

## Grant Proposal

# Global change in above-belowground multitrophic grassland communities

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## Abstract

Global change is transforming Earth's ecological communities with severe consequences for the functions and services they provide. In temperate grasslands, home to a mesmerising diversity of invertebrates controlling multiple ecosystem processes and services, land-use intensification and climate change are two of the most important global-change drivers. While we know a lot about their independent effects on grassland biodiversity and ecosystem functioning, little is known about how these stressors interact. Moreover, most research on biodiversity change focuses on decreasing biomass or species richness, while a major aspect is commonly ignored – altered ecological interactions. This is problematic because these interactions represent and control many important ecosystem processes, such as predation, herbivory or decomposition. Networks of trophic interactions, so-called food webs, link the structure and functioning of ecological communities and unravel mechanistic relationships between environmental change, ecological communities and ecosystem multifunctionality – the ability of a system to simultaneously support multiple processes. Consequently, we need to study how ecological interactions and the food webs they comprise respond to environmental change and to multiple interacting global-change drivers. Fortunately, novel tools offer

unprecedented opportunities in studying trophic interactions and their impact on ecosystem processes. In addition, we know far more about how global change impacts the aboveground world than its belowground counterpart. However, belowground communities are just as important for the overall functioning of terrestrial ecosystems. Thus, to comprehensively understand global-change impacts on temperate grasslands, we need to study above- and belowground multitrophic interactions and ecosystem processes together, also accounting for their interdependencies. Here, we propose to use the Global Change Experimental Facility (GCEF, Bad Lauchstädt, Germany) to study joint impacts of land-use intensity and climate change on above-belowground multitrophic interactions and ecosystem multifunctionality in a temperate grassland global-change experiment. We will combine novel approaches to assessing trophic interactions and basal-resource dependency with an innovative method to quantify energy flux through ecological interaction networks. We will disentangle separate and interactive effects of land use and climate change and unravel how global-change driven modifications in multitrophic interactions mechanistically translate into altered ecosystem processes and multifunctionality – above and below the ground. Combining a field-experimental approach with novel molecular and quantitative techniques will allow for a leap forward in our understanding of global-change impacts on temperate grasslands, which will be crucial to manage and conserve these important ecosystems.

## Keywords

multitrophic interactions, food webs, energy flux, climate change, land use, multiple stressors

## Starting Point

Temperate grasslands, home to a mesmerising diversity of invertebrates controlling numerous ecosystem processes, are subject to global change. Two of the most pressing global-change drivers are land-use intensification and climate change. We know that these stressors introduce filters regarding species richness, community composition, body-size patterns and the overall biomass of arthropods. What we do not know is how they jointly modulate multitrophic interactions (i.e., interactions amongst trophic levels – the steps on the trophic ladder) and what consequences altered interaction networks have for ecosystem processes. The mechanisms of how global-change drivers impact grassland multitrophic biodiversity-ecosystem functioning relationships remain unresolved. In addition, most of our knowledge on grassland biodiversity and ecosystem functioning is focused on the aboveground world, while the belowground counterpart and its responses to global change are less-well understood. Here, we propose to use a field experimental approach, together with novel molecular techniques to study feeding relationships, and an innovative approach to calculating energy flux through ecological networks, to mechanistically unravel joint impacts of land-use intensity and climate change on multitrophic, above-belowground, temperate grassland arthropod interaction networks, ecosystem processes and multifunctionality.

## State of the art and preliminary work

More than 36% of Earth's land surface is agriculturally used ([Worldbank](#), agricultural land %). With transforming these systems to meet our growing demands, human land use has severely altered their abiotic and biotic properties. We have modified their biodiversity, biogeochemical cycles and their productivity and have disrupted local to global biodiversity with consequences for ecosystem processes (Reid et al. 2005, Cardinale et al. 2012). Climate change and agricultural land-use intensification are amongst the most prominent global-change drivers (Anonymous 2018, Díaz et al. 2019). Nevertheless, the Anthropocene still comprises a diversity of agricultural systems and practices with varying land-use intensity. In 2022, Germany had 4.7 million ha grasslands (29% of its agriculturally-used area), of which ~ 42% were only mown and ~ 53% were either grazed or both mown and grazed ([Statistisches Bundesamt](#), Grünland). While grasslands are generally important for the conservation of biodiversity and ecosystem-service multifunctionality (Soliveres et al. 2016, Neyret et al. 2021) – the ability of a system to simultaneously maintain multiple processes (Jochum et al. 2012, Byrnes et al. 2013, Barnes et al. 2018, Eisenhauer et al. 2019, Jochum et al. 2021a, Jochum and Eisenhauer 2021), both aspects depend on the underlying land use (Allan et al. 2015, Eisenhauer et al. 2019). Arthropods make up a substantial part of grassland biodiversity and contribute to multiple ecosystem functions and services (Soliveres et al. 2016), but they are heavily impacted by land use (Gossner et al. 2016). We know that land-use intensity impacts multitrophic biodiversity, community composition and ecosystem processes (Newbold et al. 2015, Gossner et al. 2016). What we do not know is how land-use intensity alters grassland invertebrate multitrophic interactions and how this mechanistically changes ecosystem multifunctionality.

