Extensive grassland-use sustains high levels of soil biological activity, but does not alleviate detrimental climate change effects

Julia Siebert[a,b,*], **Madhav P. Thakur**[a,b,c], **Thomas Reitz**[a,d], **Martin Schädler**[a,e], **Elke Schulz**[d], **Rui Yin**[b,e], **Alexandra Weigelt**[a,f], **Nico Eisenhauer**[a,b]

[a]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena–Leipzig, Leipzig, Germany
[b]Institute of Biology, Leipzig University, Leipzig, Germany
[c]Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands
[d]Department of Soil Ecology, Helmholtz Centre for Environmental Research—UFZ, Halle, Germany
[e]Department of Community Ecology, Helmholtz-Centre for Environmental Research—UFZ, Halle, Germany
[f]Department of Systematic Botany and Functional Biodiversity, Institute of Biology, Leipzig University, Leipzig, Germany
*Corresponding author e-mail address: julia.siebert@idiv.de

Contents

Abstract

Climate change and intensified land use simultaneously affect the magnitude and resilience of soil-derived ecosystem functions, such as nutrient cycling and decomposition. Thus far, the responses of soil organisms to interacting global change drivers remain poorly explored and our knowledge of below-ground phenology is particularly limited. Previous studies suggest that extensive land-use management has the potential to buffer detrimental climate change impacts, via biodiversity-mediated effects. According to the insurance hypothesis of biodiversity, a higher biodiversity of soil communities and thus an elevated response diversity to climate change would facilitate a more stable provisioning of ecosystem functions under environmental stress. Here we present results of a two-year study investigating, at fine temporal resolution, the effects of predicted climate change scenarios (altered precipitation patterns; passive warming) on three grassland types, differing in land-use intensity, soil biological activity, and in resilience.

We show that future climate conditions consistently reduced soil biological activity, revealing an overall negative effect of predicted climate change. Furthermore, future climate caused earlier and significantly lower peaks of biological activity in the soil. Land-use intensity also significantly decreased soil biological activity, but contrary to general expectations, extensive land use did not alleviate the detrimental effects of simulated climate change. Instead, the greatest reduction in soil biological activity was observed in extensively-used grasslands, highlighting their potential vulnerability to predicted climate change. To assure high levels of biological activity in resilient agroecosystems, extensive land use needs to be complemented by other management approaches, such as the adoption of specific plant species compositions that secure ecosystem functioning in a changing world.

1. Introduction

Climate change is altering the composition of terrestrial ecosystems and the functions they provide (Vitousek, 1994), including soil–driven processes like nutrient cycling and decomposition (Bardgett and van der Putten, 2014; Verhoef and Brussaard, 1990). Climate change not only alters the densities and functional attributes of communities (Blankinship et al., 2011; Briones et al., 2009), but many plant and animal species also adjust their phenology to an extended growing season as a result of a modified climate (Cohen et al., 2018; Menzel and Fabian, 1999; Peñuelas and Filella, 2009). At present, however, we can only speculate on how soil organisms (e.g. microbes and invertebrates) will respond in their year–round activity patterns to changing climate conditions, as we are largely lacking data in high temporal resolution (Bakonyi et al., 2007; Briones et al., 2009;

Eisenhauer et al., 2018; Thakur et al., 2018). Knowledge of belowground activity patterns will be crucial to improve our understanding of key ecosystem functions in a changing world (Bardgett and van der Putten, 2014; Eisenhauer et al., 2018).

Decomposition of soil organic matter involves both soil microbial and invertebrate activity (Swift et al., 1979). While climate change effects on microbial-driven decomposition have been well studied in short-term assessments (A'Bear et al., 2012; Manzoni et al., 2012), the role of soil invertebrates is less well understood (Walter et al., 2013). It is often assumed that decomposition will be enhanced under warmer conditions (Fierer et al., 2005; Rustad et al., 2001), which has found empirical support from lab and field experiments (Conant et al., 2011; Melillo et al., 2002). This is generally in line with predictions of greater metabolic demands of ectothermic organisms at higher temperatures (Gillooly et al., 2001). However, there is mounting evidence that this positive relationship only holds as long as other environmental factors such as soil moisture are not limiting (Butenschoen et al., 2011; Thakur et al., 2018). As soon as higher soil temperatures are accompanied by a decrease in soil moisture, the activity levels of microorganisms and invertebrates decline and thereby potentially slow down decomposition processes (Allison and Treseder, 2008; Davidson and Janssens, 2006; Thakur et al., 2018).

It is evident that drivers of global change do not occur in isolation, but act in concert (Dukes et al., 2005). For instance, changes in temperature and precipitation coincide with dramatic alterations in land use. As the demands for raw materials and food rise with human population growth (Ingram et al., 2008; Tilman et al., 2002), large amounts of land are being converted to arable agriculture and pasture lands subjected to increasingly intensified management (Foley et al., 2005). Such practices include the adoption of a restricted pool of highly productive forage plant species that allow increased mowing frequencies, tillage, and heavy machine use, all of which can impair the functioning of managed ecosystems (Giller et al., 1997; Newbold et al., 2015; Tsiafouli et al., 2015). High tillage and grazing frequencies, and the addition of mineral fertilizers, have been shown to decrease the abundance, diversity, and activity of soil organisms as well as the functions that they drive (Treseder, 2008; Wardle et al., 2002). This means that the strength of climate change effects may depend on the management system, due to the potential interactive effects of climate change and land use (De Vries et al., 2012; Walter et al., 2013).

Extensive management strategies, with less disturbances and greater biodiversity, might be expected to buffer the detrimental effects of climate change and lead to higher resilience of the grasslands, as they represent more complex systems owing to the greater number of species and thus a higher interaction and response diversity (Goldenberg et al., 2018) with an increased likelihood of asynchronous responses of the different species within a trophic group (Craven et al., 2018; Hector et al., 2010; Mazancourt et al., 2013). Intensively-managed, often low-diversity systems, in contrast, are expected to be particularly vulnerable to changing environmental conditions, as predicted by the insurance hypothesis of biodiversity (Isbell et al., 2017; Loreau et al., 2003; Yachi and Loreau, 1999). Indeed, Walter et al. (2013) showed that decomposition rates are more susceptible to drought in grasslands with higher cutting frequency. However, multifactorial studies investigating the interactive effects of climate change and land use on decomposition processes remain scarce (Walter et al., 2013), and we particularly lack insight into the phenological patterns among below-ground soil invertebrates (Eisenhauer et al., 2018). Studying the potential interactive effects of climate change and land-use management across different seasons of the year would help gaining more realistic insights into the temporal dynamics and full-year responses of crucial ecosystem functions in a changing world (Eisenhauer et al., 2018; Bardgett and van der Putten, 2014).

Here, we test for the interactive effects of climate change and land-use management in grasslands on the average levels and phenology (shifts in activity peaks) of soil biological activity and its resilience. We do this by measuring soil microbial respiration (Scheu, 1992) and invertebrate feeding activity (Kratz, 1998), which are tightly linked to decomposition processes in the soil (Thakur et al., 2018), under modified conditions of climate and land-use management. The study was conducted within the framework of the Global Change Experimental Facility (GCEF; Fig. 1A) in Bad Lauchstädt, Germany, a large-scale experimental platform, where predicted climate conditions for the period ~2070–2100 are simulated on 16×24 m-plots: altered temperature (ambient versus ambient $+0.6\,°C$) and precipitation regimes (ambient versus ~20% reduction in summer, ~10% addition in spring and autumn, respectively) are realised with the help of fully automated, fold-out roofs (Schädler et al., 2019). The climate treatments are crossed with three different grassland types in a split-plot design: extensively-used grassland with mowing (mown two times per year, species-rich plant community, no fertilisation, hereafter: extensive meadow), extensively-used grassland with sheep grazing
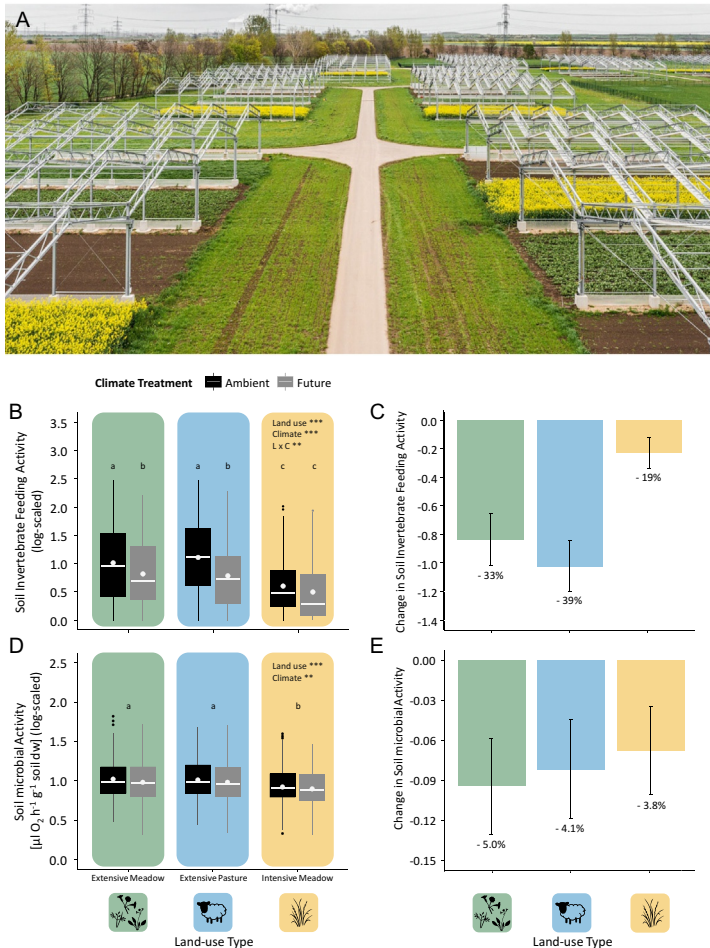
Fig. 1 Interactive effects of climate change and land use on soil biological activity and its resilience. (A) The Global Change Experimental Facility in Bad Lauchstädt, Germany. Image copyright: Tricklabor/Service Drohne. (B) Boxplots showing the interactive effects of climate change and land use on soil invertebrate feeding activity (log-scaled) across all sampling points. (C) Changes in soil invertebrate feeding activity in response to the climate treatment (compared to ambient climate conditions) for the three land-use types. Error bars ± SE based on means (ambient/future) per sampling. (D) Boxplots showing the interactive effects of climate change and land use on soil microbial activity (log-scaled) across all sampling points. (E) Changes in soil microbial activity in response to the climate treatment (compared to ambient climate conditions) for the three land-use types. Error bars ± SE based on means (ambient/future) per sampling. Boxplots show the median (horizontal line), the mean (dot), first and third quartile (rectangle), $1.5 \times$ interquartile range (whiskers), and outliers (isolated points). Letters a, b, and c on top of the boxplots indicate significant differences among treatments based on Tukey's HSD test ($P < 0.05$) run on linear mixed effects models. For interpretation of the references to color, the reader is referred to the online version of this article. $**P < 0.01$, $***P < 0.001$. Black = ambient climate; grey = future climate. Green = extensive meadow (moderately mown); blue = extensive pasture (grazed by sheep); yellow = intensive meadow (frequently mown).

