0.49	**-116.96**	**0.01**
GFH	N	-49.33	0.50	**3529.67**	**0.01**	**1324.00**	**0.01**
	S	**-21.67**	**0.01**	**-34.00**	**0.01**	**-427.00**	**0.01**
	S_n	**-20.01**	**0.01**	**-36.86**	**0.01**	**-427.81**	**0.01**
	S_{PIE}	**-8.88**	**0.01**	6.53	0.25	**-136.70**	**0.01**

c) Beta diversity

		Plants		Fungi		Bacteria	
Site	Index	Difference (D-bar)	p-value	Difference (D-bar)	p-value	Difference (D-bar)	p-value
HAR	S	-0.14	0.72	**0.46**	**0.01**	**0.11**	**0.01**
	S_n	-0.07	0.07	**0.13**	**0.03**	**0.06**	**0.01**
	S_{PIE}	-0.72	0.06	**3.35**	**0.01**	**0.05**	**0.02**
SIP	S	**0.67**	**0.01**	0.16	0.14	**0.08**	**0.02**
	S_n	**0.41**	**0.01**	**0.17**	**0.02**	**0.03**	**0.01**
	S_{PIE}	**0.74**	**0.01**	**-2.02**	**0.01**	**0.17**	**0.01**
FBG	S	-0.58	0.06	**0.21**	**0.05**	**0.07**	**0.01**
	S_n	-0.09	0.51	-0.03	0.53	-0.01	0.43
	S_{PIE}	**1.26**	**0.05**	0.27	0.52	**-0.13**	**0.01**
WAN	S	**-1.21**	**0.01**	**-1.21**	**0.02**	**-0.34**	**0.01**
	S_n	-0.18	0.14	-0.59	0.14	**-0.29**	**0.01**
	S_{PIE}	**-1.34**	**0.01**	-1.64	0.10	**-0.50**	**0.01**
GFH	S	**-0.55**	**0.01**	**-0.28**	**0.01**	-0.02	0.09
	S_n	-0.08	0.56	**-0.20**	**0.01**	-0.01	0.27
	S_{PIE}	**-0.54**	**0.01**	0.29	0.65	0.02	0.48

Chapter 3: Supplementary material

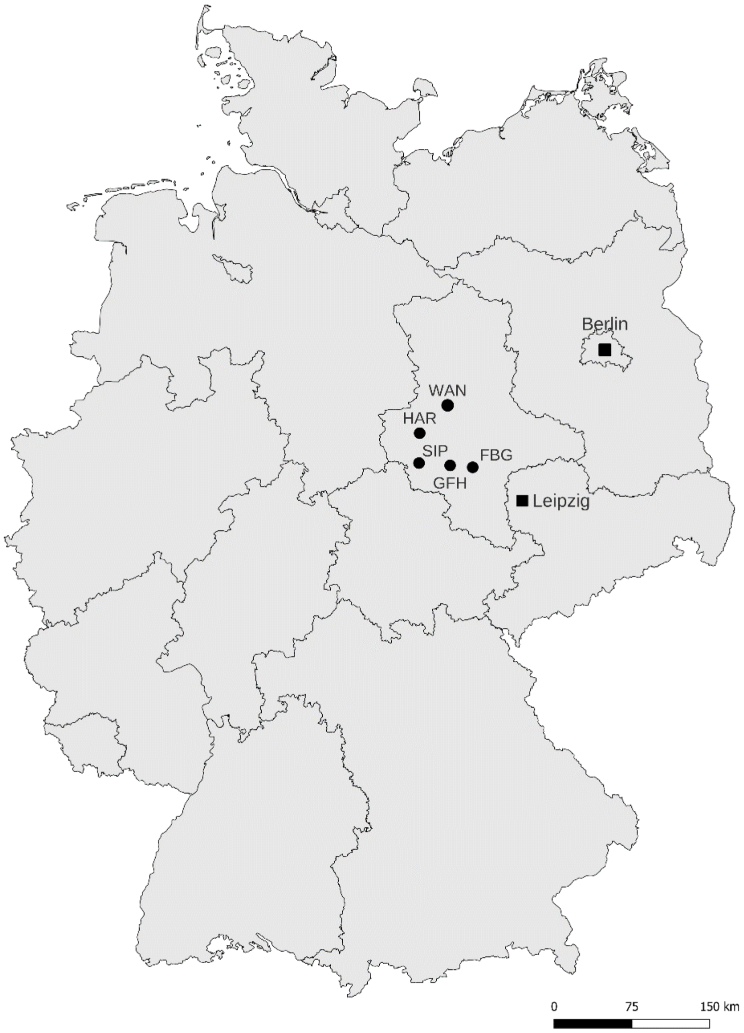

Figure S1. Map of Germany with five sites of the Terrestrial Environmental Observatories (TERENO) network in Sachsen-Anhalt where grasslands were studied. Study sites are located near Friedeburg (FBG), Greifenhagen (GFH), Wanzleben (WAN) Harsleben (HAR) and Siptenfelde (SIP). Each site covers 16 km^2. The cities of Berlin and Leipzig (squares) are provided as reference points. Map provided by M. Frenzel.

Table S1. Site and grassland descriptions of study areas that form part of the Central Germany Lowlands observatory. Habitat classification followed the revised European Nature Information System (EUNIS) (https://eunis.eea.europa.eu/habitats.jsp) to the third level.

Site name & coordinates	**Short site description**	**% arable land**	**% all semi-natural habitats (excluding forest)**	**Mean elevation [meters above sea level (asl.)]**	**Grasslands used for hay production (meadows)**	**Grasslands used for grazing livestock (pastures)**	**Number of sampling units per meadow (m) and pasture (p)**
Wanzleben 52.0803° N, 11.4518° E	The area forms part of the "Magdeburger Börde", and has high soil quality, and a relatively flat relief.	ca. 77 %	ca. 8 %	113 asl.	EUNIS: Wet grasslands Mowing frequency/a: 1-2 Area: 3.72-7.44 ha	EUNIS: Mesic grasslands Grazer: Horses Grazing intensity: 0.75-0.83 LSU/a Area: 0.75-0.83 ha	30 (m) 30 (p)
Greifenhagen 51.6329° N, 11.4340° E	The areas have a more diverse topographical profile, with valleys and rolling hills.	ca. 71 %	ca. 6 %	270 m asl.	EUNIS: Mesic grasslands Mowing frequency/a: 2 Area: 1.96 ha	EUNIS: Mesic grasslands Grazer: Cattle Grazing intensity: 0.99-2.877 LSU/a Area: 0.45-5.44 ha	10 (m) 30 (p)
Friedeburg 51.6177° N, 11.7096° E	The areas are close to the Saale river, and also has a more diverse topographical profile, with valleys and rolling hills.	ca. 71 %	ca. 10 %	122 m asl.	EUNIS: Mesic and dry grasslands Mowing frequency/a: 1-2 Area: 0.84-1.93 ha	EUNIS: Mesic grasslands Grazer: Various (cattle, goats, horses) Grazing intensity: 0.23-0.9 LSU/a Area: 1.07-1.72 ha Two of the grasslands were located in the a local nature reserve "Saaledurchbruch bei Rotenburg"	30 (m) 30 (p)

(Table S1 continues)

(Table S1 continued)

Site name & coordinates	Short site description	% arable land	% all semi-natural habitats (excluding forest)	Mean elevation [meters above sea level (asl.)]	Grasslands used for hay production (meadows)	Grasslands used for grazing livestock (pastures)	Number of sampling units per meadow (m) and pasture (p)
Harsleben 51.8423° N, 11.0753° E	Parts of the terrain is fairly flat, while others parts have more relief created by sandstone formations.	ca. 67 %	ca. 17 %	143 m asl.	EUNIS: Mesic grasslands Mowing frequency/a: 1 Area: 2.00-6.22 ha Grasslands located in the nature reserve "Harslebener Berge und Steinholz nordwestlich Quedlinburg"	EUNIS: Temperate shrub heathland Grazer: sheep Grazing intensity: 0.43 LSU/a Area: 2.29-67.00 ha One of the grasslands is located in the nature reserve "Harslebener Berge und Steinholz nordwestlich Quedlinburg", while the others are located in former military training area.	20 (m) 40 (p)
Siptenfelde 51.6491° N, 11.0526° E	In the eastern part of the Harz mountains, with distinct topology of rolling hills. Along the outer regions of the arable land and grasslands are mostly coniferous forest (ca. 61 %).	ca. 18 %	ca. 15 %	423 m asl.	EUNIS: Mesic grasslands Mowing frequency/a: 1 Area: 11.96-23.95 ha	EUNIS: Wet grasslands Grazer: Cattle Grazing intensity: 0.36-0.48 LSU/aArea: 2.53-6.76 ha	30 (m) 20 (p)
						Total:	120 (m) 150 (p)