Moreover, temperate grassland ecological communities and interactions face an additional stressor, which, because of its crucial influence on central aspects, from individual physiology to community ecology, will likely modulate land-use effects: climate change. The impacts of climate change are proposed to surpass those of other threats to biodiversity and ecosystem functioning soon (Reid et al. 2005). Mean surface temperature is increasing and precipitation regimes are shifting (IPCC 2014, Anonymous 2018) – globally, but also for Germany ([www.regionaler-klimaatlas.de](http://www.regionaler-klimaatlas.de)). Increasing temperature and altered precipitation modify arthropod communities (Yin et al. 2020, Sohlström et al. 2022) and ecosystem functions (Barnes et al. 2018, Jochum and Eisenhauer 2021). Potential mechanisms include altered species ranges and phenology (Eisenhauer et al. 2018), biodiversity (Urban et al. 2016), body-size structure (Sheridan and Bickford 2011, Yin et al. 2020), individual- to community-level energetics (Brown et al. 2004) and the resulting impacts on trophic interactions (Brose et al. 2019), community structure, ecosystem processes and multifunctionality. We know that climate change alters grassland arthropod communities. But we don't know how these changes will impact multitrophic interactions and how these community changes, together with altered interactions, will mechanistically affect ecosystem processes and multifunctionality.

Interactions are the key to understanding how communities respond to global change (Lindmark et al. 2019, Åkesson et al. 2021). When studying species interactions and their consequences for ecosystem processes, ecologists assemble trophic interaction networks – food webs (Thompson et al. 2012). Food webs comprise nodes (species or functional feeding guilds) connected by links (trophic interactions) and link the structure and functioning of ecological systems (Thompson et al. 2012). Most studies using food webs to study ecological change across biotic and abiotic gradients assemble a meta-food web comprising all species included in any studied plot and constrain this network to plot-level food webs based on species presence or absence (metaweb-subweb approach; Kortsch et al. (2018), Hines et al. (2019)). Studies rarely investigate how the underlying trophic interactions might change along these gradients. But we have good reason to assume that they will change (Montoya and Raffaelli 2010, Brose et al. 2012). Because of global-change drivers modulating trophic interactions and because of the expected impact on ecosystem processes, we urgently need to understand how trophic interactions, food webs and the corresponding ecosystem processes change with these drivers. To realistically assess global-change impacts, we must adopt approaches capable of detecting these trophic interactions and their changes along gradients of strengthening global-change drivers.

When interested in linking interactions to processes, we need to advance the question of “who eats whom” to “... and how much”? We can do this by establishing quantitative food webs that contain information on interaction strengths. To quantify these and understand how interactions and basal-resource use affect ecosystem processes, we can use the concept of matter and energy flux through ecological communities (Lindeman 1942, Odum 1968, Hunt et al. 1987, Barnes et al. 2018, Jochum et al. 2021a). As all life needs energy to live and matter to build biological structures, the transport of matter and energy through ecological communities is one of the most fundamental processes on the planet. Thanks to several recent developments, we can combine food-web theory (Thompson et al. 2012) and metabolic theory (Brown et al. 2004) to assess energy flux through complex ecological networks (Barnes et al. 2018, Gauzens et al. 2018, Jochum et al. 2021a). The resulting flux estimations link biodiversity to multiple ecosystem processes and ecosystem multifunctionality (Barnes et al. 2014, Potapov et al. 2019). Using an energy-flux approach will allow us to link global-change impacts on multitrophic biodiversity to changes in central ecosystem processes and multifunctionality in an unprecedented, comprehensively-mechanistic way.

As land use and climate change simultaneously affect temperate-grassland communities, we need to understand how these multiple stressors interactively influence the communities (De Vries et al. 2012, Urban et al. 2016, Titeux et al. 2017, Galic et al. 2018) and how this mechanistically alters ecosystem processes and multifunctionality (Barnes et al. 2018, Jochum et al. 2021a, Jochum and Eisenhauer 2021). With both stressors modulating important aspects of grassland arthropod communities (see above), it is likely that communities simultaneously experiencing both stressors will display interactive effects (Oliver and Morecroft 2014, Galic et al. 2018, Sohlström et al. 2022). As such, intensified land use could make arthropod communities either more or less susceptible to climate

change (Galic et al. 2018, Schädler et al. 2019). The expected consequences for ecosystem processes will be a result of changing biodiversity, abundance, species composition and body size, all of which impact individual metabolic demand together with a direct effect of temperature and assimilation efficiency, also affecting energy flux. Additionally, they will strongly depend on altered ecological interactions. But how do these interactions change?