(grazed two to three times per year, species-rich plant community, no fertilisation, hereafter: extensive pasture), and intensively-used grassland (mown three to four times per year, few forage species, mineral fertilizer, hereafter: intensive meadow). All grassland types represent common local management practices including specific species pools and management intervals. As for the land-use types, the climate treatments represent realistic climate scenarios that still allow for inter-annual variability in place of rigid, highly controlled conditions. The experiment started in 2014, and the present study was conducted from March 2015 to April 2017. Measurements were done every three weeks by employing rapid ecosystem function assessment methods, following Thakur et al. (2018), to obtain year-round high temporal resolution data on soil responses. While our current knowledge is predominantly based on a few short-term assessments, this comprehensive study comprises 36 (invertebrate feeding activity) and 34 (microbial activity) sampling dates in two consecutive years to address the need to continuously study the responses of soil organisms to interacting global change drivers over longer time periods (Hamel et al., 2007).

We hypothesised that future climate conditions will change the phenology of soil biological activity by increasing activity in spring and autumn and by reducing activity in summer (Thakur et al., 2018). Thus, we expected a shift towards earlier activity peaks at the beginning of the growing season under future climate conditions. Furthermore, we expected the intensive meadow to show a decrease in soil biological activity, due to frequent disturbances and the use of mineral fertilizer (Treseder, 2008). The most detrimental climate effects were expected for the intensively-managed land-use regime. Accordingly, we expected extensively-used grassland types to show greater resilience by alleviating the detrimental effects of the predicted future climate, due to substantially higher biodiversity (Isbell et al., 2015, 2017), which maintains high levels of soil biological activity.

2. Methods

2.1 Study design

The Global Change Experimental Facility was established in 2013 to study the interactive effects of climate change (including elevated temperature and changes in precipitation patterns) and land-use intensity on managed terrestrial ecosystems using realistic scenarios (Schädler et al., 2019). The study site is located at the field research station of the Helmholtz-Centre for Environmental Research (UFZ) in Bad Lauchstädt, Germany

(51° 22′ 60 N, 11° 50′ 60E, 118 m a.s.l.), and was formerly used as an arable field (last crop cultivation in 2012). Being located in the Central German dry area (Querfurter Platte), the site has a mean annual precipitation of 489 mm (1896–2013) and a mean annual temperature of 8.9 °C (1896–2013). The soil is a Haplic Chernozem with a humus layer reaching down to more than 40 cm depth. This highly fertile soil type was developed upon carbonatic loess substrates (around 70% silt and 20% clay content). The soil is known for its high water–retention capacity (nearly reaching the mean annual precipitation), ensuring comparatively low susceptibility to drought stress (Altermann et al., 2005). Within the upper 15 cm, pH values ranged from 5.8 to 7.5, while total carbon and total nitrogen varied between 1.71 and 2.09% and 0.15–0.18%, respectively.

The experiment consisted of 50 plots arranged in 10 mainplots (Schädler et al., 2019). The two experimental treatments were implemented in a split-plot design with the climate treatment carried out on the mainplot level ($n = 10$) and the land–use treatment implemented on the plot level ($n = 50$), randomly arranged within the mainplots. Thus, for each of the five land–use types, there are five plots with future climate conditions and five plots with ambient climate conditions that serve as a climate control. The spatial scale is realised by a large plot size of 16×24 m that allows the use of standard agricultural equipment. Each plot has a buffer zone of 2 m to the eastern and western sides and 4.5 m to the southern and northern sides. In addition to the buffer zones, the randomised location of plots within mainplots mimics all possible neighbourhood arrangements of land–use treatments (Schädler et al., 2019). All measurements took place in the inner plot area (15×12 m) on a specific transect for soil measurements (Fig. 2).

The climate treatments were first applied in 2014 (spring 2014: start of temperature treatment; summer 2014: start of precipitation treatment). All mainplots were equipped with a steel framework of 5 m height that allowed the mounting of equipment to impose the climate treatment. In the case of the control mainplots, the steel framework served as a control for potential infrastructure effects, such as microclimatic effects. In the case of the mainplots assigned to the climate treatment, the roof constructions included an irrigation system and mobile roof and side panels that can be closed via rain sensors/timers.

The climate treatment was chosen based on a consensus scenario across several dynamic models for Central Germany for 2070–2100, which include higher inter–annual rainfall variability with longer drought periods over summer and increased precipitation in spring and autumn (Doscher et al., 2002;
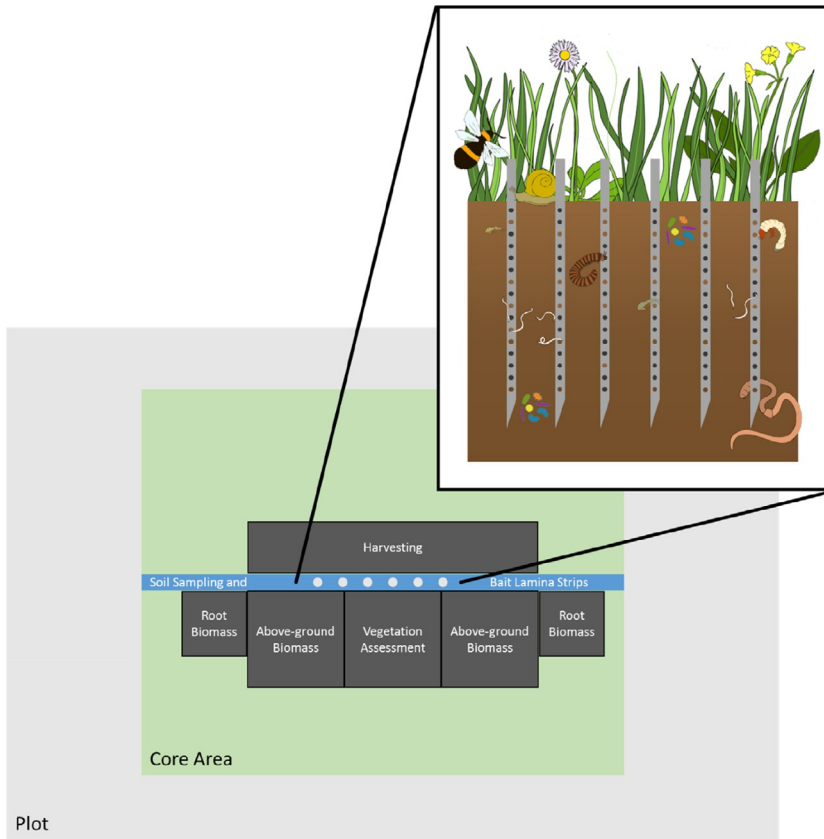
Fig. 2 The plot design of the Global Change Experimental Facility (GCEF) in Bad Lauchstädt, Germany. All 50 plots of the GCEF (24 × 16 m) have an inner core area (15 × 12 m) where the samplings took place. The area for soil measurements describes a north-south transect (in blue, 15 × 0.5 m in total). Six bait lamina strips were placed on the transect in a distance of approximately 20 cm to each other. Above-ground biomass was harvested on a 9 × 1.6 m area. Root biomass was sampled on 2 m × 2 m areas using multiple soil cores.

Jacob and Podzun, 1997; Rockel et al., 2008). Furthermore, the mean annual temperature is predicted to rise by up to 3 °C (Kerr, 2007; Meinke et al., 2010). The treatments are applied as realistic climate scenarios, which include natural variability instead of highly controlled conditions. Thus, the climate treatments are applied relative to the ambient conditions and allow for inter-annual variability. Over summer (June–August), the climate treatment includes a reduction of precipitation by ~20% (closing of roof and side panels via rain sensors). In spring (March–May) and autumn

(September–November), the precipitation is increased by ∼10% by the use of an irrigation system that uses water from a large rain water reservoir (Fig. 3).

Passive warming by reducing heat emission during the night with mobile roofs became a standard method in climate change experiments and mimics
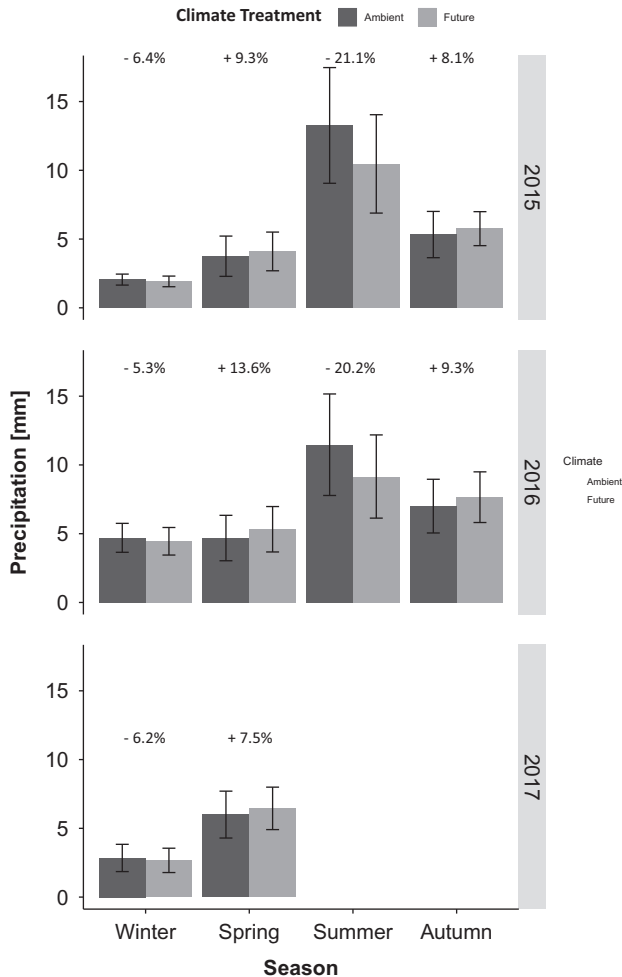

Fig. 3 The precipitation treatment of the Global Change Experimental Facility. Panels show ambient and future climate conditions for each season and year in which the study took place. Intended reduction in summer: ∼20%, intended increase in spring and autumn: ∼10% (small reduction in winter can be explained by a decrease of vegetation cover on plots with future climate, see Schädler et al. (2019)). Dark grey = ambient climate; light grey = future climate. Percentages above the bar plots indicate the changes in precipitation under future climate conditions compared to ambient climate conditions. Error bars ±SE.

Table 1 The temperature treatment of the global change experimental facility. Shown are average deviations of daily means in air and soil temperature for future climate conditions compared to ambient climate conditions during active and inactive roof phases within the study period ($\pm$ SE). Values different from zero (t-test, $P < 0.05$) are given in bold.