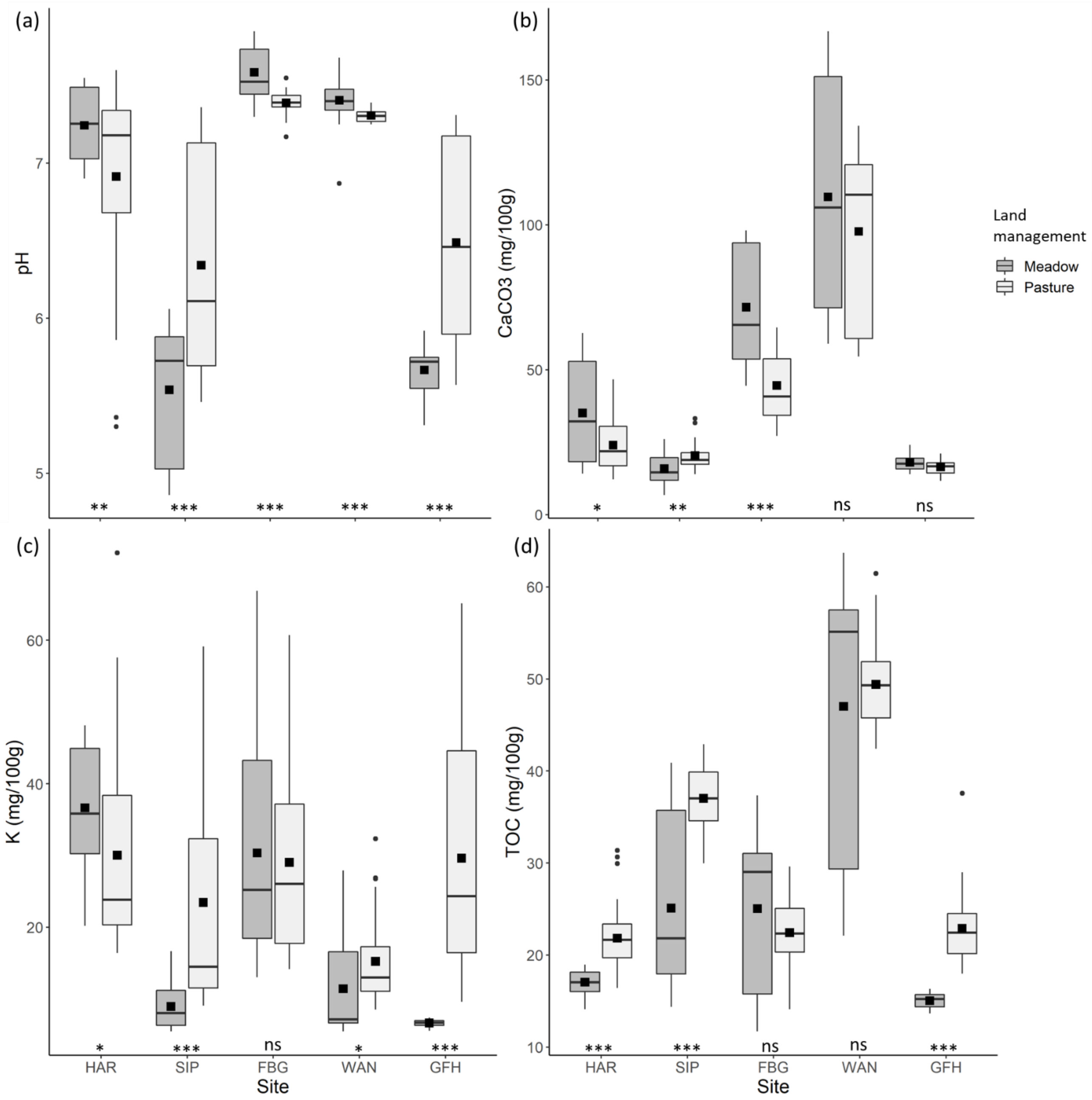

Figure S2. Boxplots of soil properties across grassland land management (LM) types (meadow and pasture) within and across study sites. Abbreviated site names refer to the closest large village [Harsleben (HAR), Siptenfelde (SIP), Friedeburg (FBG), Wanzleben (WAN) and Greifenhagen (GHF)]. Soil parameters reported include the soil acidity (pH), calcium carbonate ($CaCO_3$), plant available potassium (K) and total organic carbon (TOC). Asterisks' indicate significance differences ('*', $p < 0.05$; '**', $p < 0.01$; '***', $p < 0.001$ and ns, no significance) between management types based on a Welch t-test.

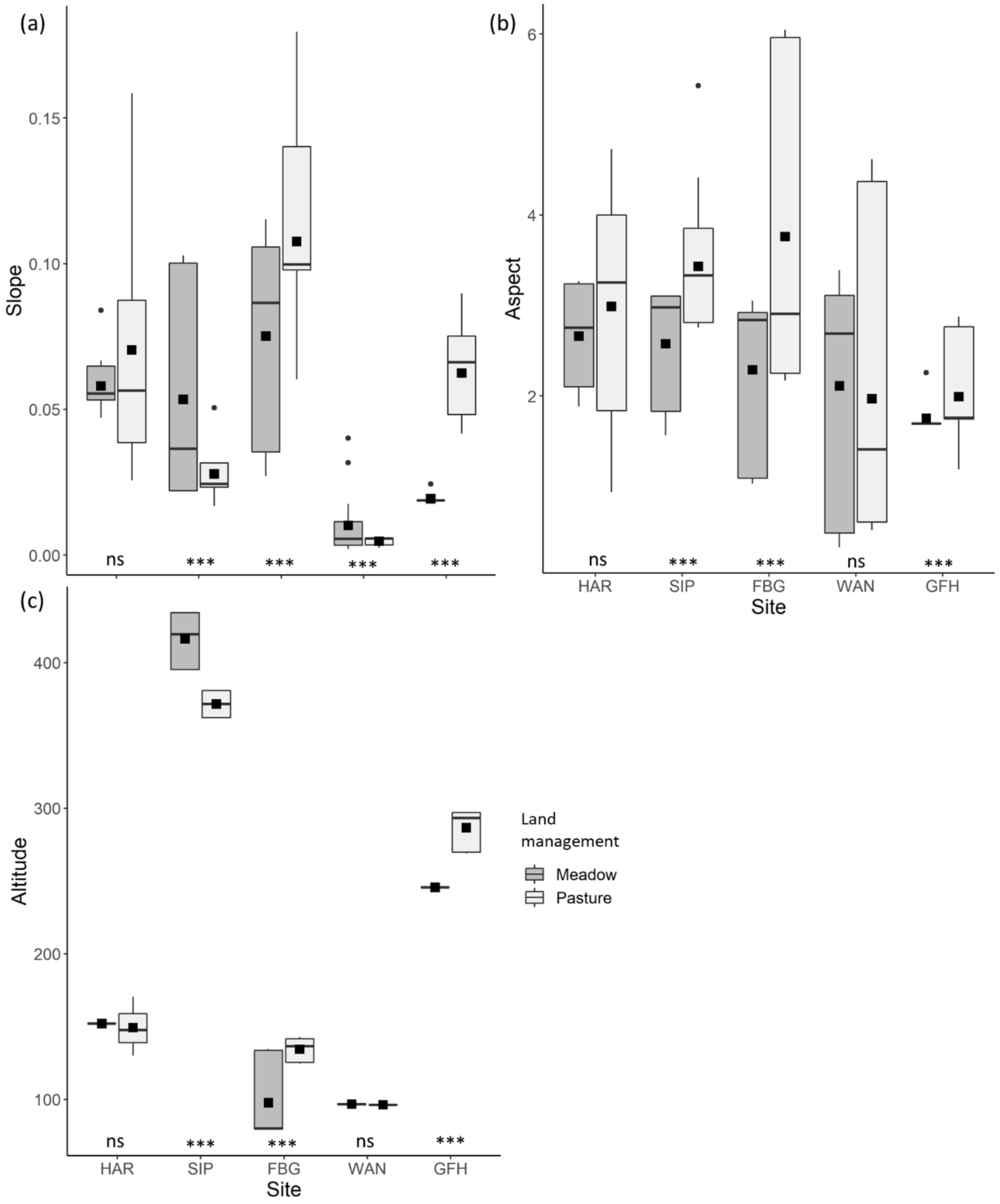

Figure S3. Boxplots of topographical variation in (a) slope, (b) aspect (compass direction a terrain surface faces, measured in degrees from north) and (c) altitude across grassland land management (LM) types (meadow and pasture) within and across study sites. Abbreviated site names refer to the closest large village [Harsleben (HAR), Siptenfelde (SIP), Friedeburg (FBG), Wanzleben (WAN) and Greifenhagen (GHF)]. Asterisks' indicate significance differences ('*', $p < 0.05$; '**', $p < 0.01$; '***', $p < 0.001$ and ns, no significance) between management types based on a Welch t-test.

Table S2. Overview of clade level classification for plant species used in the analysis, see APG IV (2016) for more details.

Clade	**Order**	**Family**	**No. of species per family**	**Total no. of species per clade**
Commelinids	Poales	Cyperaceae	3	
	Poales	Juncaceae	1	
	Poales	Poaceae	23	27
Ranunculales	Ranunculales	Ranunculaceae	2	2
Rosids	Brassicales	Brassicaceae	2	
	Fabales	Leguminosae	20	
	Geraniales	Geraniaceae	1	
	Malpighiales	Euphorbiaceae	1	
	Malpighiales	Hypericaceae	1	
	Malpighiales	Linaceae	1	
	Rosales	Rosaceae	7	
	Rosales	Urticaceae	1	34
Superasterids	Caryophyllales	Caryophyllaceae	5	
	Caryophyllales	Polygonaceae	4	9
Asterids	Apiales	Apiaceae	7	
	Asterales	Compositae	17	
	Boraginales	Boraginaceae	2	
	Dipsacales	Caprifoliaceae	1	
	Gentianales	Rubiaceae	4	
	Lamiales	Lamiaceae	3	
	Lamiales	Oleaceae	1	
	Lamiales	Orobanchaceae	1	
	Lamiales	Plantaginaceae	5	
	Solanales	Convolvulaceae	1	42
			Total no. of species:	114

Table S3. Overview of phylum, class and family level classification, see Köljalg et al. (2013) for more detail.