Despite all previous research on land-use and climate-change impacts on temperate grasslands, there are two main aspects that require substantial further investigation. First, while we know that multitrophic biodiversity and community composition change with land-use intensity and climate change, we know very little about the corresponding changes in ecological interactions and the interaction networks they comprise – as well as how these changes mechanistically impact ecosystem functioning and multifunctionality. This lack of knowledge is driven by previous technological constraints to an in-depth assessment of changing feeding interactions in complex communities. Fortunately, novel analytical techniques, such as gut content DNA metabarcoding (Sousa et al. 2019) and compound-specific isotope analysis of amino acids (CSIA-AA, Pollierer et al. (2019)) allow for unprecedented insights when uncovering trophic interactions and the relative importance of basal resources, such as bacteria, fungi and plants, in the food chains. We will combine these techniques with a powerful energy-flux approach (Barnes et al. 2018, Jochum et al. 2021a) to reveal how global change impacts interaction networks and how these changes mechanistically alter ecosystem processes. Information on how changing biodiversity, trophic interactions, food-web properties, ecosystem processes and multifunctionality are mechanistically linked will represent a leap in our understanding of global-change impacts on temperate grasslands which are key for biodiversity conservation and landscape multifunctionality.

Second, in comparison to the aboveground world, knowledge on biodiversity and ecosystem functioning below the ground is scarce (Guerra et al. 2020). This is problematic because belowground systems are vital for many ecosystem processes and services (Bardgett and van der Putten 2014, FAO et al. 2020) and because they do not necessarily resemble aboveground systems in their status or response to disturbances (Cameron et al. 2019, Thakur 2020). But even where we have information on both realms, we rarely have data on how they interact. This undermines our understanding of terrestrial systems as a whole, including the links between realms (Hooper et al. 2000, Wardle et al. 2004, Mulder et al. 2013, Jochum and Eisenhauer 2021) and their control of how terrestrial systems will respond to future global change (Thakur 2020, Jochum and Eisenhauer 2021). To comprehensively understand the joint impacts of land-use intensity and climate change on terrestrial ecosystems, we need to study above- and belowground realms together and assess their inter-dependencies. Here, we propose to study the joint impacts of land-use intensity and climate change on above-belowground multitrophic arthropod communities in temperate grassland systems and subsequent changes in ecosystem processes and ecosystem multifunctionality that both the integrity of the natural system and our human society depend on.

## Preliminary work

The first author, Malte Jochum, has a broad background in global-change impacts on multitrophic communities and ecosystem functioning (Jochum et al. 2012, Barnes et al. 2014, Eisenhauer et al. 2019, Jochum et al. 2021b, Jochum et al. 2022). He is experienced in analysing land-use impacts on multitrophic terrestrial communities, ecosystem functioning and multifunctionality (Barnes et al. 2014, Jochum et al. 2017a, Jochum et al. 2017b, Grass et al. 2020). Over the past years, he has advanced upon the research areas outlined above. Specifically, he has studied multitrophic arthropod communities above and below the ground (Barnes et al. 2014, Jochum et al. 2021b, Jochum et al. 2022) and has worked with large data sets on biodiversity and ecosystem functioning in temperate grasslands (Felipe-Lucia et al. 2020, Jochum et al. 2020). He co-developed an approach for calculating energy flux through food webs (Barnes et al. 2014, Barnes et al. 2018, Gauzens et al. 2018, Jochum et al. 2021a) that integrates organism size and environmental conditions via metabolic rates and is thus perfectly suited for assessing energy flux under global change (Barnes et al. 2018, Jochum et al. 2021a). More recently, he started working on above-belowground linkages (Jochum et al. 2022) and, together with co-author Nico Eisenhauer, called for combining the energy-flux approach with joint above- and belowground community assessments to understand global-change impacts on ecosystems (Jochum and Eisenhauer 2021). The first author recently started integrating novel approaches on assessing trophic interactions in his research. He is currently using compound-specific isotope analysis of amino acids (CSIA-AA) and gut content DNA metabarcoding on arthropods from the [EcoStressWeb](#) experiment that he led in the [iDiv Ecotron](#) (Schmidt et al. 2021). Because he does not have the necessary experience with these techniques, he collaborates with co-authors M. Pollierer and S. Scheu (Göttingen), both experts for the CSIA-AA approach, and with co-author V. Zizka in Bonn, an expert in DNA metabarcoding. Malte Jochum has co-supervised two PhD students working on above- and belowground biodiversity in the Global Change Experimental Facility (GCEF, details below) as thesis advisory committee member and last author on one PhD chapter, respectively. Co-authors Scheu and Eisenhauer and collaborator Schädler, are experts in terrestrial arthropod trophic ecology, above-belowground biodiversity and ecosystem functioning.