	June 1st 2015[a]—December 11th 2015	December 12th 2015—March 23rd 2016	March 24th 2016—November 22nd 2016	November 23rd 2016—December 31st 2017
	Roofs active	Roofs inactive	Roofs active	Roofs inactive
Daily mean air temperature at 5 cm height	**+0.55 ± 0.03 °C**	+0.006 ± 0.006 °C	**+0.55 ± 0.03 °C**	**+0.08 ± 0.03 °C**
Daily mean soil temperature at 1 cm depth	**+0.65 ± 0.02 °C**	**+0.11 ± 0.01 °C**	**+0.44 ± 0.02 °C**	**+0.31 ± 0.03 °C**

[a]Active roof phase started on February 25th, but data from temperature loggers is only available from June 2015 onwards.

the realistic phenomenon of stronger increases of minimal rather than maximal temperatures (Beier et al., 2004). In our experiment, passive warming overnight was realised on future climate mainplots by closing the roof and side panels automatically from calendrical sundown to sunrise (within the active roofing phase), which increased air and soil temperature on average by ~0.6 °C (Table 1). In addition to the direct warming effects of roof closing, we could also observe a slight increase of soil and air temperatures near the soil surface during inactive roofing phases. This can be explained by a decrease of vegetation cover on plots with future climate and the accompanying direct insolation on the soil surface (Schädler et al., 2019). This can be interpreted as a realistic side effect of climate change on the microclimate.

In 2015, the roofs were in place from February 25th to December 11th (roofs were closed 79% of night time, deviations were due to frost and wind). In 2016, the roofing phase started on March 23rd and ended on November 23rd (roofs were closed 82% of night time). In 2017, the roofing phase started on March 11th. The exact timing of the inactive roofing phase over winter (i.e. no climate treatment intended) was determined based on the forecasts of longer frost periods. Within the active roofing phase, roofs and side panels open automatically at wind speeds above $7\,\mathrm{ms}^{-1}$ and frost to avoid damages (Schädler et al., 2019).

Within each mainplot there were plots representing five different land-use treatments, each with different levels of land-use intensity: (1) conventional farmland; (2) organic farmland; (3) intensive meadow; (4) extensive meadow; and, (5) extensive pasture (the two last-mentioned summarised

as extensively-used grasslands). In place of an experimental gradient, each land-use scenario represented a commonly-used management type in the locality around Bad Lauchstädt that has specific combinations of plant diversity and community structure, management intervals, and fertilisation.

The intensive meadow consisted of typical forage plant species, fertilised with mineral fertilizer and mown frequently (three times in 2015, four times in 2016). The extensively-used grasslands were either mown at a moderate frequency (two times in 2015 and 2016, no fertilisation) or moderately grazed by sheep (two times in 2015, three times in 2016, by a group of 20 sheep grazing on each plot for 24 h). After each mowing event, the cut plant biomass was removed from the plots as would normally happen during hay harvest. In the extensive meadow, the mown biomass was left on the plots for some days to enable natural shed of seeds back onto the soil. While the extensively-used grasslands contained 53.1 ± 2.0 plant species per $9 m^2$, the intensive meadow had 10.1 ± 3.6 plant species per $9 m^2$ (mean $\pm$ SD for 2015–2017). For details on the sown plant species pools, see Schädler et al. (2019). Owing to methodological constraints in making the soil measurements, due to management such as repeated ploughing events, and to a focus on the hypothesis for the potential buffering effects of more species-rich, extensively-used grasslands compared to intensively-used grasslands (De Vries et al., 2012; Isbell et al., 2015), the data presented in this paper is restricted to the extensive meadows, the extensive pastures, and the intensive meadows (i.e. 30 plots arranged within the 10 mainplots) and does not include the two farmlands.

2.2 Soil animal feeding activity and soil microbial activity

We monitored soil invertebrate feeding activity and soil microbial activity every three weeks over a two-year period (March 2015 to April 2017), resulting in 36 and 34 sampling time points with 1080 and 1020 observations of invertebrate feeding activity and microbial activity, respectively. Soil invertebrate feeding activity was assessed using the bait lamina test (Terra Protecta GmbH, Berlin, Germany) as a commonly-used rapid ecosystem function assessment method (Kratz, 1998; Thakur et al., 2018). The bait strips are made of PVC ($1 mm \times 6 mm \times 120 mm$) and have 16 holes (1.5 mm diameter). Original sticks were ordered from Terra Protecta and filled with an artificial organic bait substrate, which was prepared according to the recommendations of Terra Protecta, consisting of 70% cellulose powder, 27% wheat bran, and 3% activated carbon. The bait substrate is primarily consumed by mites, collembolans, enchytraeids, millipedes, and earthworms

(Gardi et al., 2009; Hamel et al., 2007; Harding and Stuttard, 1974), whereas microbial activity plays a minor role in bait substrate loss (Hamel et al., 2007; Rożen et al., 2010; Simpson et al., 2012).

The bait lamina strips were inserted vertically into the soil with the uppermost hole just beneath the soil surface. A steel knife was used to make a slot in the soil into which the strips were carefully inserted. Six strips were placed at a distance of approximately 20 cm from one another per plot to account for spatial heterogeneity (Fig. 2). After three weeks of exposure, the bait lamina strips were removed from the soil, directly evaluated in the field, and replaced by a new bait strip. Each hole was carefully inspected and rated as 0 (no invertebrate feeding activity), 0.5 (intermediate feeding activity), or 1 (high invertebrate feeding activity). Soil invertebrate feeding activity can therefore range from 0 (no feeding activity) to 16 (maximum feeding activity) per strip. Mean bait consumption of the six strips was cal‐ culated per plot prior to statistical analysis.

To measure soil microbial activity, soil samples were taken every three weeks using a steel corer (1 cm diameter; 15 cm deep). Seven subsamples per plot were homogenised, sieved through a 2 mm sieve, and stored at 4 °C. Basal respiration (without addition of substrate) was measured using an O_2-microcompensation apparatus in the lab (Scheu, 1992). Soil microbial respiration was measured at hourly intervals for 24 h at 20 °C (i.e. at constant temperature), and basal respiration as a measure of microbial activity was cal‐ culated as the mean O_2 consumption rate 14–24 h after the start of the mea‐ surements (μl O_2 h^{-1} per g soil dry weight). Since we were able to monitor the phenology of invertebrate feeding activity in situ, we focused on these results hereafter. Nevertheless, we performed time series analyses for both response variables (Table 2).

Table 2 Results from generalised additive mixed-effects models (GAMMs) for soil invertebrate feeding activity and soil microbial activity (both log-scaled). Climate, land use, and time were incorporated as smooth terms. Statistically significant results are given in bold.

Treatment	Soil invertebrate feeding activity			Soil microbial activity		
	edf	*F*-value	*P*-value	edf	*F*-value	*P*-value
s (Time, Land use)	2.63	1.38	0.24	17.61	0.47	0.98
s (Time, Climate)	**21.91**	**4.55**	**<0.0001**	12.83	0.08	1
s (Time, Land use, Climate)	**24.63**	**6.74**	**<0.0001**	**3.96**	**6.92**	**<0.0001**

2.3 Assessments of potential explanatory variables

On the two meadow types, plant shoot biomass was assessed on subplots of 9 m × 1.6 m (Fig. 2) using a rotary mower with a cutting height of 5–8 cm. The intensive meadow was mown four times per year, whereas the extensive meadow was mown twice in 2016. On the extensive pasture (i.e. sheep grazing), such data is not available. Plant root biomass was sampled in April and June 2016 on all three grassland types. Using a soil corer of 3.5 cm diameter, four subsamples were taken per plot (see Fig. 2 for the specific location) at a depth of 0–15 cm. All subsamples were pooled and repeatedly rinsed in water to obtain the fraction of fine roots (<2 mm), which was then dried at 70 °C. Root mass density was calculated per dm^3 soil.

To analyse soil microbial biomass and abiotic soil parameters, soil samples were taken in April, June, and October 2016 by using a steel corer (1 cm diameter; 15 cm deep). Seven subsamples per plot were homogenised, sieved at 2 mm, and stored at 4 °C. An O_2-microcompensation system (Scheu, 1992) was used to estimate the maximal respiratory response of soil microorganisms following the addition of a glucose standard ($4 mg g^{-1}$ dry weight soil, solved in 1.5 mL distilled water) to determine soil microbial biomass (μg Cmic g^{-1} dry weight soil). Gravimetric soil moisture contents were determined using a fully automatic moisture analyser (Kern DBS60–3 from Kern & Sohn GmbH, Germany). Soil pH was measured with a pH electrode (Mettler Toledo InLab Expert Pro-ISM) after shaking the soil for 1 h in 0.01 M $CaCl_2$ (1:2.5 w/v). Hot water extractable carbon (HWC) and nitrogen (HWN), which represent the labile organic C and N pools, were determined from 10 g of air-dried soil following the method of Schulz (2002) and analysed using an elemental analyser for liquid samples (Multi N/C, Analytik Jena, Germany).

Soil mesofauna (mostly Collembola and Acari) was sampled in June and October 2016. Three soil cores (6 cm diameter, 5 cm depth) were randomly taken per subplot on a strip of 15 m × 0.5 m (Fig. 2) and extracted in a MacFadyen high-gradient extractor for 10 days (Macfadyen, 1961) before the abundances were determined.

2.4 Statistical analysis

Soil invertebrate feeding activity was measured at 36 time points, and soil microbial activity was measured at 34 time points. Given that we expected treatment effects to vary with time in a nonlinear way, we used generalised

additive mixed–effects models (GAMMs) to test the interactive effects of climate, land use, and time on soil biological activity. We chose GAMMs due to their flexibility in including smooth functions of covariates without restricting the relationships to be linear, quadratic, or cubic. The model structure of the GAMM was: soil biological activity ~s (time, climate) * s (time, land use) * s (time, climate, land use) + (1 | mainplot/plot), with 's' indicating smoothing functions for GAMM. Experimental plots were nested within mainplots and incorporated as a random intercept for the experimental design. We applied GAMMs using the 'gamm4' package (Wood and Scheipl, 2017). The test statistics for GAMMs were obtained from the 'itsadug' package (van Rij et al., 2017). In addition, we compared the results from GAMMs with linear mixed effects models (LMMs), in which we tested the treatment effects across time on soil biological activity using the package 'nlme' (Pinheiro et al., 2017). For LMMs, a random intercept with mainplots nested within sampling time points, nested within years was included in the models. We accounted for repeated measurements by including a compound symmetry covariance structure, which fitted the data better than a first–order autoregressive covariance structure based on the difference in their Akaike information criterion (AIC) value. Invertebrate feeding activity and microbial activity were log-transformed (log $(x + 1)$) to improve the fit of the model. The raw means and standard errors of both response variables are presented in Table 3.

The 'quantmod' package (Ryan et al., 2017) was used to identify the nearest peaks (using the 15 closest data points) in the time series data of soil invertebrate feeding activity under both ambient and future climate conditions.

Table 3 Mean values of soil invertebrate feeding activity and soil microbial activity. Shown are means of the non-transformed data ($\pm$ SE) for the different land-use types (extensive meadow, extensive pasture, and intensive meadow) under ambient and future climate conditions.