Phylum	Class	Family	No. of species per family	No. of species per phylum
Ascomycota	Archaeorhizomycetes	Archaeorhizomycetaceae	1	
	Dothideomycetes	Aureobasidiaceae	1	
		Capnodiaceae	1	
		Cladosporiaceae	1	
		Corynesporascaceae	1	
		Cucurbitariaceae	5	
		Dictyosporiaceae	1	
		Didymellaceae	1	
		Didymosphaeriaceae	3	
		Dissoconiaceae	1	
		Lentitheciaceae	1	
		Leptosphaeriaceae	2	
		Lophiostomataceae	1	
		Massarinaceae	4	
		Minutisphaeraceae	1	
		Periconiaceae	3	
		Phaeosphaeriaceae	11	
		Pleomassariaceae	1	
		Pleosporaceae	7	
		Sporormiaceae	5	
		Teratosphaeriaceae	3	
		Testudinaceae	1	
		Torulaceae	5	
	Eurotiomycetes	Arachnomycetaceae	3	
(Table S3 continues)		Cyphellophoraceae	2	
(Table S3 continued)				

Phylum	**Class**	**Family**	**No. of species per family**	**No. of species per phylum**
Ascomycota	Eurotiomycetes	Gymnoascaceae	1	
		Herpotrichiellaceae	9	
		Onygenales fam Incertae sedis	9	
		Thermoascaceae	1	
		Trichocomaceae	9	
	Geoglossomycetes	Geoglossaceae	1	
	Laboulbeniomycetes	Pyxidiophoraceae	1	
	Lecanoromycetes	Ramalinaceae	1	
	Leotiomycetes	Helotiaceae	12	
		Helotiales fam Incertae sedis	8	
		Hyaloscyphaceae	10	
		Leotiaceae	1	
		Myxotrichaceae	3	
		Phacidiaceae	1	
		Pseudeurotiaceae	2	
		Sclerotiniaceae	1	
		Thelebolaceae	1	
		Vibrisseaceae	1	
	Orbiliomycetes	Orbiliaceae	4	
	Pezizomycetes	Ascobolaceae	2	
		Ascodesmidaceae	1	
		Pyronemataceae	10	
		Sarcoscyphaceae	1	
		Tuberaceae	1	

(Table S3 continues)
(Table S3 continued)

Phylum	Class	Family	No. of species per family	No. of species per phylum
Ascomycota	Sordariomycetes	Chaetomiaceae	8	
		Chaetosphaeriaceae	3	
		Clavicipitaceae	7	
		Coniochaetaceae	3	
		Cordycipitaceae	7	
		Diaporthaceae	1	
		Diatrypaceae	1	
		Glomerellaceae	1	
		Hypocreaceae	5	
		Hypocreales fam Incertae sedis	18	
		Lasiosphaeriaceae	20	
		Lulworthiaceae	1	
		Magnaporthaceae	1	
		Microascaceae	8	
		Microdochiaceae	6	
		Nectriaceae	19	
		Ophiocordycipitaceae	6	
		Phomatosporaceae	1	
		Phyllachoraceae	1	
		Plectosphaerellaceae	10	
		Savoryellaceae	1	
		Sordariales fam Incertae sedis	2	
		Stachybotryaceae	2	
		Xylariaceae	2	
		Xylariales fam Incertae sedis	1	

(Table S3 continues)

Phylum	**Class**	**Family**	**No. of species per family**	**No. of species per phylum**
Ascomycota	Taphrinomycetes	Protomycetaceae	1	299
Basidiomycota	Agaricomycetes	Agaricaceae	2	
		Agaricomycetes fam Incertae sedis	1	
		Auriculariaceae	1	
		Auriculariales fam Incertae sedis	1	
		Bolbitiaceae	24	
		Cantharellales fam Incertae sedis	1	
		Ceratobasidiaceae	5	
		Clavariaceae	9	
		Corticiaceae	4	
		Cortinariaceae	1	
		Crepidotaceae	1	
		Entolomataceae	8	
		Fomitopsidaceae	1	
		Hydnodontaceae	5	
		Hymenogastraceae	3	
		Lycoperdaceae	2	
		Marasmiaceae	3	
		Omphalotaceae	1	
		Pluteaceae	5	
		Podoscyphaceae	2	
		Psathyrellaceae	10	
		Schizoporaceae	1	
		Sebacinaceae	1	

(Table S3 continues)
(Table S3 continued)

Phylum	Class	Family	No. of species per family	No. of species per phylum
Basidiomycota	Agaricomycetes	Serendipitaceae	3	
		Stephanosporaceae	2	
		Strophariaceae	9	
		Thelephoraceae	2	
		Tremellodendropsidaceae	1	
		Tricholomataceae	13	
		Typhulaceae	1	
	Atractiellomycetes	Hoehnelomycetaceae	1	
	Cystobasidiomycetes	Cystobasidiaceae	1	
		Erythrobasidiales fam Incertae sedis	1	
	Exobasidiomycetes	Entylomataceae	1	
		Entylomatales fam Incertae sedis	1	
		Tilletiariaceae	1	
	Geminibasidiomycetes	Geminibasidiaceae	1	
	Microbotryomycetes	Chrysozymaceae	1	
		Leucosporidiaceae	4	
		Sporidiobolaceae	4	
		Ustilentylomataceae	1	
	Pucciniomycetes	Eocronartiaceae	1	
	Tremellomycetes	Cystofilobasidiaceae	3	
		Filobasidiaceae	3	
		Mrakiaceae	2	
		Tetragoniomycetaceae	1	
		Tremellaceae	1	

(Table S3 continues)
(Table S3 continued)

Phylum	Class	Family	No. of species per family	No. of species per phylum
Basidiomycota	Tremellomycetes	Ustilaginaceae	3	159
Calcarisporiellomycota	Calcarisporiellomycetes	Calcarisporiellaceae	1	1
Chytridiomycota	Chytridiomycetes	Chytridiaceae	2	
Chytridiomycota	Rhizophlyctidomycetes	Rhizophlyctidaceae	1	
		Alphamycetaceae	1	
		Rhizophydiaceae	1	
	Spizellomycetes	Powellomycetaceae	2	
		Spizellomycetaceae	1	8
Entorrhizomycota	Entorrhizomycetes	Entorrhizaceae	1	1
Glomeromycota	Archaeosporomycetes	Ambisporaceae	2	
		Archaeosporaceae	1	
	Glomeromycetes	Acaulosporaceae	1	
		Claroideoglomeraceae	3	
		Diversisporaceae	1	
		Glomeraceae	6	14
Kickxellomycota	Kickxellomycetes	Kickxellaceae	1	1
			Total no. of species:	483

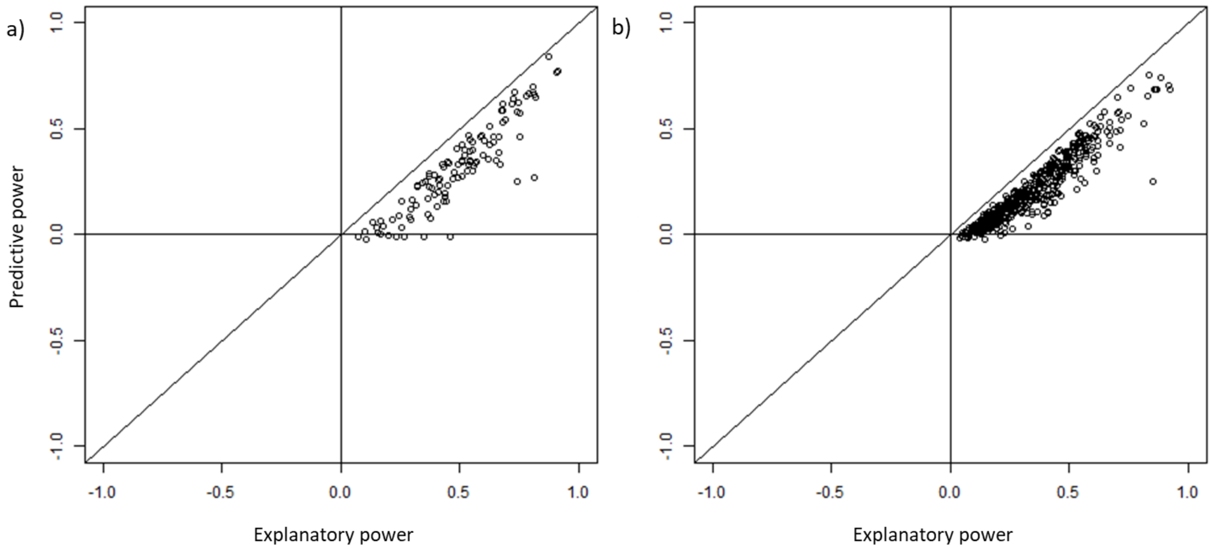

Figure S4. Explanatory versus predictive power of the HMSC presence-absence models for (a) plants and (b) soil fungi. The plant model had a transient phase with 1250 000 iterations before sufficient MCMC convergence was reached, soil fungi 12 500 iterations.