## Objectives and work programme

### Objectives

Overarching goal: Understand how land-use intensity and climate change jointly alter above-belowground multitrophic communities and ecosystem multifunctionality in temperate grasslands. Objective 1 (**OB1**): Explore how above- and belowground fauna communities (richness, density, biomass, average body mass, composition) differ in response to multiple stressors (i.e., under simultaneous climate change and land-use intensification). **OB2**: Assess climate- and land-use related changes in trophic interactions and basal-resource dependency of high-trophic level consumers above and below the

ground. **OB3**: Quantify climate- and land-use impacts on above-belowground energy flux, ecosystem processes and grassland ecosystem multifunctionality.

Overarching hypotheses: **HA**: Detrimental effects of climate change on above-belowground communities will be more pronounced at high land-use intensity (Oliver and Morecroft 2014, Titeux et al. 2017), with climate-change impacts buffered belowground (Le Provost et al. 2021). **HB**: Global-change drivers will modulate trophic relationships (Lindmark et al. 2019, Åkesson et al. 2021) shifting basal-resource dependence of consumers towards stronger dependence on bacteria under high land-use intensity and fungi under intensifying climate change (De Vries et al. 2012, Bloor et al. 2021). **HC**: Altered trophic interactions have energetic consequences translating into modulated ecosystem processes (e.g. increased herbivory), shifted relative importance of energy channels and reduced multifunctionality under higher land-use intensity and future-climate conditions (Barnes et al. 2018, Jochum et al. 2021a). **HD**: Different community properties, such as average body mass, total biomass, species richness and food-web metrics, jointly control energy flux, ecosystem processes and ecosystem multifunctionality (Barnes et al. 2018, Jochum et al. 2021a), with, for example, land-use driving changes via composition and climate change via altered body-size structure. More detailed hypotheses are formulated in the work packages below.

## Work programme including proposed research methods

We propose to use an existing field experiment (see below) to mechanistically link two of the most prominent global-change drivers in temperate grasslands, land-use intensity and climate change, to changes in above-belowground multitrophic interaction networks and ecosystem multifunctionality. Instead of merely describing how communities change, we will obtain mechanistic insights on how these changes translate into altered ecosystem processes and multifunctionality – which is what society ultimately depends on.

We will investigate how land-use intensity and climate change jointly impact above-belowground communities and ecosystem processes. This is important because both stressors affect individual- to community-level aspects of biology and ecology and are likely to interact, i.e. to influence each other's impact (Oliver and Morecroft 2014). We will obtain a mechanistic understanding of these joint impacts by using two state-of-the-art molecular methods to assess how multitrophic interactions change and combine the resulting information on altered interactions and basal resources with a powerful method for calculating energy flux through food webs. We will use the Global Change Experimental Facility (GCEF, Helmholtz-Zentrum für Umweltforschung – UFZ, Bad Lauchstädt, Fig. 1a), established in 2012 (Schädler et al. 2019), which combines a land-use intensity treatment with a climate-change treatment in a temperate-grassland context. The GCEF features two climate levels (current vs. future climate – the latter with shifted precipitation patterns, ~ 20% reduction in summer and ~ 10% increase in spring and autumn and increased temperature – 0.55°C increased daily mean temperature, increased minimum temperature, longer frost-free periods and more growing degree days), enabled via automatic roofs and irrigation systems and five land-use types spanning common management options for

croplands and grasslands. Each of the 10 main plots (80 x 24 m) represents either current or future climate and consists of five randomly-ordered plots (16 x 24 m) for each of the land-use types (Schädler et al. 2019). We will test the overarching hypothesis that land-use intensity and climate change magnify each other's impact on above-belowground communities and functioning. We will use the climate treatment together with three land-use types: intensively-used meadow (sown with 5 species/cultivars in 2013, moderately NPK fertilised, mown four times a year), extensively-used meadow (sown with a 56-species mix, mown twice a year) and extensively-used pasture (as ext. meadow, but grazed three times a year by ~ 20 sheep for 24 h).