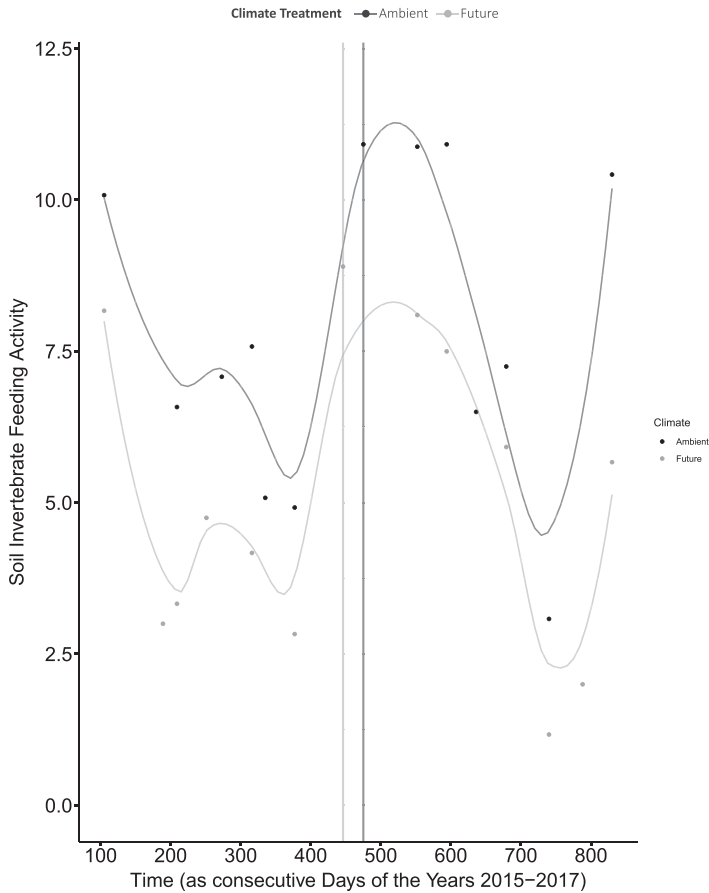|	Extensive meadow				Extensive pasture				Intensive meadow			
	Ambient		Future		Ambient		Future		Ambient		Future	
	mean	$\pm$SE	mean	$\pm$SE	mean	$\pm$SE	mean	$\pm$SE	mean	$\pm$SE	mean	$\pm$SE
Soil invertebrate feeding activity	2.51	0.20	1.69	0.13	2.61	0.16	1.59	0.13	1.10	0.10	0.89	0.09
Soil microbial activity	1.87	0.06	1.78	0.06	1.84	0.06	1.77	0.06	1.59	0.05	1.53	0.05

Fig. 4 Peak values of soil invertebrate feeding activity under ambient (dark grey) and future (light grey) climatic conditions within the entire measurement period. The nearest peaks were identified using the 15 closest data points. The grey shaded area represents the difference in days between the two highest peak values of invertebrate feeding activity for the two climate scenarios (29 days).

After the identification of all peaks in the time series (i.e. the local maxima after restricting the search to the nearest 15 data points for each climate condition), we calculated the day difference between the two highest peaks (among all the identified peaks, see Fig. 4) of invertebrate feeding activity for the two climate scenarios. Finally, LMMs (Pinheiro et al., 2017) were used to analyse the effects of climate, land use, season, and their interactions on potential explanatory
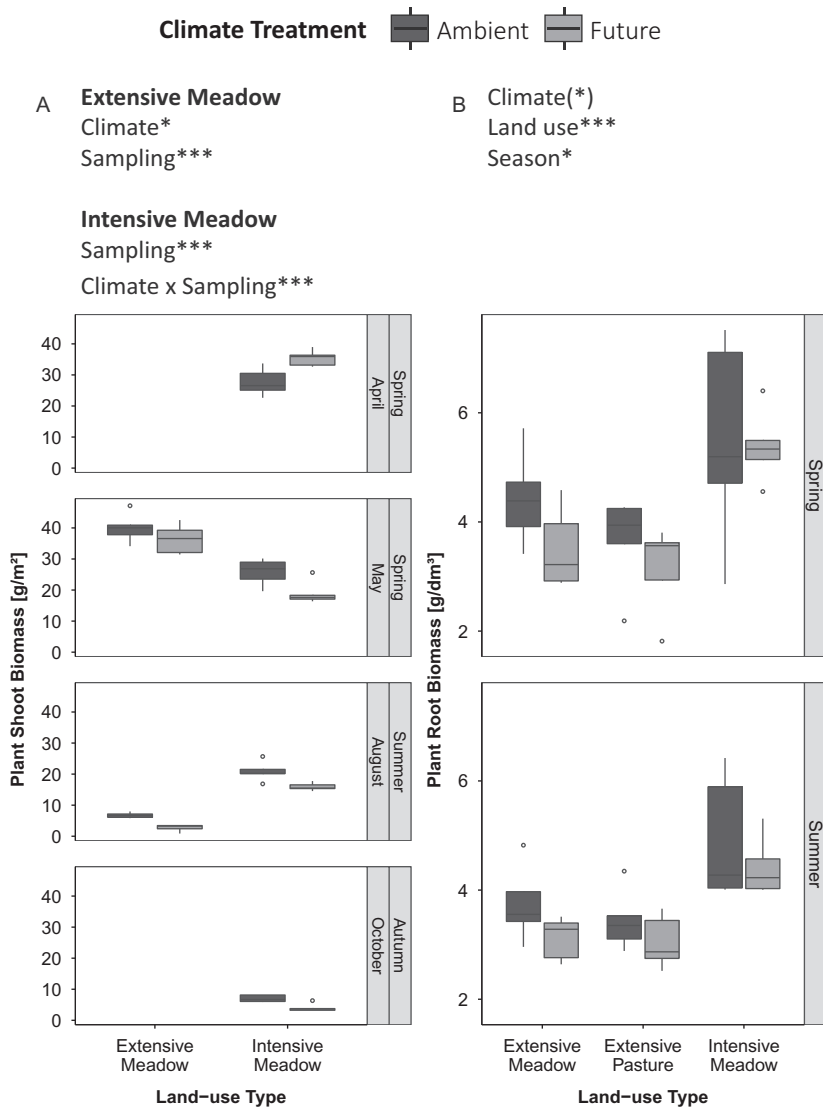
Climate Treatment ◼ Ambient ◼ Future

A **Extensive Meadow**
Climate*
Sampling***

B Climate(*)
Land use***
Season*

Intensive Meadow
Sampling***
Climate x Sampling***

Fig. 5 The effects of climate, land use, and season on plant shoot biomass, plant root biomass, soil microbial biomass, and soil water content. (A) Plant shoot biomass. Extensive meadow was mown two times (May and August); intensive meadow was mown four times (April, May, August, and October). Both land-use types were analysed separately. (B) Plant root biomass from 0 to 15 cm depth. Spring = April; summer = June. (C) Soil microbial biomass. Measured using substrate-induced respiration (Scheu, 1992). Spring = April; summer 1 = June; autumn = October. (D) Soil water content. Spring = April; summer = June; autumn = October. Data from 2016 were used. EM = extensive meadow; ES = extensive pasture; IG = intensive meadow. Dark grey = ambient climate; light grey = future climate. (*) $P < 0.1$; *$P < 0.05$; ***$P < 0.001$.

C Land use(*)
Season***

D Climate***
Land use***
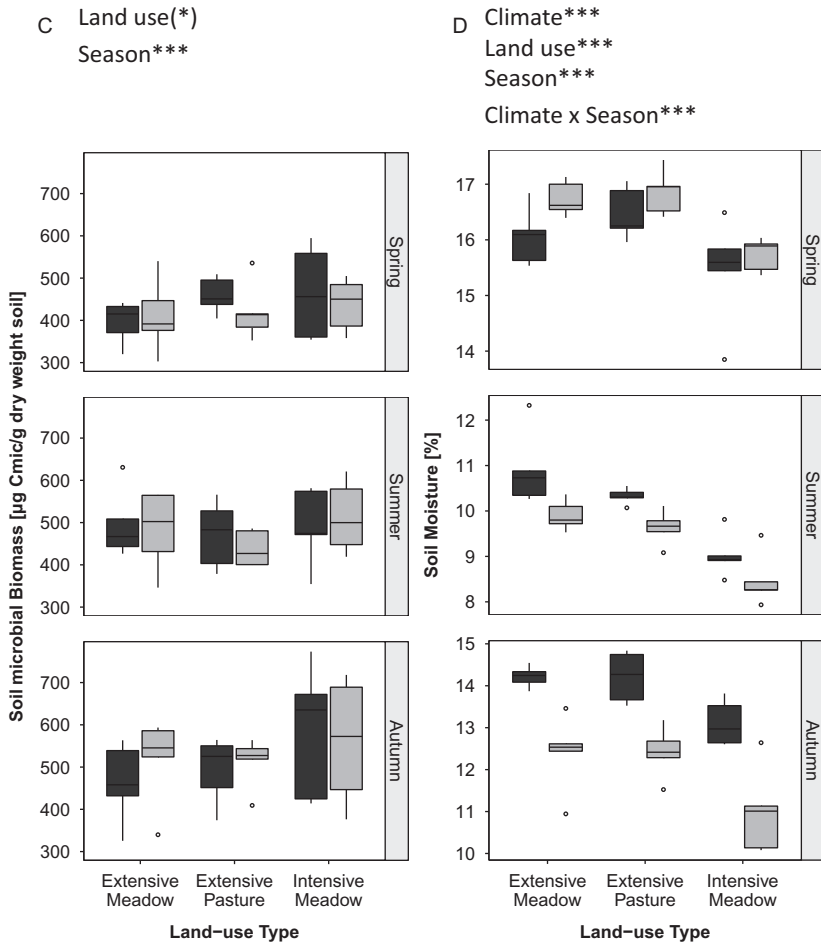Season***
Climate x Season***

Fig. 5—cont'd

variables (i.e. plant root biomass, microbial biomass, soil water content, soil fauna groups, pH, available C and N) using data available for spring, summer, and autumn 2016 (Figs 5–7). In the case of plant shoot biomass, the effects of climate and sampling were analysed separately for each land–use type because of the different mowing frequencies. A random intercept with plots nested within mainplots was included in the models. All statistical analyses were performed using the R statistical software version 3.5.1 (R Core Team, 2017).
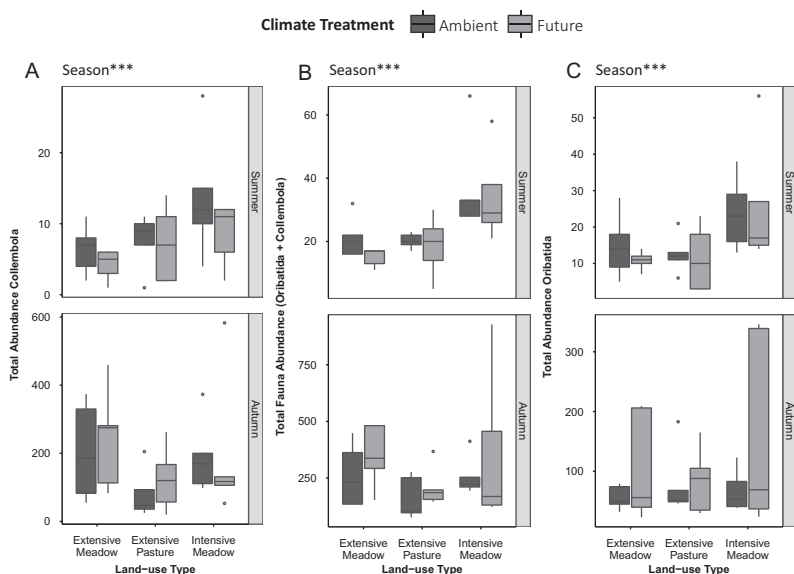
Fig. 6 The effects of climate, land use, and season on soil fauna groups. (A) Total fauna (Oribatida + Collembola). (B) Collembola. (C) Oribatida. Data from 2016 were used: summer = June; autumn = October. EM = extensive meadow; ES = extensive pasture; IG = intensive meadow. Dark grey = ambient climate; light grey = future climate. ***$P < 0.001$.