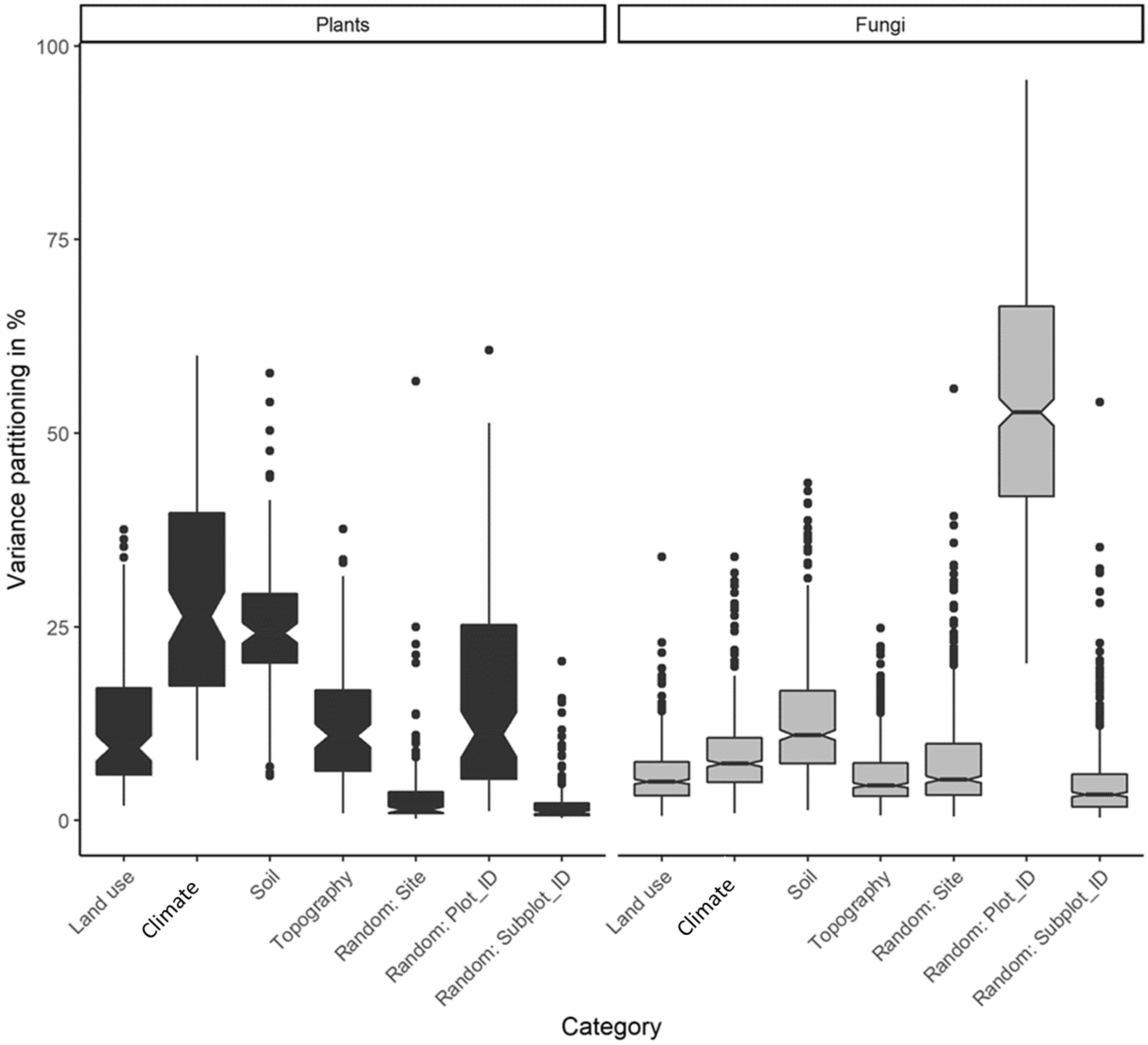

Figure S5. Relative importance of land use and biogeographical variables, and random effects, in explaining variance of species occurrence for plants and fungi species in semi-natural grasslands. Data collected from central Germany sites part of Terrestrial Environmental Observatories (TERENO) and analyzed as presence-absence data in a HMSC model. The respective categories contain two variables each, land use = land management as pasture or meadow and standardized land use intensity; climate = mean annual precipitation and temperature; soil = first two PCA loadings of a suit of soil parameters, ecologically representing soil carbon content (PC1) and soil pH and potassium (PC2); and topography = topographic index and amount of hill shading.

Table S4. Proportion (%) of variation in niche response associated with the taxon classification grouping variable for the presence-absence HMSC models of plant and fungi species, respectively, in semi-natural grasslands. PC1 and 2 are the first and second axis loading of a principal component analysis of a suit of standard soil variables (see main text for details).

Variable	Plants	Fungi
(Intercept)	1.8	4.3
Land management	7.6	1.6
Land use intensity	4.9	2.7
Temperature	11.9	5.2
Precipitation	11.8	4.8
Soil C (PC1)	13.9	3.6
Soil pH & K (PC2)	4.7	4.0
Topographic index	15.7	3.1
Hill shading	1.6	3.0

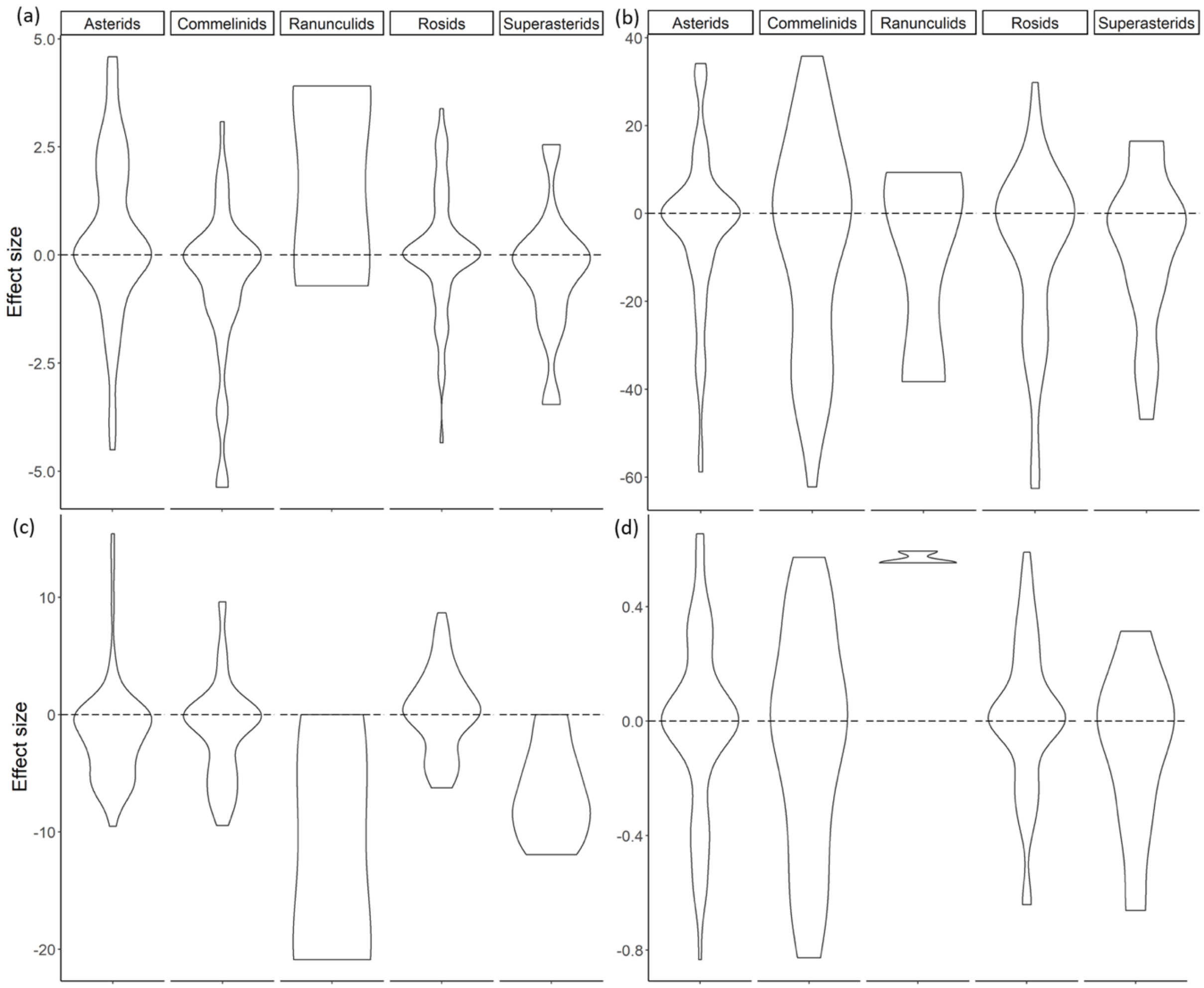

Figure S6. Effect size and direction of vascular plant clade responses to environmental variables (β parameter) (a) land use intensity (LUI) (positive values indicate higher probability of species occurrence under high LUI), (b) hill shading (positive values indicate higher probability of species occurrence with higher shading, (c) topographic index (positive values indicate higher probability of species occurrence at higher lying locations) and (d) soil acidity and concentration of potassium (K) (positive values indicate higher probability of species occurrence in acidic soils with higher soil K). Only responses with a posterior probability of at least 85% are reported.