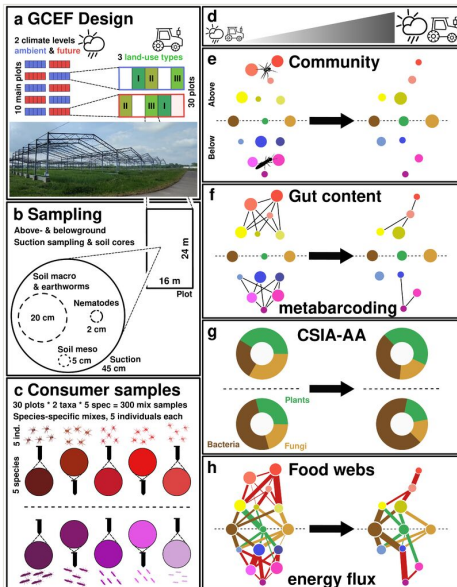


Figure 1. [doi](#)

**a** The Global Change Experimental Facility (GCEF) Bad Lauchstädt, Germany, has 10 main plots, five in each climate level (ambient, blue; future, red). Each main plot is split into five plots (16 x 24 m) with different land-use types. We will use three of these (I-III, green shades), 30 plots overall. **b** On each plot, we will sample (**WP1**) vegetation- and ground-dwelling fauna (suction sampling, 45 cm diameter), soil macrofauna (20 cm diameter), mesofauna (5 cm diameter) and nematodes (2 cm diameter), each to 10 cm depth. We will extract earthworms (mustard extraction) in the 20-cm hole, below the 10-cm core. **c** Spiders and staphylinid beetles (top consumers) will be stored at -20°C, in molecular-grade ethanol. After extraction, sorting and identification, we will create multi-individual samples (**WP2**) for the five most common spider and staphylinid species (red and purple shades, respectively). These multi-individual samples will be used for gut content metabarcoding (**f**) and compound specific isotope analysis of amino acids (CSIA-AA, **g**). We will analyse how climate and land-use intensity (**d**) alter above- and belowground invertebrate communities (density, biomass, diversity, etc.) (**e**) and, using the molecular techniques, above- and belowground consumer trophic interactions (resource pool, **f**) and basal-resource dependency (**g**). Based on **WP1** and **WP2**, we will build above-belowground food webs to calculate energy flux under different climates and land-use intensity (**h**, **WP3**).



The GCEF was set up to investigate how climate change and land-use intensity interactively impact ecosystem functioning via above-belowground biodiversity. GCEF research has shown that climate and land-use intensification independently and interactively modify aboveground arthropod species richness, abundance and community composition (Sohlström et al. 2022). The two global-change drivers were found to alter soil-fauna biomass via different pathways (climate change via body-size reductions, land-use intensity via density reductions; Yin et al. (2020)). Despite this previous research, we know little about: i) how these community changes translate into altered ecosystem processes and multifunctionality and ii) how above- and belowground systems interact in their response to global change. To answer these questions, we propose to use the GCEF to simultaneously sample above- and belowground invertebrate communities (**WP1 and OB1**), use gut-content metabarcoding (Sousa et al. 2019) and CSIA-AA (Pollierer et al. 2019) for assessing trophic interactions (**WP2 and OB2**) and establish plot-level food webs, calculate above-belowground energy flux, ecosystem processes, energy channels (Potapov 2022) and multifunctionality to unravel the mechanisms of global-change effects on grassland communities and ecosystems (**WP3 and OB3**; Barnes et al. (2018), Potapov et al. (2019), Jochum and Eisenhauer (2021)).

### **WP1 - Above-belowground invertebrate communities**

In **WP1**, our aim is to simultaneously assess the responses of above- and belowground invertebrate communities in temperate grasslands to the joint influence of land-use intensity and climate change (**OB1**). To achieve this goal, we (PhD & student helpers) will sample above- and belowground invertebrates in 30 GCEF plots (10 main plots, three land-use plots each: intensive and extensive meadow, extensive pasture) in two consecutive years (1 and 2, see Fig. 1b). Aboveground fauna will be suction-sampled and belowground fauna will be extracted from soil cores or using mustard extraction directly from the ground (earthworms). Suction samplers are effective tools to quantitatively sample aboveground grassland arthropods. We will use the ecoVac (ecoTech, Bonn, Germany) device which has been successfully used in temperate grasslands before (Sohlström et al. 2022). On each plot, in each year, we will sample one randomly-selected 45-cm-diameter area for aboveground (vegetation and ground) arthropods. When approaching the sampling spot, we will put a modified circular laundry basket (45 cm diameter, IKEA Fyllen, 50 cm high, Polyester) on the ground to prevent mobile arthropods from escaping. Subsequently, we will suction-sample the vegetation and ground inside the basket for four minutes and afterwards empty out the upper cage (Jochum et al. 2022, Sohlström et al. 2022). Suction samples will be cooled in the field, frozen at -20°C as soon as possible and subsequently transferred to 70% ethanol (spiders will be placed in molecular-grade ethanol for subsequent molecular analyses, i.e. to avoid DNA breakdown) for later identification and analyses. We will measure sward height to be used as a correction parameter for aboveground arthropod suction sampling.