Fig. 7 The effects of climate, land use, and season on abiotic soil parameters. (A) pH-value. (B) Available carbon (hot-water extractable fraction). (C) Available nitrogen (hot water extractable fraction). Data from 2016 were used: spring = April; summer = June; autumn = October. EM = extensive meadow; ES = extensive pasture; IG = intensive meadow. Dark grey = ambient climate; light grey = future climate. ***$P < 0.001$.
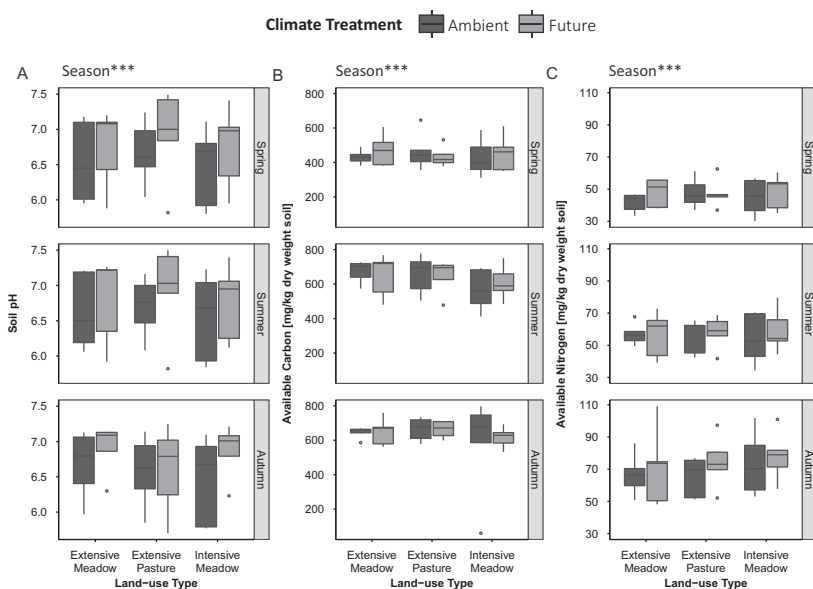
3. Results

3.1 Land use and climate change effects on soil biological activity

Overall, future climate conditions significantly reduced soil invertebrate feeding activity in both extensively-used grasslands, whereas the intensive meadow showed the lowest activity levels under both climate conditions without significant differences (Fig. 1B; Table 4). The strongest climate change–induced reduction was observed in the extensive pasture, the weakest reduction in the intensive meadow (Fig. 1C). Similarly, soil microbial activity was significantly reduced by future climate conditions across all grassland types, with significantly lower activity levels in intensive meadows than in the two extensively-used grasslands (Fig. 1D; Table 4). The strongest climate change–induced reduction was observed for the extensive meadow, the weakest reduction in the intensive meadow (Fig. 1E).

3.2 Interactive effects of climate, land use, and time on soil biological activity

We found a significant three-way interaction effect of time, climate, and land use on both soil invertebrate feeding activity and soil microbial activity (GAMM, Table 2). Future climate conditions decreased soil invertebrate feeding activity for most parts of the study period, except for spring 2016 (Fig. 8). However, changes of average levels of activity depended on the season though. Soil invertebrate feeding activity showed an earlier, but lower peak under future climate conditions in spring 2016. That is, the overall

Table 4 Results of linear mixed effects models (LMMs) for the effects of climate, land use, and their interaction on soil invertebrate feeding activity and soil microbial activity (both log-scaled) across all samplings. Mainplots nested within samplings nested within years served as a random intercept in the model. A compound symmetry covariance structure was used to account for repeated measurements. F-values are given with numerator and denominator degrees of freedom. Significant results are shown in bold.

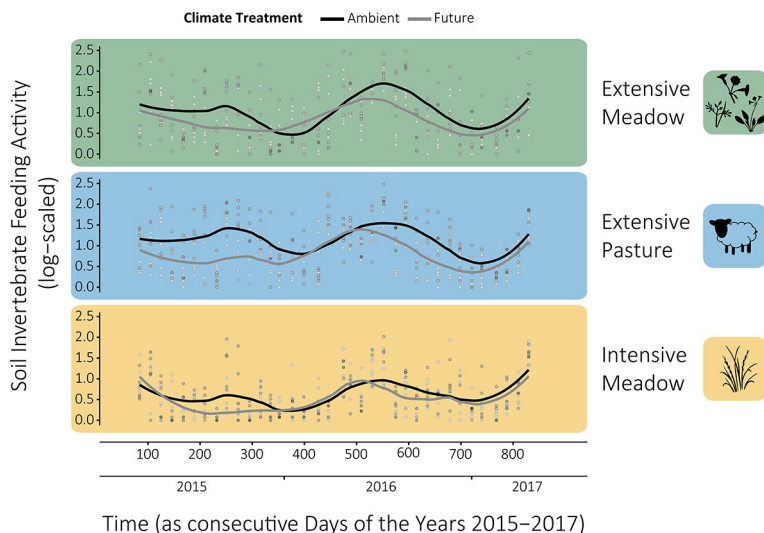|	Climate		Land use		Climate x Land use	
	F-value	P-value	F-value	P-value	F-value	P-value
Soil invertebrate feeding activity	50.61 (1, 323)	**<0.0001**	102.51 (2, 712)	**<0.0001**	6.47 (2, 712)	**0.0016**
Soil microbial activity	16.16 (1, 305)	**0.0001**	65.30 (2, 666)	**<0.0001**	0.11 (2, 666)	0.90

Fig. 8 Temporal patterns of the interactive effects of climate and land use on soil invertebrate feeding activity. The panels show the treatment effects over time, separated by the three land-use types (climate × land use × time: $F = 6.74$, $P \leq 0.0001$). The curves are based on the 'loess' smoothing function from the 'ggplot2' package in R with lambda = 0.4. For interpretation of the references to color, the reader is referred to the online version of this article. Black = ambient climate; grey = future climate. Green = extensive meadow (moderately mown); blue = extensive pasture (grazed by sheep); yellow = intensive meadow (frequently mown).

highest value of invertebrate feeding activity under future climate conditions was reached 29 days earlier than the overall highest value recorded under ambient climate conditions (Figs 4 and 8). Despite seasonal fluctuations, intensive meadows showed the lowest activity patterns under both climate conditions throughout the study period. With respect to the interactive effects of land use and climate, intensive meadows were less affected by climate change compared to the two extensively-used grassland types, which showed an equally strong decline (Fig. 8). Soil microbial activity showed similar, although weaker responses to the treatments (Fig. 9).

3.3 Responses of additional plant and soil variables

Future climate consistently reduced plant shoot biomass on the extensive meadow. The intensive meadow benefitted from future climate conditions in April, but shoot biomass was strongly reduced by the climate treatment on all other harvest dates in 2016 (Fig. 5A; Table 5). Plant root biomass was strongly affected by land use, showing the highest biomass under intensive
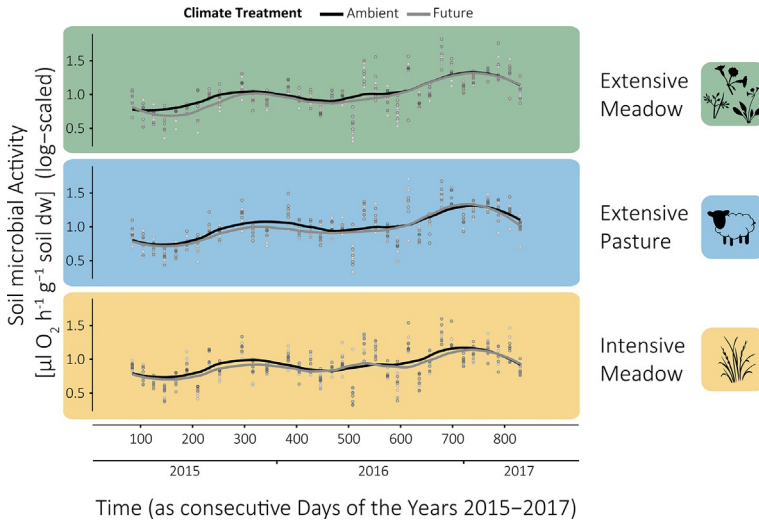
Fig. 9 Temporal patterns of the interactive effects of climate, land use, and time on soil microbial activity. The panels show the treatment effects over time, separated by the three land-use types (climate × land use × time: $F = 6.92$, $P \leq 0.0001$). The curves are based on the 'loess' smoothing function from the 'ggplot2' package in R with lambda = 0.4. For interpretation of the references to color, the reader is referred to the online version of this article. Black = ambient climate; grey = future climate. Green = extensive meadow (moderately mown); blue = extensive pasture (grazed by sheep); yellow = intensive meadow (frequently mown).

Table 5 Results of linear mixed effects models (LMMs) for the effects of climate, sampling, and their interaction on plant shoot biomass. Plots nested within mainplots served as a random intercept in the model. Each land-use type was analysed separately because of the different mowing frequencies (Extensive meadow: May and August 2016; Intensive meadow: April, May, August, October 2016). *F*-values are given with numerator and denominator degrees of freedom. Significant results are shown in bold.

	Climate		Sampling		Climate × Sampling	
	F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Extensive meadow	6.25 (1, 8)	**0.04**	476.39 (1, 8)	**<0.0001**	0.02 (1, 8)	0.89
Intensive meadow	2.42 (1, 8)	0.16	146.05 (3, 24)	**<0.0001**	13.23 (3, 24)	**<0.0001**

management. There was some evidence of an effect, at the 10% level of significance, of future climate on plant root biomass, especially leading to reduced biomass on the extensively-used grasslands (Fig. 5B; Table 6). Another trend was observed for land-use effects on soil microbial biomass,

Table 6 Results of linear mixed effects models (LMMs) for the effects of climate, land use, season, and their interactions on additional explanatory variables. Data from spring, summer, and autumn 2016 were included. Plots nested within mainplots served as a random intercept in the model. F-values are given with numerator and denominator degrees of freedom. Significant results are shown in bold.