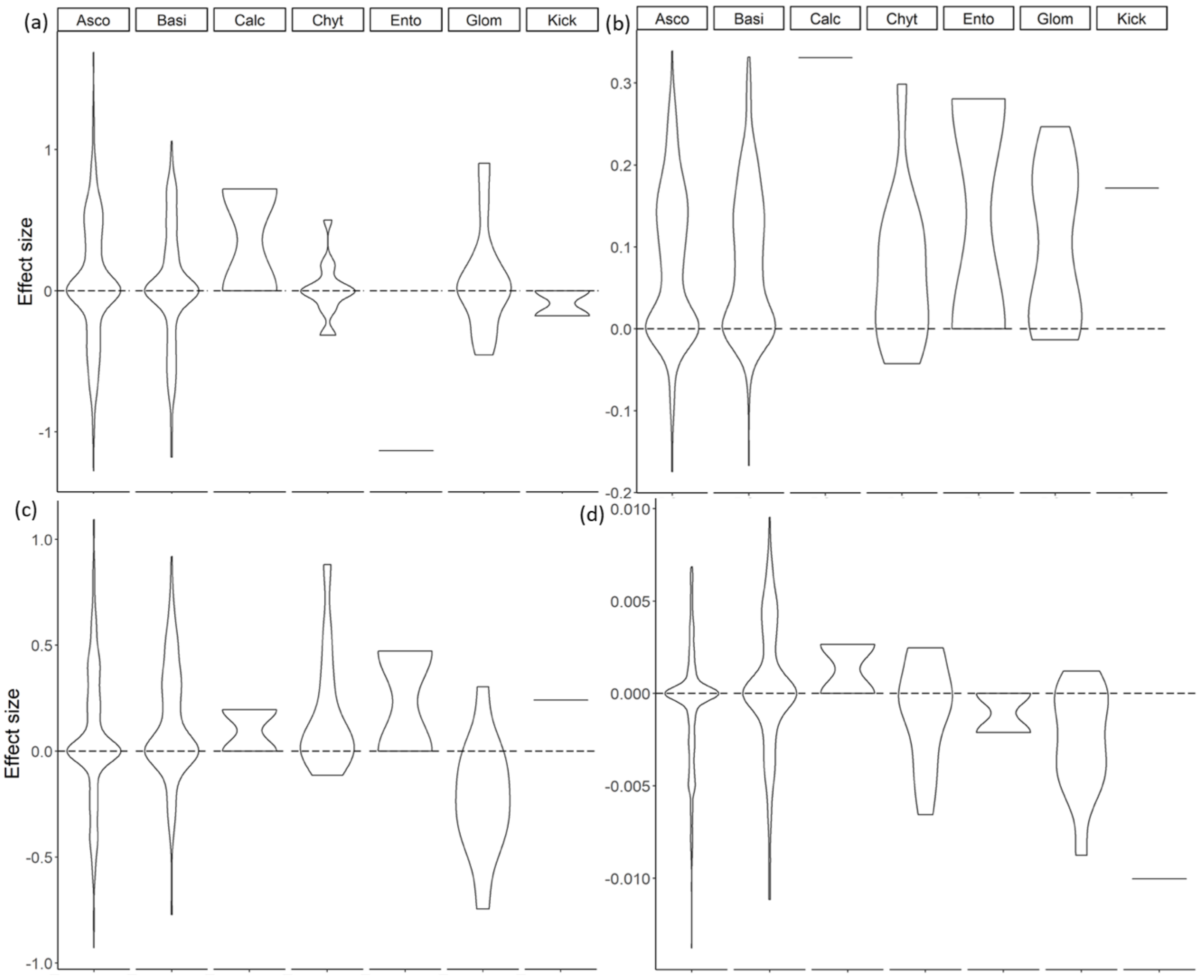

Figure S7. Effect size and direction of fungi phylum responses to environmental variables (β parameter) (a) land management with meadows as reference (positive values indicate higher probability of species occurrence in pastures), (b) soil carbon (PC1) (positive values indicate higher probability of species occurrence with higher soil C levels), (c) average air temperature (positive values indicate higher probability of species occurrence under warmer temperatures) and (d) average precipitation (positive values indicate higher probability of species occurrence under wetter conditions). Only responses with a posterior probability of at least 85% are reported. Phylum names abbreviated: Ascomycota (Asco); Basidiomycota (Basi); Calcarisporiellomycota (Calc); Chytridiomycota (Chyt); Entorrhizomycota (Ento); Glomeromycota (Glom) and Kickxellomycota (Kick).

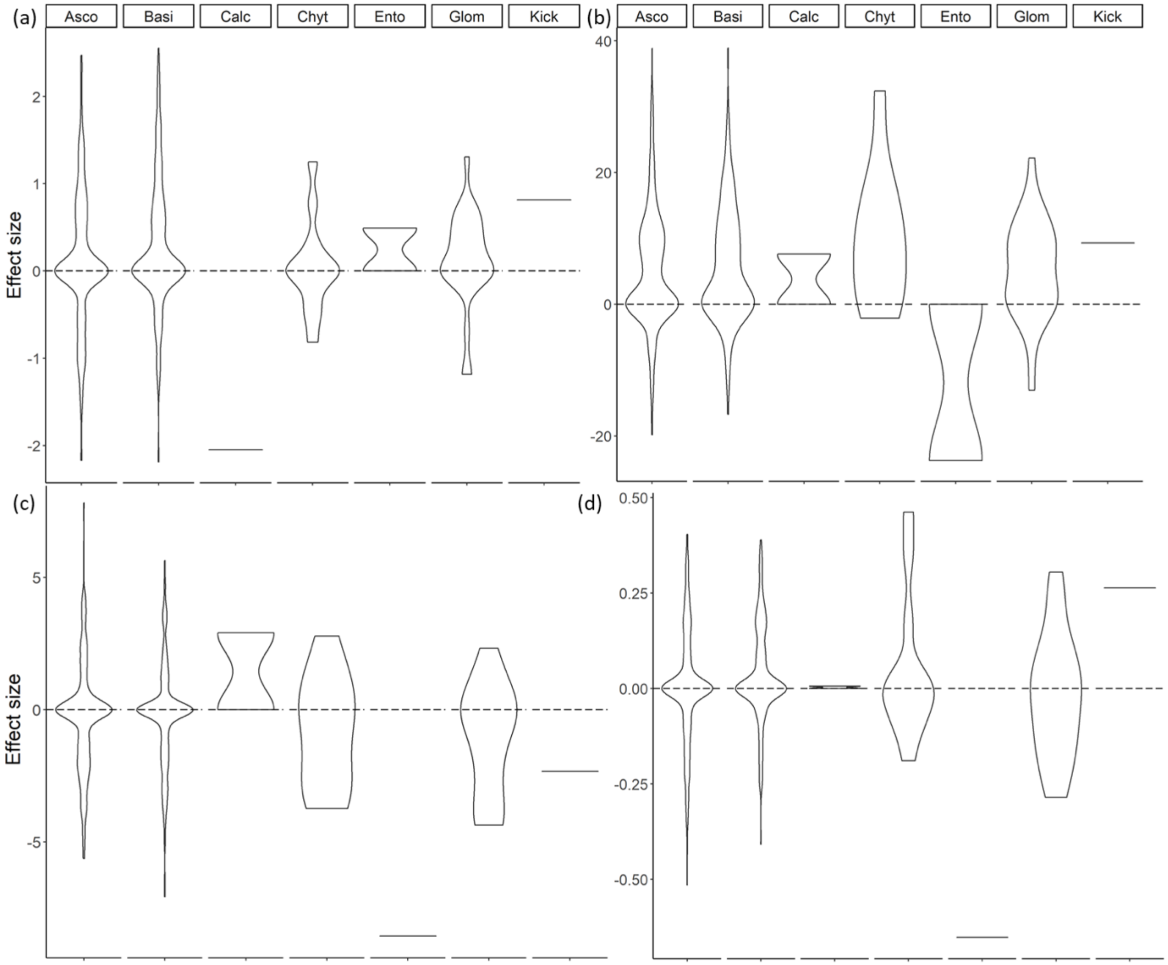

Figure S8. Effect size and direction of fungi clade responses to environmental variables (β parameter) (a) land use intensity (LUI) (positive values indicate higher probability of species occurrence under high LUI), (b) hill shading (positive values indicate higher probability of species occurrence with higher shading, (c) topographic index (positive values indicate higher probability of species occurrence at higher lying locations) and (d) soil acidity and concentration of potassium (K) (positive values indicate higher probability of species occurrence in acidic soils with higher soil K). Only responses with a posterior probability of at least 85% are reported. Phylum names abbreviated: Ascomycota (Asco); Basidiomycota (Basi); Calcarisporiellomycota (Calc); Chytridiomycota (Chyt); Entorrhizomycota (Ento); Glomeromycota (Glom) and Kickxellomycota (Kick).