To quantitatively sample soil fauna at peak biomass, and in concert with the simultaneous aboveground-fauna assessment, we will take one large (20 cm diameter) and one small (5 cm diameter) soil core, both to a depth of 10 cm, to adequately assess soil macro- and

mesofauna, respectively (Potapov et al. 2022). All cores will be taken inside the suction-sampled area right after suction sampling. Soil cores will be stored in sealed plastic containers and transported to Leipzig (Eisenhauer lab, iDiv), where we will use heat to quantitatively extract belowground fauna using modified Macfadyen and Kempson heat extraction schemes (8 d, starting at 20°C with 5°C steps/24 h, until going from 50°C - 60°C at day 7; Birkhofer et al. (2017)). After extraction, soil fauna will be stored in 70% ethanol for later identification and analyses (staphylinids will be placed in molecular-grade ethanol and be frozen at -20°C because of subsequent molecular analyses). To complement soil-fauna data from these soil cores, we will quantitatively sample earthworms from deeper layers by twice applying 2 l of mustard solution (with 5 min break) to the 20-cm soil-core holes and collecting earthworms until 5 min after the application (Eisenhauer et al. 2008). Additionally, soil nematodes will be extracted by wet extraction (additional core; 2-cm diameter, 10 cm depth). In addition to this fauna sampling, we will take pictures of the vegetation inside the suction cage – and of the direct surroundings in a standardised way, to later assess dominant plant species in this exact patch of the plot. Overall, we estimate fieldwork to take 5 days per year for the team (PhD, student helpers). To complement the data collected here, we will have access to GCEF joint data on plant communities, soil abiotics and microclimate.

Macro- and mesofauna will be pre-sorted to order or higher-level taxon by the PhD student and student helpers. All taxa, including nematodes and earthworms, will then be identified to species- or functional-group level by specialists to ascribe them to trophic species for food-web construction. We will measure body lengths of five individuals per species/highest identification level and plot to calculate body masses with allometric regressions (Sohlström et al. 2018). We will calculate plot-level taxon richness, individual density (ind/m<sup>2</sup>), fresh biomass (mg/m<sup>2</sup>) and community composition, split into above- and belowground communities and for the overall community. We will analyse the impact of climate, land use and their interaction on above-belowground community properties (**HA**). We expect above- and belowground communities and different community properties to respond differently to the stressors (Barnes et al. 2014, Jochum et al. 2017a, Le Provost et al. 2021, Jochum et al. 2021b). More specifically, we expect aboveground communities (**H1.1**; Le Provost et al. (2021)) and higher trophic levels to respond most strongly (**H1.2**; Brose et al. (2012)) and density to respond more strongly than species richness (**H1.3**; Barnes et al. (2014), Jochum et al. (2021b), Jochum et al. (2022)). We expect land use to more-strongly affect communities via community composition and climate change to more strongly affect their body-size structure (**H1.4**; Yin et al. (2020), Sohlström et al. (2022)). Structural-equation models will assess joint impacts of climate and land use on above-belowground interdependencies. We expect decoupling between above-belowground communities and their properties (e.g., diversity of above- and belowground taxa) in response to combined stressors (**H1.5**; Manning et al. (2015), Ochoa-Hueso et al. (2020)).

## WP2 - Molecular analyses of trophic interactions

To assess global-change impacts on multitrophic interactions and energy channels (**OB2**), we will use two state-of-the-art methods, gut-content metabarcoding for assessing short-

term, direct trophic interactions (Who eats whom?) and compound-specific isotope analysis of amino acids (CSIA-AA) to quantify the relative dietary contribution of long-term basal resources, such as bacteria, fungi and plants, for consumers (... and how much?). The little information we have on global-change impacts on grassland-interaction networks is commonly constrained to plant-pollinator (Weiner et al. 2014) or plant-herbivore networks (Neff et al. 2021), with higher trophic levels typically neglected. However, to understand how global change alters ecosystems, these higher trophic levels and their community-wide impacts are crucial (Brose et al. 2012, Jochum et al. 2012) and ignoring them could result in misinterpreting the overall patterns (Jochum et al. 2021a). Consequently, both molecular methods will be used on above- and belowground predators. As we need time to extract and sort the invertebrate samples and run the molecular analyses, we will focus these analyses on samples taken in year 1 and later expand the obtained information on feeding relationships and basal resources to the community data from both years in **WP3**. We know from two previous PhD projects that spiders and staphylinid beetles are the most common above- and belowground predators in the GCEF grasslands, respectively. We will focus on these taxa, present across all plots and important for subsequent flux calculations, to assess how the treatments change their trophic interactions and basal resources.