	Climate		Land use		Season		Climate x Land use		Climate x Season		Land use x Season		Climate x Land use x Season	
	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
Plant root biomass [g/dm^3]	4.16 (1, 8)	0.08	18.04 (2, 16)	**0.0001**	5.23 (1, 24)	**0.03**	0.32 (2, 16)	0.73	0.0001 (1, 24)	0.99	0.70 (2, 24)	0.51	0.24 (2, 24)	0.79
Microbial biomass [μg Cmic/g dry weight soil]	0.0041 (1, 8)	0.95	3.13 (2, 16)	0.07	19.94 (2, 48)	**<0.0001**	0.42 (2, 16)	0.66	0.75 (2, 48)	0.48	1.76 (4, 48)	0.15	0.82 (4, 48)	0.52
Total abundance soil fauna	1.38 (1, 16)	0.26	1.88 (2, 16)	0.19	57.55 (1, 24)	**<0.0001**	0.06 (2, 16)	0.94	1.71 (1, 24)	0.20	1.45 (2, 24)	0.26	0.07 (2, 24)	0.93
Total abundance Collembola	0.27 (1, 16)	0.61	2.00 (2, 16)	0.17	42.46 (1, 24)	**<0.0001**	0.06 (2, 16)	0.94	0.40 (1, 24)	0.54	2.06 (2, 24)	0.15	0.04 (2, 24)	0.96
Total abundance Oribatida	2.47 (1, 16)	0.14	0.96 (2, 16)	0.40	23.59 (1, 24)	**0.0001**	0.73 (2, 16)	0.50	2.69 (1, 24)	0.11	0.21 (2, 24)	0.82	0.64 (2, 24)	0.54
Soil moisture [%]	33.53 (1, 8)	**0.0004**	41.96 (2, 16)	**<0.0001**	904.38 (2, 48)	**<0.0001**	0.05 (2, 16)	0.95	29.79 (2, 48)	**<0.0001**	1.48 (4, 48)	0.22	0.43 (4, 48)	0.79
Soil pH	0.40 (1, 8)	0.55	1.62 (2, 16)	0.23	16.69 (2, 43)	**<0.0001**	0.09 (2, 16)	0.91	0.93 (2, 43)	0.40	1.33 (4, 43)	0.28	0.16 (4, 43)	0.96
Available carbon [mg/kg dry weight soil]	0.03 (1, 8)	0.86	2.58 (2, 16)	0.11	69.66 (2, 48)	**<0.0001**	0.59 (2, 16)	0.57	0.07 (2, 48)	0.93	0.78 (4, 48)	0.54	0.30 (4, 48)	0.88
Available nitrogen [mg/kg dry weight soil]	0.27 (1, 8)	0.62	0.97 (2, 16)	0.40	129.87 (2, 48)	**<0.0001**	0.03 (2, 16)	0.97	0.83 (2, 48)	0.44	1.33 (4, 48)	0.27	0.87 (4, 48)	0.49

resulting in highest levels under intensive management, and soil microbial biomass varied significantly among seasons, with highest values in autumn and lowest values in spring (Fig. 5C; Table 6). Soil water content was higher on future climate plots in spring, but decreased substantially in summer and autumn. Furthermore, the intensive meadow had the lowest soil water content of all land-use types (Fig. 5D; Table 6). The densities of detritivores (collembolans and oribatid mites; Fig. 6, Table 6) as well as pH–value, available carbon, and available nitrogen (Fig. 7; Table 6) varied significantly among seasons, but were not significantly affected by the experimental treatments in 2016.

4. Discussion

The present study reveals that two key response variables for soil biological activity showed similar responses to climate change and land-use management, which are the two main global change drivers affecting terrestrial ecosystems (Sala et al., 2000). By covering a full two-year period, with continuous measurements across all seasons, we show that future climate conditions and intensive land use can be expected to significantly reduce soil biological activity with changing magnitudes across time. Extensive-land use sustained high levels of soil biological activity, but contrary to our expectations and general assumptions, did not alleviate the detrimental effects of climate change. Instead, the decrease in soil biological activity under future climate conditions was most pronounced under extensive management.

Overall, our results show that climate change, simulated by a combination of $\sim0.6\,^\circ\text{C}$ warming and shifts in precipitation patterns across the growing season, consistently reduced soil biological activity throughout the study period, while the magnitude of this reduction depended on the season. This was likely caused by a significantly lower soil water content under the future climate scenario (Fig. 5D), in line with the general expectation that a concurrence of warming and reduced summer rainfall has detrimental effects on soil biological activity (Allison and Treseder, 2008; Davidson and Janssens, 2006; Thakur et al., 2018). We found that the detrimental effects of summer drought exceeded those of elevated precipitation in spring and autumn.

There are potentially a number of explanations for the lower level of invertebrate feeding activity in response to the climate treatment. First, many soil organisms live in a pore system with extensive surfaces of water films and are depending on a water-saturated atmosphere, which might be scarce under future climate conditions (Coleman et al., 2004; Verhoef and Brussaard, 1990).

Second, mobile soil organisms may move to more favourable habitats, e.g., to deeper soil layers (Briones et al., 2007), therefore not contributing to bait perforation within the upper 15 cm that we sampled with our methods. Third, there might be indirect climate effects on soil organisms via altered substrate characteristics, as dry soil is more difficult to ingest and to digest for soil invertebrates (Thakur et al., 2018). The latter explanation may be further exacerbated by the increased metabolic demands of soil organisms under warmed conditions (Brown et al., 2004), which put additional pressure on foraging success under already detrimental conditions (Thakur et al., 2018).

Surprisingly, we did not find higher soil biological activity levels in spring and autumn under future climate conditions, which were expected based on increased precipitation during these seasons. Substantially higher percentages of bare soil cover on future climate plots (Fig. 10) and lower plant shoot and root biomass (Fig. 5A and B) may explain these results. Bare soil is known to strongly reduce bacterial and fungal decomposition rates as well as soil enzyme activities, which may lead to bottom–up–induced changes at higher trophic levels, highlighting the importance of vegetation cover for soil biological activity (Birkhofer et al., 2011; Moreno et al., 2009; Sánchez–Moreno et al., 2015). Summer drought–induced reductions in vegetation cover are unlikely to be compensated by elevated growth in other seasons (Fig. 5A); thus, soil biological activity on future climate plots may still be restrained during more favourable (wet) conditions in spring and autumn. This finding suggests that shifts in precipitation patterns can impair crucial ecosystem functions without any significant net changes in annual precipitation amounts.

In March 2016, we detected a shift towards earlier, and lower peaks in invertebrate feeding activity under future climate conditions (29 days; Figs 4 and 8), indicating a potential shift in the phenology of soil biological activity. This phenological shift may be a direct response to altered soil moisture and temperature and/or indirectly mediated via changes in plant phenology in response to the climate treatment (Eisenhauer et al., 2018). As the timing of plant inputs to the soil advances earlier in the growing season under climate change (Delbart et al., 2008; Menzel and Fabian, 1999; Nord and Lynch, 2009), decomposers are forced to synchronize with plants to optimize resource consumption. This is also supported by higher plant shoot biomass on intensive meadows under future climate in spring 2016 (Fig. 5A), which may be a consequence of accelerated plant growth early in the year. Shifts in soil biological activity may also induce alterations in nutrient cycling by changing the time at which nutrients are made available
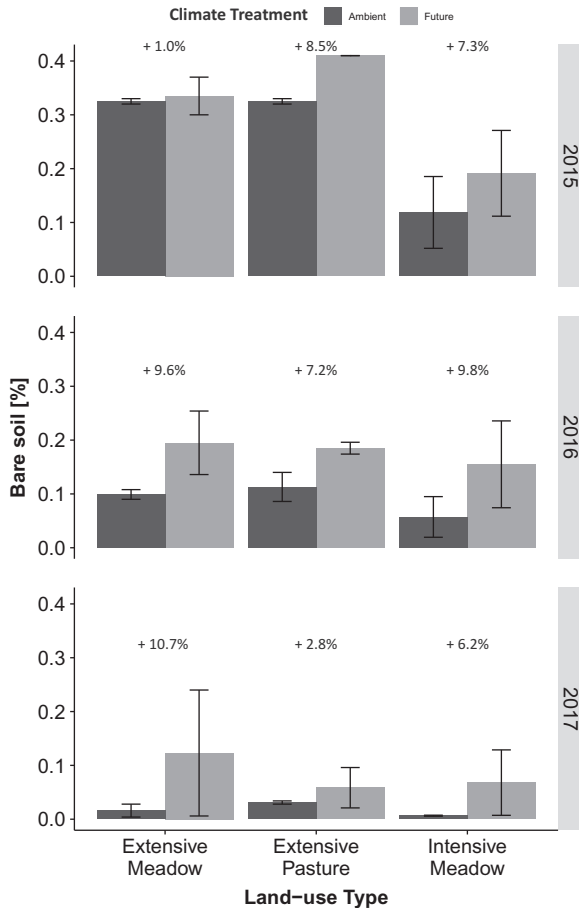
Fig. 10 Percentage bare soil cover. All panels show ambient and future climatic conditions for each year in which the study took place. Dark grey = ambient climate; light grey = future climate. Percentages above the bar plots indicate the increase in bare soil under future climatic conditions compared to ambient climatic conditions. Error bars ±SE.

for plants (Bardgett and Wardle, 2010). Where certain groups of organisms follow this climate-induced shift in phenology and others do not, this effect could potentially lead to temporal mismatches between above- and below-ground components of the community that affect ecosystem functioning (Eisenhauer et al., 2018) and may even lead to changes in community composition and species extinctions (Durant et al., 2007; Thackeray et al., 2016). Temporal mismatches might alter interactions among trophic groups, such

as predator-prey relationships, whose synchrony is crucial for natural pest control in agricultural systems (Durant et al., 2007; Thomson et al., 2010). We did, however, not detect any significant changes in detritivore densities in response to the climate and land-use treatments, which may have been due to the snap-shot nature of these assessments. Nevertheless, our study provides compelling evidence for climate change-induced shifts in the phenology of soil biological activity, mainly for soil invertebrate activity patterns. We encourage future studies to investigate the causes and consequences of phenological shifts below-ground for terrestrial ecosystem functioning, which has rarely been considered compared to phenological shifts in above-ground taxa (Eisenhauer et al., 2018).

Extensive management is known to facilitate the abundance and diversity of a wide range of organisms above and below the ground (Bengtsson et al., 2005). This was for example shown for soil organisms, as enhanced microbial activity and diversity of arbuscular-mycorrhizal fungi (França et al., 2007) or higher densities of invertebrate predators (Birkhofer et al., 2008) and carabid beetles (Döring and Kromp, 2003). In the case of grasslands, these positive effects can be connected to higher plant species richness, typically realised in conditions of extensive management that promote soil organisms and processes (Balvanera et al., 2006; Eisenhauer et al., 2013; Lange et al., 2015). Land-use intensification, on the other hand, has been found to have negative effects on soil fauna (Birkhofer et al., 2012; Decaëns and Jiménez, 2002) by reducing taxonomic richness, subsequently leading to less complex and functionally depauperate soil communities (Tsiafouli et al., 2015). Indeed, our results confirm that intensive land use led to the lowest activity levels throughout the study period. Our study also shows that extensive management supported higher absolute levels of soil biological activity than intensive management under both climate scenarios, but with no effect of extensive mowing and sheep grazing. This would support the value of extensive grassland management for enhancing soil biological activity.

It is assumed that extensive management, with higher plant species richness, lower disturbance and reduced tillage, leads to more resilient systems that have the potential to mitigate climate change effects and assure sustainable agricultural productivity (Isbell et al., 2017). Despite the beneficial net effect of extensive management described above, our study revealed that, contrary to our expectations, the extensively-managed systems experienced the greatest losses in soil biological activity. Extensively managed systems had reduced functions under future climate conditions, particularly for soil

invertebrate feeding activity. Activity levels in extensive grasslands thus seemed more vulnerable to climate change than in intensive grasslands. These results contradict a large body of literature reporting buffering effects of high-biodiversity systems under environmental stress (Isbell et al., 2015). However, it should also be noted that extensive grasslands showed high soil biological activity under ambient climate conditions, which means that they may have responded more to the climate treatment, because they have 'more to lose' (Pfisterer and Schmid, 2002; Wright et al., 2015).