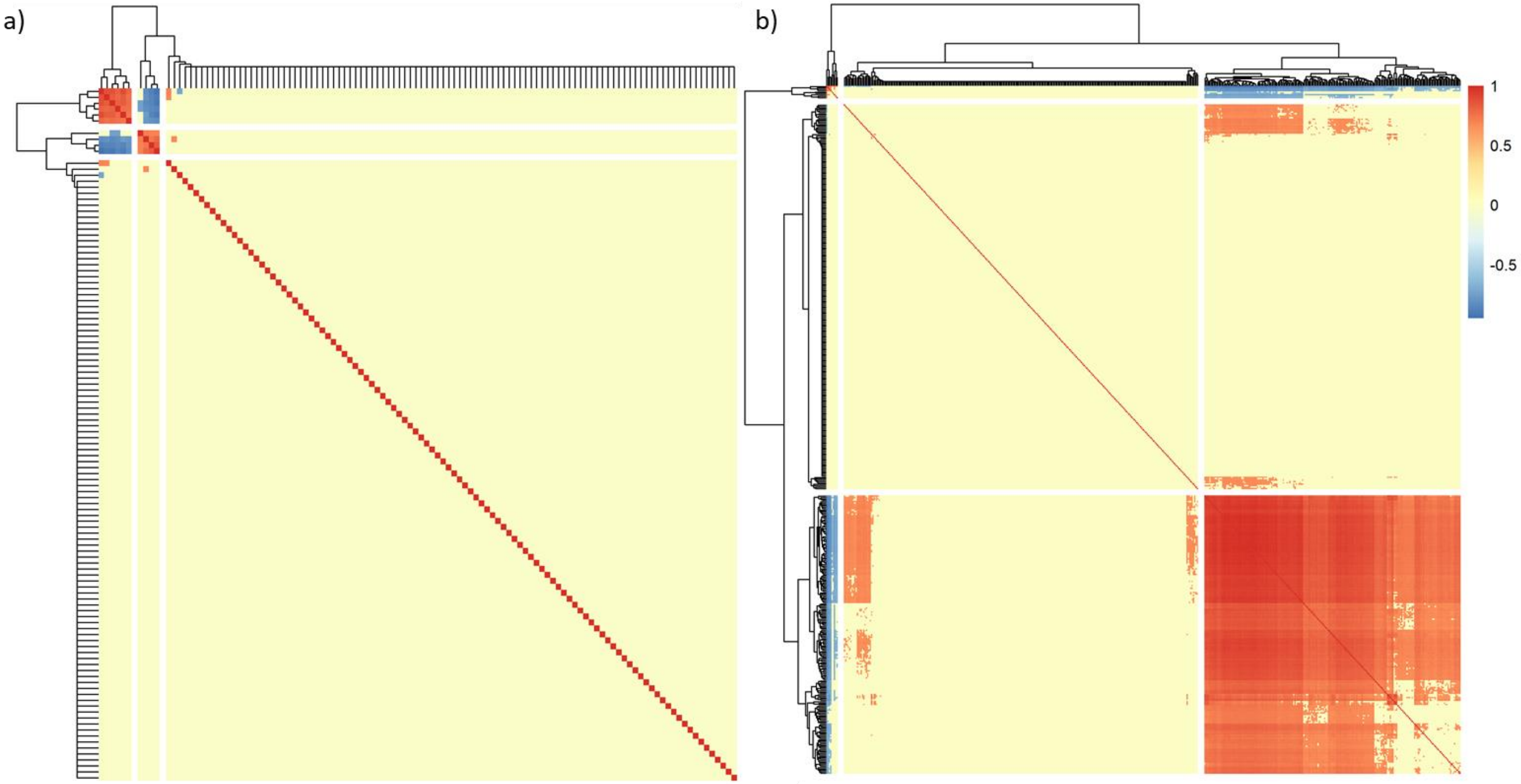

Figure S9. Residual variance of the HMSC analysis plotted as co-occurrence patterns for (a) plants and (b) soil fungi representing potential plant-plant and fungi-fungi interactions. Only co-occurrence patterns with a posterior probability of at least 0.85 are plotted as being stronger than expected (warmer colors towards red) or weaker than expected at random (cooler colors towards blue). Species are arranged based on Euclidian clustering and here visualized by the tree diagrams on the margins of the heatmaps.

Chapter 4: Supplementary material

Table S1. Brief overview of study sites that form part of the TERENO Harz/Central Germany project. Study sites are names with reference to the nearest largest town. Shannon diversity index was used to calculate the site-level diversity of European Nature Information System (classified to the 3rd level) land cover types. See main text for more details. Additional metadata, including photos and a map overview, of the sites are available on the DEIMS Repository for Research Sites and Datasets (https://deims.org > search TERENO) and TERENO website (https://www.tereno.net > harz-north-german-lowland-observatory.

Study site and location	Brief description	Arable land (km^2)	Forested area (km^2)	Managed grassland (km^2)	Site-level diversity in land cover	Site-level proportion of semi-natural habitat	Mean elevation (meters above sea level)	Number of sampling points
Schafstädt (SST) 51.3770° N, 11.7224° E	Area with rich soils (part of the “Querfurter Platte”) with flat topography. Highly cultivated, with large arable fields.	25.21	0.16	0.04	0.20	0.04	177 (±11)	16
Wanzleben (WAN) 52.0803° N, 11.4518° E	Area of high soil quality (part of the “Magdeburger Börde”) with flat topography. Highly cultivated.	20.60	0.99	0.68	0.82	6.79	113(±10)	16
Greifenhagen (GFH) 51.6329° N, 11.4340° E	Agricultural dominated landscape, with topography of valleys and rolling hills.	17.81	2.79	1.39	0.98	13.87	270 (±27)	15
Friedeburg (FBG) 51.6177° N, 11.7096° E	Agricultural dominated landscape, close to the Saale river. Topography of valleys and rolling hills.	18.16	0.78	1.95	0.95	19.47	122 (±31)	14

(Table S1 continues)

(Table S1 continued)

Study site and location	Brief description	Arable land (km²)	Forested area (km²)	Managed grassland (km²)	Site-level diversity in land cover	Site-level proportion of semi-natural habitat	Mean elevation (meters above sea level)	Number of sampling points
Harsleben (HAR) 51.8423° N, 11.0753° E	Part of the area includes a former military training area that has been occasionally grazed by sheep over the last 30 years. Topography mostly flat.	17.69	3.52	0.20	0.93	2.03	143 (±14)	16
Siptenfelde (SIP) 51.6491° N, 11.0526° E	In the eastern part of the Harz mountains, with distinct topography of rolling hills. Agricultural area surrounded by predominantly coniferous forest.	4.50	15.83	1.42	1.17	14.16	423 (±31)	15
							Total:	92

Table S2. Overview of average plot-level richness per taxa group and the total number of species (ASVs for soil bacteria and fungi) per taxonomic group, and the number of genera represented by the recorded species.

Taxa	Mean spp. Richness per sampling unit	Std	Total number of species	Genera (Order/Family) represented
Vascular plants	12	4	227	139 (24 Orders)
Wild bees	35	11	172	15 (5 Families)
Ground beetles	9	4	76	32 (1 Family)
Soil bacteria	1.206	252	6121	464 (201 Orders)
Soil fungi	248	68	1484	327 (81 Orders)

Table S3. Structural equation model results of the five taxonomic groups and various large- (site-level) and small-scale (plot-level) predictors per response variable (species richness, Shannon diversity index, and change in community composition). Site-level variables included the proportion of semi-natural habitat (Pro. semi-natural); Shannon diversity of EUNIS land cover types (Land cover diversity); mean annual temperature (MAT) and precipitation (MAP) of the preceding year. Plot-level predictors included: percentage of soil water content (scaled), soil texture, soil nutrients and local topography (as captured by the 1st axis of a principal component analysis of the respective categories). See main text for further details. Asterisks indicate the level of statistical significance: 0, '***'; 0.001, '**'; 0.01, '*' 0.05.

Richness (standardized per taxa group to highest species richness at plot-level)

Response	**Predictor**	**Estimate**	**Std. Error**	**DF**	**Std. Estimate**	
Vascular plants	Pro. semi-natural	0.05	0.01	86	0.68	***
Vascular plants	MAP (scaled)	-0.02	0.02	86	-0.15	
Vascular plants	MAT (scaled)	0.04	0.02	86	0.29	*
Vascular plants	Soil texture (PC1)	0.01	0.01	86	0.11	
Vascular plants	Soil water content (scaled)	-0.02	0.01	86	-0.14	
Wild bees	Pro. semi-natural	0.07	0.02	86	0.92	**
Wild bees	Land cover diversity	-0.33	0.10	86	-0.59	**
Wild bees	MAP (scaled)	-0.14	0.04	86	-0.76	***
Wild bees	Soil texture (PC1)	-0.03	0.01	86	-0.22	*
Wild bees	Soil pH	0.03	0.02	86	0.19	
Carabids	Pro. semi-natural	0.11	0.03	85	1.03	***
Carabids	Land cover diversity	-0.64	0.12	85	-0.86	***
Carabids	MAP (scaled)	-0.15	0.05	85	-0.67	***
Carabids	MAT (scaled)	0.11	0.04	85	0.47	**
Carabids	Topography (PC1)	0.04	0.02	85	0.19	*
Carabids	Soil pH	-0.06	0.03	85	-0.28	
Soil bacteria	MAP (scaled)	0.02	0.01	84	0.11	
Soil bacteria	Topography (PC1)	0.01	0.01	84	0.06	
Soil bacteria	Soil texture (PC1)	-0.01	0.01	84	-0.08	
Soil bacteria	Soil pH	0.06	0.01	84	0.42	***
Soil bacteria	Soil fungi	0.29	0.07	84	0.38	***
Soil bacteria	Vascular plants	0.07	0.07	84	0.07	
Soil bacteria	Land cover diversity	-0.08	0.04	84	-0.18	*
Soil fungi	MAT (scaled)	-0.04	0.03	85	-0.20	
Soil fungi	MAP (scaled)	-0.04	0.02	85	-0.19	
Soil fungi	topo_PC1	0.02	0.01	85	0.09	
Soil fungi	Soil pH	0.13	0.03	85	0.70	***
Soil fungi	Soil water content (scaled)	-0.02	0.02	85	-0.12	
Soil fungi	Vascular plants	-0.12	0.11	85	-0.09	
Soil pH	MAT (scaled)	0.95	0.07	87	0.96	***
Soil pH	Soil texture (PC1)	-0.16	0.05	87	-0.23	***
Soil pH	Soil nutrients (PC1)	-0.06	0.05	87	-0.10	
Soil pH	MAP (scaled)	0.22	0.07	87	0.22	**

(Table S3 continues)

(Table S3 continued)