Gut-content metabarcoding (Sousa et al. 2019) will be used to detect changes in predator-prey interactions. We use this method on spiders (aboveground) and staphylinids (belowground), taken from suction and heat-extraction samples, to test how their trophic interactions change with land-use intensity and climate change. We will use whole-body DNA extraction linked with predator-specific blocking primers during PCR to increase prey-DNA amplification and subsequent detection of prey species. Such primers are available for spiders (Lafage et al. 2020) and we have tested them successfully (EcoStressWeb). Blocking primers for staphylinids will be designed together with collaborators. As a back-up solution, we could use beetle regurgitates for gut-content metabarcoding as has successfully been done before (Tiede et al. 2016). On each plot ( $n = 30$ ), we will use the five most common spider and staphylinid species, respectively and analyse one multiple-individual sample ( $30 \text{ plots} * 2 \text{ consumers} * 5 \text{ mix-samples} = 300 \text{ metabarcoding samples}$ , Fig. 1c). Metabarcoding will be done by a company specialised in high-throughput sample processing and sequencing, including specimen preparation, DNA extraction and amplification, marker gene library preparation and sequencing. We will obtain plot-level data regarding above- and belowground consumer prey spectra in response to two stressors. This will allow us to analyse if and how trophic interactions change (**HB**). We expect land-use intensity and climate change to interactively affect the number of trophic interactions (diversity of prey items), with a reduced number of trophic links for predators under future-climate conditions (**H2.1**) and higher-intensity land use (**H2.2**) and the effect of one stressor being dependent on the other (**H2.3**; Lindmark et al. (2019), Åkesson et al. (2021)). We expect changes in trophic interactions to be more pronounced for above- than belowground consumers (**H2.4**; Le Provost et al. (2021)). Finally, to improve our understanding of the mechanisms behind global-change impacts on altered trophic links, we will quantify how well consumer prey choice matches prey relative abundance patterns (links to most abundant prey) or body-size changes (optimal prey size), based on data from

**WP1** (Gauzens et al. (2021)). Here, we expect both altered body size and shifted relative abundance patterns to impact consumer trophic links, with land use having a stronger impact via community composition and climate via body-size changes (**H2.5**; Yin et al. (2020), Sohlström et al. (2022)).

Compound-specific isotope analysis of amino acids (Pollierer et al. 2019) will be used to assess global-change driven shifts in the long-term relative-importance of basal resources, such as plants, fungi and bacteria. The method is based on the fact that essential amino acids are synthesised by these producers and then recycled up the food chain. Since producer-derived amino acids differ in their carbon (C) isotopic signatures given differing biosynthetic pathways, we can use the isotopic signatures of essential amino acids from consumer-body tissue to indirectly assess the relative importance of basal resources for specific consumers (Pollierer et al. 2019). Furthermore, nitrogen (N) isotopic signatures of “trophic” and “source” amino acids, which are either strongly or very slightly enriched via trophic transfer, can be used to assess consumer trophic positions (Pollierer et al. 2019). We will use predators as indicators for the communities’ overall dependence on the three basal resources. We will analyse multi-individual samples for each of the five most common spider and staphylinid species per plot (300 CSIA-AA samples). The PhD student will acquire the skills to perform these analyses and analyse these samples supervised by one of the collaborators. Generally, we expect global change to shift basal-resource dependence more strongly in below- than aboveground consumers, as we expect the aboveground system to remain strongly based on the plants as their main basal resource (**H2.6**). We expect the belowground communities to be shifted towards a higher dependence on bacteria as basal resource under higher land-use intensity (**H2.7**; Bloor et al. (2021)) and on fungi under future-climate conditions (**H2.8**; De Vries et al. (2012)). We will combine the results from **WP2** into one paper on multiple-stressor impacts on above-belowground multitrophic interactions and basal-resource dependency (**HB**).

### **WP3 - Food webs, energy flux and ecosystem multifunctionality**

We know that global change impacts communities and ecosystem processes, but we lack the mechanistic understanding of how the two things are linked. In **WP3**, we aim to establish plot-level food webs to calculate above-belowground energy flux, ecosystem processes (e.g., predation, herbivory, decomposition), energy channels (plant-, bacteria-, fungi-based) and multifunctionality and unravel the mechanisms of global-change effects on grassland communities and ecosystems (**OB3**). We will combine the community data from **WP1** (both years) with the trophic information from **WP2** (based on sampling in year 1) to establish plot-specific food webs for both years. More specifically, we will use a combination of taxonomic and functional information together with novel, plot-specific data on predator-prey interactions from **WP2** to build food webs (see Hines et al. (2019), similar approach without molecular methods). Hence, rather than using a metaweb-subweb approach, we will have plot-specific data on body sizes (**WP1**), trophic interactions and relative importance of basal resources (both **WP2**) that we can use with the taxonomic information to build plot-specific food webs. These food webs will be used to calculate plot-

level energy fluxes providing information on ecosystem processes, energy channels (Potapov 2022) and multifunctionality.