There is broad evidence that systems with higher plant diversity are better capable of resisting environmental disturbances, e.g., based on their greater range of (asynchronous) responses (Craven et al., 2018; Hector et al., 2010; Mazancourt et al., 2013) and the higher probability of containing tolerant species able to access limited resources (Mueller et al., 2013), thus facilitating the reliable provisioning of ecosystem functions under environmental change (Hautier et al., 2015; Keith et al., 2008; Milcu et al., 2010). However, we could not confirm such plant diversity- and/or management-mediated resilience effects on soil biological activity in our two-year study, in which climate change as well as land use were simulated in realistic scenarios. Despite the evidence of alterations in soil biological activities in our two-year study, it is still difficult to predict how much time those impaired functions may need to recover to pre-treatment levels in the different land-use types. For drawing such conclusions, long-term monitoring of soil biological activities after the cessation of treatments would be required.

What makes our findings particularly interesting is that they are derived from an experimental framework with rather conservative assumptions. First, the climate treatment applied in this GCEF experiment was moderate, at less than +1 °C, when compared to most climate warming experiments and the stated aim of the Paris Agreement to limit temperature rise to below 2 °C in order to avoid the most detrimental climate change effects (Paris Agreement, 2015). Second, the experiment was situated on chernozem soil, which is highly fertile and has a higher water-holding capacity than many other soil types that might be more susceptible to environmental stress (Altermann et al., 2005). Accordingly, future studies should investigate the context-dependency of climate change effects on soil communities and functions. For instance, globally coordinated networks of experiments, such as Drought-Net (Knapp et al., 2017), provide the ideal set-up to explore climate change effects across different climates and soils.

Our results would suggest that the high levels of soil biological activity in extensively-used grasslands are driven by organisms that are particularly

vulnerable to environmental stress and whose function provisioning cannot be solely preserved via increases in or the maintenance of plant diversity. In intensive meadows, by contrast, activity levels are presumably driven by a soil community already adapted to disturbances and therefore only little affected by climate change. However, even in non-changed conditions, these intensive meadows reflect the low biological activity level of an already functionally deteriorated ecosystem. As Tsiafouli et al. (2015) demonstrated, intensive management results in a dramatic reduction in soil functioning, including nutrient cycling, decomposition, and natural pest control. This would make the case for adopting practices that promote highly diverse systems, even if they appear to be less resilient to environmental stress (Pfisterer and Schmid, 2002, Wright et al., 2015).

We would argue that new management approaches, besides simply increasing plant diversity, are needed to complement the beneficial effects of extensive management. This could include the selection of specific plant species compositions that are more resistant to drought periods and other climate extremes (Madani et al., 2018). In this vein, related ideas like engineered plant communities (Storkey et al., 2015) or targeted diversified agroecosystems (Isbell et al., 2017) are promising future applied research directions to balance productivity and stability of ecosystem functioning above- and below-ground. Both are based on the notion that a stable provisioning of agroecosystem services (e.g. food production, soil fertility, and pest control) can best if not only be achieved if we foster functionally diverse communities with contrasting traits, e.g., regarding phenology or growth type (Storkey et al., 2015). By implementing diversification strategies, such as increased genetic diversity or crop rotations in agroecosystems, we might be able to overcome declining yields that are predicted for monocultures within the next decades (Isbell et al., 2017). Moreover, such combined approaches might be key to secure ecosystem functioning and food provisioning in the future by supporting systems that hold a vital level of below-ground functionality.

5. Conclusions and outlook

We conclude that climate change consistently reduced soil biological activity throughout the year, without any detectable compensation among seasons. Furthermore, future climate conditions may lead to significant phenological shifts in soil organisms that may cause as yet unexplored community changes and potential mismatches of above- and below-ground

interactions (Eisenhauer et al., 2018). Our findings call for future research on the potential context-dependencies of climate-change effects on soil organisms and functions, such as by employing globally distributed experiments covering different environmental conditions (Knapp et al., 2017). Moreover, in the present study soil animal activity showed more pronounced responses to the climate change treatment than our soil microbial activity measurement. Although the applied methods are not straightforward to compare, varying vulnerabilities of different groups of soil organisms should be explored in future studies (George et al., 2019; Siebert et al., 2019).

Our work would corroborate the expectation that extensive management can support higher levels of soil biological activity and related functions than intensive management practices. However, current extensive management practice, as tested here, may not be sufficient to alleviate predicted climate change effects and therefore needs to be complemented by other approaches. We encourage future research to investigate new avenues, such as the use of targeted plant species compositions, to maintain high levels of soil biological activity in agricultural landscapes in a changing world.

Acknowledgements

Author contributions

M.S. and T.R. are part of the GCEF steering committee that developed the experimental platform. N.E. conceived the study on soil microbial and invertebrate activity. J.S. and T.R. collected the data. J.S. and M.P.T. analysed the data. J.S. wrote the manuscript with contributions from all authors.

Competing interests

The authors declare no competing interests.

References

A'Bear, A.D., Boddy, L., Hefin Jones, T., 2012. Impacts of elevated temperature on the growth and functioning of decomposer fungi are influenced by grazing collembola. Glob. Chang. Biol. 18, 1823–1832.

Allison, S.D., Treseder, K.K., 2008. Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. Glob. Chang. Biol. 14, 2898–2909.

Altermann, M., Rinklebe, J., Merbach, I., Körschens, M., Langer, U., Hofmann, B., 2005. Chernozem—soil of the year 2005. J. Plant Nutr. Soil Sci. 168, 725–740.

Bakonyi, G., Nagy, P., Kovacs-Lang, E., Kovacs, E., Barabás, S., Répási, V., Seres, A., 2007. Soil nematode community structure as affected by temperature and moisture in a temperate semiarid shrubland. Appl. Soil Ecol. 37, 31–40.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol. Lett. 9, 1146–1156.

Bardgett, R.D., Van Der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. Nature 515, 505–511.

Bardgett, R.D., Wardle, D.A., 2010. Aboveground-Belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change. Oxford University Press Oxford.

Beier, C., Emmett, B., Gundersen, P., Tietema, A., Penuelas, J., Estiarte, M., Gordon, C., Gorissen, A., Llorens, L., Roda, F., 2004. Novel approaches to study climate change effects on terrestrial ecosystems in the field: drought and passive nighttime warming. Ecosystems 7, 583–597.

Bengtsson, J., Ahnström, J., Weibull, A.C., 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. J. Appl. Ecol. 42, 261–269.

Birkhofer, K., Bezemer, T.M., Bloem, J., Bonkowski, M., Christensen, S., Dubois, D., Ekelund, F., Fließbach, A., Gunst, L., Hedlund, K., 2008. Long-term organic farming fosters below and aboveground biota: implications for soil quality, biological control and productivity. Soil Biol. Biochem. 40, 2297–2308.

Birkhofer, K., Diekötter, T., Boch, S., Fischer, M., Müller, J., Socher, S., Wolters, V., 2011. Soil fauna feeding activity in temperate grassland soils increases with legume and grass species richness. Soil Biol. Biochem. 43, 2200–2207.

Birkhofer, K., Bezemer, T.M., Hedlund, K., Setälä, H., 2012. Community composition of soil organisms under different wheat farming systems. In: Cheeke, T.E., Coleman, D.C., Wall, D.H. (Eds.), Microbial Ecology in Sustainable Agroecosystems. Crc Press Taylor & Francis Group, Boca Raton.

Blankinship, J.C., Niklaus, P.A., Hungate, B.A., 2011. A meta-analysis of responses of soil biota to global change. Oecologia 165, 553–565.

Briones, M.J.I., Ineson, P., Heinemeyer, A., 2007. Predicting potential impacts of climate change on the geographical distribution of enchytraeids: a meta-analysis approach. Glob. Chang. Biol. 13, 2252–2269.

Briones, M.J.I., Ostle, N.J., McNamara, N.P., Poskitt, J., 2009. Functional shifts of grassland soil communities in response to soil warming. Soil Biol. Biochem. 41, 315–322.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Butenschoen, O., Scheu, S., Eisenhauer, N., 2011. Interactive effects of warming, soil humidity and plant diversity on litter decomposition and microbial activity. Soil Biol. Biochem. 43, 1902–1907.

Cohen, J.M., Lajeunesse, M.J., Rohr, J.R., 2018. A global synthesis of animal phenological responses to climate change. Nat Climate Change 8, 224–228.

Coleman, D.C., Crossley Jr., D.A., Hendrix, P.F., 2004. Fundamentals of Soil Ecology. Academic press.

Conant, R.T., Ryan, M.G., Ågren, G.I., Birge, H.E., Davidson, E.A., Eliasson, P.E., Evans, S.E., Frey, S.D., Giardina, C.P., Hopkins, F.M., 2011. Temperature and soil organic matter decomposition rates–synthesis of current knowledge and a way forward. Glob. Chang. Biol. 17, 3392–3404.

Craven, D., Eisenhauer, N., Pearse, W.D., Hautier, Y., Roscher, C., Boenisch, A.H., Kattge, J., Kreyling, J., Lanta, V., Enrica De Luca, H.W., 2018. Multiple facets of biodiversity drive the diversity-stability relationship. Nat. Ecol. Evol. 2, 1579–1587.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

De Vries, F.T., Liiri, M.E., Bjørnlund, L., Bowker, M.A., Christensen, S., Setälä, H.M., Bardgett, R.D., 2012. Land use alters the resistance and resilience of soil food webs to drought. Nat. Clim. Chang. 2, 276–280.

Decaëns, T., Jiménez, J., 2002. Earthworm communities under an agricultural intensification gradient in Colombia. Plant Soil 240, 133–143.

Delbart, N., Picard, G., Le Toan, T., Kergoat, L., Quegan, S., Woodward, I., Dye, D., Fedotova, V., 2008. Spring phenology in boreal Eurasia over a nearly century time scale. Glob. Chang. Biol. 14, 603–614.

Döring, T.F., Kromp, B., 2003. Which carabid species benefit from organic agriculture?—a review of comparative studies in winter cereals from Germany and Switzerland. Agric. Ecosyst. Environ. 98, 153–161.

Doscher, R., Willén, U., Jones, C., Rutgersson, A., Meier, H.M., Hansson, U., Graham, L.P., 2002. The development of the regional coupled ocean-atmosphere model Rcao. Boreal Environ. Res. 7, 183–192.

Dukes, J.S., Chiariello, N.R., Cleland, E.E., Moore, L.A., Shaw, M.R., Thayer, S., Tobeck, T., Mooney, H.A., Field, C.B., 2005. Responses of grassland production to single and multiple global environmental changes. PLoS Biol. 3 e319.

Durant, J.M., Hjermann, D.Ø., Ottersen, G., Stenseth, N.C., 2007. Climate and the match or mismatch between predator requirements and resource availability. Climate Res. 33, 271–283.

Eisenhauer, N., Dobies, T., Cesarz, S., Hobbie, S.E., Meyer, R.J., Worm, K., Reich, P.B., 2013. Plant diversity effects on soil food webs are stronger than those of elevated CO_2 and N deposition in a long-term grassland experiment. Proc. Natl. Acad. Sci. 110 (17), 6889–6894.

Eisenhauer, N., Herrmann, S., Hines, J., Buscot, F., Siebert, J., Thakur, M.P., 2018. The dark side of animal phenology. Trends Ecol. Evol. 33 (12), 898–901.