Response	Predictor	Estimate	Std. Error	DF	Std. Estimate	
Vascular plants	Pro. semi-natural	0.31	0.14	85	0.66	*
Vascular plants	Land cover diversity	0.56	0.58	85	0.17	
Vascular plants	MAP (scaled)	-0.41	0.21	85	-0.39	
Vascular plants	Soil texture (PC1)	0.10	0.07	85	0.13	
Vascular plants	Soil pH	0.32	0.10	85	0.31	**
Vascular plants	Soil water content (scaled)	-0.17	0.10	85	-0.16	
Wild bees	Pro. semi-natural	0.09	0.06	87	0.41	
Wild bees	Land cover diversity	0,3842	0.27	87	0.26	
Wild bees	MAP (scaled)	-0.18	0.09	87	-0.38	
Wild bees	MAT (scaled)	-0.04	0.05	87	-0.09	
Carabids	Pro. semi-natural	0.25	0.09	83	0.85	**
Carabids	Land cover diversity	-0.88	0.383	83	-0.43	*
Carabids	MAP (scaled)	-0.51	0.14	83	-0.79	***
Carabids	MAT (scaled)	0.15	0.13	83	0.24	
Carabids	Topography (PC1)	0.12	0.05	83	0.22	*
Carabids	Soil texture (PC1)	0.06	0.06	83	0.13	
Carabids	Soil pH	-0.28	0.12	83	-0.44	*
Carabids	Soil fungi	0.39	0.17	83	0.26	*
Soil bacteria	MAP (scaled)	0.05	0.02	84	0.16	*
Soil bacteria	Topography (PC1)	0.01	0.01	84	0.05	
Soil bacteria	Soil texture (PC1)	-0.02	0.01	84	-0.10	
Soil bacteria	Soil pH	0.13	0.02	84	0.47	***
Soil bacteria	Soil fungi	0.31	0.05	84	0.45	***
Soil bacteria	Vascular plants	0.03	0.02	84	0.14	
Soil bacteria	Land cover diversity	-0.12	0.07	84	-0.14	
Soil fungi	MAT (scaled)	-0.15	0.07	85	-0.35	*
Soil fungi	MAP (scaled)	-0.09	0.05	85	-0.22	
Soil fungi	Topography (PC1)	0.03	0.03	85	0.07	
Soil fungi	Soil nutrients (PC1)	0.02	0.03	85	0.08	
Soil fungi	Soil pH	0.30	0.06	85	0.71	***
Soil fungi	Soil water content (scaled)	-0.07	0.04	85	-0.17	
Soil pH	MAT (scaled)	0.95	0.07	87	1.00	***
Soil pH	Soil texture (PC1)	-0.16	0.05	87	-0.23	***
Soil pH	Soil nutrients (PC1)	-0.06	0.04	87	-0.10	
Soil pH	MAP (scaled)	0.22	0.07	87	0.22	**

(Table S3 continues)

(Table S3 continued)

Community composition (captured by axis loading of principal component analysis that best captured variation in community composition)

Response	Predictor	Estimate	Std. Error	DF	Std. Estimate	
Vascular plants (PC1)	Land cover diversity	0.11	0.03	86	0.33	**
Vascular plants (PC1)	MAP (scaled)	-0.03	0.01	86	-0.25	*
Vascular plants (PC1)	MAT (scaled)	0.04	0.01	86	0.40	***
Vascular plants (PC1)	Soil texture (PC1)	-0.01	0.01	86	-0.15	
Vascular plants (PC1)	Soil water content (scaled)	-0.02	0.01	86	-0.15	
Wild bees (PC2)	Pro. semi-natural	-0.04	0.01	86	-0.74	**
Wild bees (PC2)	Land cover diversity	-0.13	0.05	86	-0.37	**
Wild bees (PC2)	MAP (scaled)	0.07	0.02	86	0.67	***
Wild bees (PC2)	MAT (scaled)	0.02	0.01	86	0.22	
Wild bees (PC2)	Soil pH	-0.03	0.01	86	-0.30	*
Carabids (PC1)	Pro. semi-natural	-0.03	0.01	86	-0.53	
Carabids (PC1)	Land cover diversity	0.06	0.06	86	0.19	
Carabids (PC1)	MAP (scaled)	0.07	0.02	86	0.65	**
Carabids (PC1)	Soil texture (PC1)	-0.01	0.01	86	-0.16	
Carabids (PC1)	Soil pH	0.04	0.01	86	0.39	***
Soil bacteria (PC1)	MAP (scaled)	-0.01	0.00	85	-0.06	*
Soil bacteria (PC1)	Topography (PC1)	0.00	0.00	85	0.03	
Soil bacteria (PC1)	Soil texture (PC1)	-0.00	0.00	85	-0.04	*
Soil bacteria (PC1)	Soil nutrients (PC1)	-0.00	0.00	85	-0.02	
Soil bacteria (PC1)	Soil fungi (PC1)	1.03	0.02	85	1.03	***
Soil bacteria (PC1)	Vascular plants (PC1)	0.03	0.02	85	0.03	
Soil fungi (PC1)	MAT (scaled)	-0.02	0.01	82	-0.19	*
Soil fungi (PC1)	MAP (scaled)	0.01	0.01	82	0.11	
Soil fungi (PC1)	Soil texture (PC1)	0.01	0.00	82	0.07	
Soil fungi (PC1)	Soil nutrients (PC1)	0.01	0.00	82	0.07	
Soil fungi (PC1)	Soil pH	-0.06	0.00	82	-0.60	***
Soil fungi (PC1)	Soil water content (scaled)	0.00	0.00	82	0.04	
Soil fungi (PC1)	Vascular plants (PC1)	-0.09	0.05	82	-0.09	*
Soil fungi (PC1)	Pro. semi-natural	-0.01	0.01	82	-0.23	
Soil fungi (PC1)	Land cover diversity	0.14	0.02	82	0.41	***
Soil pH	MAT (scaled)	0.95	0.07	87	1.00	***
Soil pH	Soil texture (PC1)	-0.16	0.05	87	-0.23	***
Soil pH	Soil nutrients (PC1)	-0.06	0.04	87	-0.09	
Soil pH	MAP (scaled)	0.22	0.07	87	0.22	**

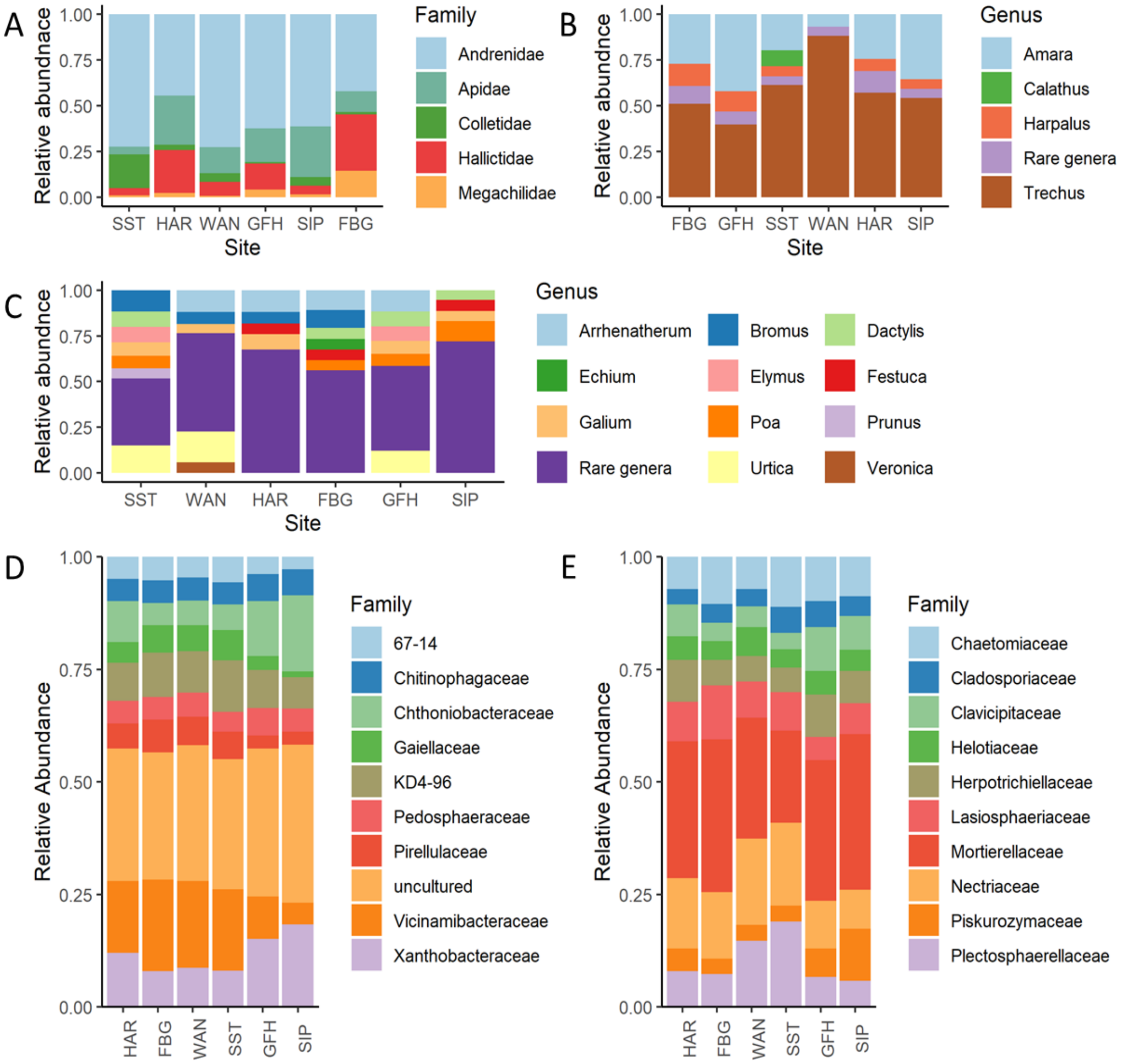

Figure S1. Relative abundance per taxa group across the respective sites, named after the next largest town [Schäfstädt (SST), Hartzleben (HAR), Wanzleben (WAN), Greifenhagen (GFH), Siptenfelde (SIP), Friedeburg (FBG)]. Ordering of the sites differ based on the main drivers of community composition according to the results of the structural equation model (see main text for details). For wild bees (A) sites are arranged from lowest to highest proportion of semi-natural habitat. For carabid beetles (B), the sites are arranged from lowest to the highest mean annual precipitation of the preceding year. For vascular plants (C), sites are arranged with increasing land cover diversity. For soil bacteria (D) and fungi (E), sites are arranged according to decreasing mean annual temperature of the preceding year. Taxa are grouped at the finest possible taxonomic level classification to ease interpretation. For carabids and vascular plants, we pooled across rare genera where the relative abundance was less than 0.05. For soil fungi and bacteria, for plotting purposes we only plotted the top 10 most abundant families as representative of the broader community.