Based on the pre-sorting and expert identification of all invertebrates (**WP1**), we will group them into trophically-consistent feeding types, such as carnivores, herbivores, detritivores or omnivores, within taxonomic orders. Omnivores will be further specified into carnivore-herbivores, carnivore-detritivores, herbivore-detritivores or generalistic omnivores consuming animal, plant and detritus resources (Lind et al. 2015, Barnes et al. 2020). We use this combined taxonomic-functional approach, because feeding relationships in grasslands are highly phylogenetically conserved and taxonomic groups provide information on the trophic behaviour and prey vulnerability, for example, due to morphological traits, such as sclerotisation (Lind et al. 2015, Potapov et al. 2018, Barnes et al. 2020). These taxonomic-functional entities will be the trophic nodes in the food webs and energy-flux calculation. We will calculate energy flux through plot-level food webs and use the resulting fluxes to quantify processes, energy channels and multifunctionality. Energy flux will be calculated following a well-established routine, the adapted food-web energetics approach (Barnes et al. 2018, Gauzens et al. 2018, Jochum and Eisenhauer 2021, Jochum et al. 2021a). It will be based on the community and trophic data assembled in **WP1** and **WP2**, providing plot- and taxon-specific individual density and body size, as well as trophic-link information for spiders and staphylinid beetles. We will calculate individual-level metabolic rates based on taxonomy, body size (from **WP1**) and plot-level temperature (plot-level soil- and vegetation-level temperature available from GCEF) using well-established regressions for arthropods (Ehnes et al. 2011). On each plot, we will scale the data obtained from different above- and belowground sampling techniques (**Fig. 1b**) to one square metre. Subsequently, for each of the food-web nodes present in a plot, we will sum up the individual metabolic rates of the respective individuals resulting in the metabolic demand of the whole node (Barnes et al. 2014, Jochum et al. 2021a). We will assign link-level assimilation efficiencies, based on the respective resource type and ambient temperature (Lang et al. 2017). We will apply consumer preferences taking into account the relative abundance of prey types (**WP1**), as well as information on relative importance of basal resources (from **WP2**). Subsequently, we will use the “fluxweb” R package (Gauzens et al. 2018) to calculate energy flux through the plot-level food webs, resulting in flux estimations for each consumer-resource interaction, i.e. every single food-web link.

Based on this information, we will quantify ecosystem processes, such as primary and intraguild predation, herbivory and decomposition as all fluxes going out of the respective resource types, for example, out of autotroph nodes for herbivory. We will quantify energy channels by summing up all fluxes upstream of plants, bacteria and fungi, respectively. These assessments are based on established routines (Barnes et al. 2018, Jochum et al. 2021a, Potapov 2022). We will use flux-based ecosystem processes (predation, herbivory etc.) to calculate trophic multifunctionality (Potapov et al. 2019) with the averaging and multiple-threshold approaches (Byrnes et al. 2013). Subsequently, the calculated ecosystem processes, energy channels and multifunctionality will be related back to the underlying climate and land-use treatments (**HC**). We will identify differences and

similarities between treatment impacts on the belowground and aboveground parts of the response variables (belowground vs. aboveground ecosystem processes, channels, multifunctionality) and on energy fluxes across the above-belowground boundary (e.g., predation of aboveground predators on predominantly-belowground prey).

Generally, we expect higher land-use intensity and future climate to reduce total energy flux, but more severely above than below the ground (**H3.1**; Le Provost et al. (2021)). Single ecosystem processes will respond to the treatments, with, for example, increased herbivory at high land-use intensity (**H3.2**; Barnes et al. (2020)). We expect functions associated with higher trophic levels, for example, predation, to be more-heavily affected than those associated with lower trophic levels (**H3.3**; Potapov et al. (2019)). The bacterial energy channel will likely be strengthened under high land-use intensity (Bloor et al. 2021) and the fungal channel will be strengthened under future climate conditions (De Vries et al. 2012) (**H3.4**). Finally, we hypothesise land-use intensity and climate change to reduce above- and belowground ecosystem multifunctionality (**H3.5**; Allan et al. (2015)), mediated via several community properties. We will analyse how average body mass, total biomass, taxon richness, food-web properties and taxonomic composition mechanistically drive energy flux, ecosystem processes and multifunctionality (**HD**; Barnes et al. (2018), Jochum et al. (2021a), Wan et al. (2022)). The results on land-use and climate impacts on grassland above-belowground energy flux, ecosystem processes and multifunctionality will be summarised in one paper.

In summary, we will obtain fundamentally-novel information on how land-use intensity and climate change jointly alter above-belowground communities and trophic interactions and how this mechanistically modulates above-belowground ecosystem functions, energy channels and multifunctionality. Our results will offer unprecedented insights into how exactly multiple global-change drivers alter ecosystem performance, which is important to understand, manage and mitigate global-change impacts on temperate grasslands.

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## Conflicts of interest

The authors have declared that no competing interests exist.

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