Curriculum Vitae:

Eleonore Slabbert

Full name:
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21 January 1991

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Driver's license:
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Languages:
Bilingual (English & Afrikaans); German (B1)

Highest qualification:
Masters of Science
Applied Entomology,
Stellenbosch University

Previous position:
PhD researcher
@ Helmholtz Centre for Environmental Research - UFZ

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PERSONAL PROFILE

Eleonore is a young professional interested in applied science in the fields of agroecology, ecosystem services, natural resource management, sustainable agriculture, socio-ecological systems, and conservation ecology. She has an academic background in conservation (B.Sc. Conservation Ecology) and applied science (M.Sc. Entomology) from Stellenbosch University (US), South Africa. Currently she is finishing her doctoral studies in community ecology while based at the Helmholtz Centre for Environmental Research - UFZ, Germany. Her research investigates the scale-dependent and mechanistic impact of land use on multiple trophic groups toward advancing multifunctionality within agroecosystems.

Eleonore is dedicated to excellence, in scientific research and its implementation. She also holds high esteem for local community engagement and capacity development through participatory approaches. She has well-developed communication, facilitation, co-ordination, critical thinking, problem solving and team work skills. Other key areas of interests include, among others, the science-policy interface, ecological restoration, community-bases resource management, human capacity development and integrated pest management.

KEY ACHIEVEMENTS

GreenMatter fellowship and grant (2014 – 2015)

NRF Innovation Research Grant (2013 – 2015)

Role player in the establishment of a community-based Honeybush Knowledge Partnership between Stellenbosch University and small-scale land users in the Overberg, SA (2013 – 2015)

Rectors' award for excellent academic achievement (2014)

Departmental and Entomological Society of Southern Africa awards for top entomology graduate (2013), US

Consistent academic distinction on secondary (2005-2009) and tertiary level (2010 – 2013, US)

EDUCATION & TRAINING

M.Sc. Entomology
Stellenbosch University,
2014 – March 2016
(research on the ecosystem services and disservices of Honeybush (*Cyclopia*) associated insects)

B.Sc. Conservation Ecology
Stellenbosch University,
2010 – 2013
(Passed cum laude)

Senior certificate
Rhenish Girls' High School, 2005 -2009
(Passed with distinction, academic record available upon request)

Short courses:

Statistical & soft skill courses via UFZ graduate school
During PhD, more details upon request

Starting and managing a small business
Get Smarter, University of Cape Town, April – June 2016

Turn Down the Heat: From Climate Science to Action
Coursera, May – June 2016

Community Interaction
Frederik Van Zyl Slabbert Leadership Institute,
Oct – Nov 2015

RESEARCH & OTHER RELEVANT WORK EXPERIENCE

- Project coordination for interdisciplinary research collaborations within the UFZ as part of doctoral research, including some fieldwork
(Jun 2017 – March 2022)

- Experience working on international teams for developing and following through on a research collaboration. ESCALATE (UFZ) driven collaboration (Biffi et al. 2021)
(Jun 2019 – May 2021)

- Project coordination of Cape Winelands Environmental Education (EE) program (Junior LandCare)
(Jul – Dec 2016)

- Intern & consultant @ non-profit organization based in the Northern Cape (Indigo development & change)
(Mar – May 2016, Aug '16 – Mar 2017)

- Project coordination for applied entomology masters and honors-level research project at Stellenbosch University, including fieldwork and community workshops
(2012 – 2015)

- Teaching assistant for undergraduate entomology course
(2013 – 2015)

CORE SKILLS

ADMINISTRATIVE

- Scientific and informal report/article writing
- Project coordination
- Interactive workshop development & facilitation
- Team management
- Administration and marketing
- Competent in Microsoft Office 2010: Word, Excel, Power Point, Project, Access, Outlook and Explorer
- Interpersonal skills: Effective communication and time management; conflict management and resolution; effective team player

RESEARCH

- Fieldwork experience related to community ecology
- Insect identification
- Use of R as a statistical tool
- Knowledge and experience working with frequency statistics, and initial exposure to Bayesian statistics
- Use of ArcGIS & QGIS
- Critical problem solving and strategic thinking
- Creative and innovative

FUTURE PROSPECTS

In future I hope to contribute to biodiversity conservation through inspiring and equipping communities with practical knowledge and skills to advance sustainable resource use practices within their spheres of influence, whether that be in their backyard, neighborhood or broader community. The concept of working toward eco-tipping points through community-based natural resource management is, for example, an area of interest I hope to learn and engage more with in the near future. I would like to also contribute to more informed policy development through my research. Additionally, I am interested in working on socio-ecological integration and the science-society interface. I would also like to contribute towards more effective communication and collaboration between research institutes, policy makers and practitioners and other land users, including local communities. I could also envision bringing my theatre related skills and experiences into the social-ecological sphere, using participatory theatre games and processes to engage different stakeholders and initiating platforms for more active engagement and discussion about topics relevant to the community.

"I believe in servant leadership and have a passion to see others inspired and empowered to realize their capacity to make a difference."

-El Slabbert

PUBLICATIONS

Slabbert, EL; Knight, TM; Wubet, T; Kautzner, A; Baessler, C; Auge, H; Roscher, C; Schweiger, O (2022). Abiotic factors are more important than land management and biotic interactions in shaping vascular plant and soil fungal communities. *Global Ecology and Conservation*, 33, e01960. https://doi.org/10.1016/j.gecco.2021.e01960

Slabbert, EL; Schweiger, O; Wubet, T; Kautzner, A; Baessler, C; Auge, H; Roscher, C; Knight, TM (2020). Scale-dependent impact of land management on above- and belowground biodiversity. *Ecology and Evolution*, 10, 1139-10149. https://doi.org/10.1002/ece3.6675

Biffi, S; Traldi, B; Crezee, B; Beckmann, M; Egli, L; Schmidt, DE; Motzer, N; Okumah, M; Seppelt, R; **Slabbert, EL**; Tiedeman, K, Wang, H; Ziv, G. (2021) Aligning agri-environmental subsidies and environmental needs: A comparative analysis between the US and EU. *Environmental Research letters,* 16, 054067. https://iopscience.iop.org/article/10.1088/1748-9326/abfa4e

Slabbert, EL; Malgas, RR; Veldtman, R; Addison, P (2019) Honeybush (*Cyclopia* spp.) phenology and associated arthropod diversity in the Overberg region, South Africa. *Bothalia*, 49(1), a2430. https://doi.org/10.4102/abc.v49i1.2430

Koelle, B; **Slabbert, EL**; Koopman, A; Oettle, N; Archer, E; Kotze, D. (2016) Livestock Farming under Climate Change Conditions. *Indigo development and change*. URL link (Field guide)

CONFERENCE PARTICIPATION

50th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GFÖ) conference, Virtual Annual Meeting, 30 August-1 September 2021 (talk)

German Centre for Integrative Biodiversity (iDiv) Annual conference, Leipzig – UFZ, KUBUS, 29 -30 August 2019 (poster)

49th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GFÖ) conference, University of Münster, 9-13 September 2019 (talk)

Integrative Projects (IP) seminar, 22-23 November 2018 (poster)

Entomological Society of Southern Africa congress, July 2015

Fynbos Forum, August 2015

Declaration of Independence / Eigenständigkeitserklärung

I hereby declare that the thesis entitled "Impacts of small- and large-scale drivers of agroecosystems on multi-trophic diversity across the soil surface" has not previously been submitted to the Faculty of Natural Sciences I Biosciences of the Martin Luther University Halle-Wittenberg or to any other scientific institution for the purpose of a doctorate. Furthermore, I declare that I am the sole author of this thesis (save to the extent explicitly stated otherwise). I have not used any sources or aids other than those indicated in the text. Text passages that have been taken over verbatim or used to inform my content have been referenced. I further declare that I have never applied for a doctoral degree before.

Hiermit erkläre ich, dass die Arbeit mit dem Titel "Impacts of small- and large-scale drivers of agroecosystems on multi-trophic diversity across the soil surface" bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde. Außerdem erkläre ich, dass ich der alleinige Autor dieser Arbeit bin (sofern nicht ausdrücklich anders angegeben). Andere als die im Text angegebenen Quellen und Hilfsmittel habe ich nicht benutzt. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), ___________

Eleonore Louise Slabbert

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