Fierer, N., Craine, J.M., Mclauchlan, K., Schimel, J.P., 2005. Litter quality and the temperature sensitivity of decomposition. Ecology 86, 320–326.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., 2005. Global consequences of land use. Science 309, 570–574.

França, S.C., Gomes-Da-Costa, S.M., Silveira, A.P., 2007. Microbial activity and arbuscular mycorrhizal fungal diversity in conventional and organic citrus orchards. Biol. Agric. Hortic. 25, 91–102.

Gardi, C., Montanarella, L., Arrouays, D., Bispo, A., Lemanceau, P., Jolivet, C., Mulder, C., Ranjard, L., Römbke, J., Rutgers, M., 2009. Soil biodiversity monitoring in Europe: ongoing activities and challenges. Eur. J. Soil Sci. 60, 807–819.

George, P.B., Lallias, D., Creer, S., Seaton, F.M., Kenny, J.G., Eccles, R.M., Griffiths, R.I., Lebron, I., Emmett, B.A., Robinson, D.A., 2019. Divergent national-scale trends of microbial and animal biodiversity revealed across diverse temperate soil ecosystems. Nat. Commun. 10, 1107.

Giller, K., Beare, M., Lavelle, P., Izac, A.-M., Swift, M., 1997. Agricultural intensification, soil biodiversity and agroecosystem function. Appl. Soil Ecol. 6, 3–16.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of size and temperature on metabolic rate. Science 293, 2248–2251.

Goldenberg, S.U., Nagelkerken, I., Marangon, E., Bonnet, A., Ferreira, C.M., Connell, S.D., 2018. Ecological complexity buffers the impacts of future climate on marine consumers. Nat. Clim. Change 8, 229–233.

Hamel, C., Schellenberg, M.P., Hanson, K., Wang, H., 2007. Evaluation of the "bait-lamina test" to assess soil microfauna feeding activity in mixed grassland. Appl. Soil Ecol. 36, 199–204.

Harding, D., Stuttard, R., 1974. Microarthropods. In: Dickinson, C.H., Pugh, G.J.F. (Eds.), Biology of Plant Litter Decomposition. Academic Press, pp. 489–532.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T., Reich, P.B., 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. Science 348, 336–340.

Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenzen, M., Spehn, E.M., Bazeley-White, E., Weilenmann, M., 2010. General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. Ecology 91, 2213–2220.

Ingram, J., Gregory, P., Izac, A.-M., 2008. The role of agronomic research in climate change and food security policy. Agr Ecosyst Environ 126, 4–12.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T.M., Bonin, C., Bruelheide, H., De Luca, E., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526, 574–577.

Isbell, F., Adler, P.R., Eisenhauer, N., Fornara, D., Kimmel, K., Kremen, C., Letourneau, D.K., Liebman, M., Polley, H.W., Quijas, S., Scherer-Lorenzen, M., 2017. Benefits of increasing plant diversity in sustainable agroecosystems. J. Ecol. 105, 871–879.

Jacob, D., Podzun, R., 1997. Sensitivity studies with the regional climate model REMO. Meteorol. Atmos. Phys. 63, 119–129.

Keith, A.M., Van Der Wal, R., Brooker, R.W., Osler, G.H., Chapman, S.J., Burslem, D.F., Elston, D.A., 2008. Increasing litter species richness reduces variability in a terrestrial decomposer system. Ecology 89, 2657–2664.

Kerr, R.A., 2007. Global warming is changing the world. Science 316, 188–190.

Knapp, A.K., Avolio, M.L., Beier, C., Carroll, C.J., Collins, S.L., Dukes, J.S., Fraser, L.H., Griffin-Nolan, R.J., Hoover, D.L., Jentsch, A., 2017. Pushing precipitation to the extremes in distributed experiments: recommendations for simulating wet and dry years. Glob. Chang. Biol. 23, 1774–1782.

Kratz, W., 1998. The bait-lamina test. Environ. Sci. Pollut. Res. 5, 94–96.

Lange, M., Eisenhauer, N., Sierra, C.A., Bessler, H., Engels, C., Griffiths, R.I., Mellado-Vázquez, P.G., Malik, A.A., Roy, J., Scheu, S., 2015. Plant diversity increases soil microbial activity and soil carbon storage. Nat. Commun. 6, 6707.

Loreau, M., Mouquet, N., Gonzalez, A., 2003. Biodiversity as spatial insurance in heterogeneous landscapes. Proc. Natl. Acad. Sci. 100, 12765–12770.

Macfadyen, A., 1961. Improved funnel-type extractors for soil arthropods. J. Anim. Ecol. 30, 171–184.

Madani, N., Kimball, J.S., Ballantyne, A.P., Affleck, D.L., Bodegom, P.M., Reich, P.B., Kattge, J., Sala, A., Nazeri, M., Jones, M.O., 2018. Future global productivity will be affected by plant trait response to climate. Sci. Rep. 8, 2870.

Manzoni, S., Schimel, J.P., Porporato, A., 2012. Responses of soil microbial communities to water stress: results from a meta-analysis. Ecology 93, 930–938.

Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., Luca, E., Grace, J.B., Haegeman, B., Wayne Polley, H., Roscher, C., Schmid, B., 2013. Predicting ecosystem stability from community composition and biodiversity. Ecol. Lett. 16, 617–625.

Meinke, I., Gerstner, E., von Storch, H., Marx, A., Schipper, H., Kottmeier, C., Treffeisen, R., Lemke, P., 2010. Regionaler klimaatlas deutschland der Helmholtz-Gemeinschaft informiert im Internet über möglichen künftigen Klimawandel. Mitt. DMG 2, 5–7.

Melillo, J., Steudler, P., Aber, J., Newkirk, K., Lux, H., Bowles, F., Catricala, C., Magill, A., Ahrens, T., Morrisseau, S., 2002. Soil warming and carbon-cycle feedbacks to the climate system. Science 298, 2173–2176.

Menzel, A., Fabian, P., 1999. Growing season extended in Europe. Nature 397, 659.

Milcu, A., Thebault, E., Scheu, S., Eisenhauer, N., 2010. Plant diversity enhances the reliability of belowground processes. Soil Biol. Biochem. 42, 2102–2110.

Moreno, B., Garcia-Rodriguez, S., Cañizares, R., Castro, J., Benítez, E., 2009. Rainfed olive farming in South-Eastern Spain: long-term effect of soil management on biological indicators of soil quality. Agric. Ecosyst. Environ.rgg 131, 333–339.

Mueller, K.E., Tilman, D., Fornara, D.A., Hobbie, S.E., 2013. Root depth distribution and the diversity–productivity relationship in a long-term grassland experiment. Ecology 94, 787–793.

Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50.

Nord, E.A., Lynch, J.P., 2009. Plant phenology: a critical controller of soil resource acquisition. J. Exp. Bot. 60, 1927–1937.

Paris Agreement, 2015. United Nations Framework Convention on Climate Change. Paris, France.

Peñuelas, J., Filella, I., 2009. Phenology feedbacks on climate change. Science 324, 887–888.

Pfisterer, A.B., Schmid, B., 2002. Diversity-dependent production can decrease the stability of ecosystem functioning. Nature 416, 84.

Pinheiro J., Bates D., DebRoy S., Sarkar D., R Core Team (2017). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-128

R Core Team, R. C. T, 2017. R: A Language and Environment for Statistical Computing. Vienna, Austria; 2014.

Rockel, B., Will, A., Hense, A., 2008. The regional climate model COSMO-CLM (CCLM). Meteorol. Z. 17, 347–348.

Rożen, A., Sobczyk, Ł., Liszka, K., Weiner, J., 2010. Soil faunal activity as measured by the bait-lamina test in monocultures of 14 tree species in the Siemianice common-garden experiment, Poland. Appl. Soil Ecol. 45, 160–167.

Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J., Gurevitch, J., 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562.

Ryan, J.A., Ulrich, J.M., Thielen, W., Teetor, P., Ulrich, M.J.M., 2017. Package 'quantmod'.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Sánchez-Moreno, S., Castro, J., Alonso-Prados, E., Alonso-Prados, J.L., García-Baudín, J.M., Talavera, M., Durán-Zuazo, V.H., 2015. Tillage and herbicide decrease soil biodiversity in olive orchards. Agron. Sustain. Dev. 35, 691–700.

Schädler, M., Buscot, F., Klotz, S., Reitz, T., Durka, W., Bumberger, J., Merbach, I., Michalski, S.G., Kirsch, K., Remmler, P., Schulz, E., Auge, H., 2019. Investigating the Consequences of Climate Change under Different Land-Use Regimes—A Novel Experimental Infrastructure. Ecosphere 10 (3), e02635.

Scheu, S., 1992. Automated measurement of the respiratory response of soil micro-compartments: active microbial biomass in earthworm faeces. Soil Biol. Biochem. 24, 1113–1118.

Schulz, E., 2002. Influence of extreme management on decomposable soil organic matter pool. Arch. Agron. Soil Sci. 48, 101–105.

Siebert, J., Suennemann, M., Auge, H., Berger, S., Cesarz, S., Ciobanu, M., Guerrero-Ramirez, N.R., Eisenhauer, N., 2018. The effects of drought and nutrient addition on soil organisms vary across taxonomic groups, but are constant across seasons. Sci. Rep. 9 (1), 639.

Simpson, J.E., Slade, E., Riutta, T., Taylor, M.E., 2012. Factors affecting soil fauna feeding activity in a fragmented lowland temperate deciduous woodland. PLoS One 7, e29616.

Storkey, J., Döring, T., Baddeley, J., Collins, R., Roderick, S., Jones, H., Watson, C., 2015. Engineering a plant community to deliver multiple ecosystem services. Ecol. Appl. 25, 1034–1043.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. Univ of California Press.

Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., Helaouet, P., Johns, D.G., Jones, I.D., Leech, D.I., 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature 535, 241.

Thakur, M.P., Reich, P.B., Hobbie, S.E., Stefanski, A., Rich, R., Rice, K.E., Eddy, W.C., Eisenhauer, N., 2018. Reduced feeding activity of soil detritivores under warmer and drier conditions. Nat. Clim. Change 8, 75–78.

Thomson, L.J., Macfadyen, S., Hoffmann, A.A., 2010. Predicting the effects of climate change on natural enemies of agricultural pests. Biol. Control 52, 296–306.

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S., 2002. Agricultural sustainability and intensive production practices. Nature 418, 671–677.

Treseder, K.K., 2008. Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. Ecol. Lett. 11, 1111–1120.

Tsiafouli, M.A., Thébault, E., Sgardelis, S.P., Ruiter, P.C., Putten, W.H., Birkhofer, K., Hemerik, L., Vries, F.T., Bardgett, R.D., Brady, M.V., 2015. Intensive agriculture reduces soil biodiversity across Europe. Glob. Chang. Biol. 21, 973–985.

van Rij, J., Wieling, M., Baayen, R., van Rijn, H., 2017. itsadug: Interpreting Time Series and Autocorrelated Data Using GAMMs. R package version 2.3.

Verhoef, H., Brussaard, L., 1990. Decomposition and nitrogen mineralization in natural and agroecosystems: the contribution of soil animals. Biogeochemistry 11, 175–211.

Vitousek, P.M., 1994. Beyond global warming: ecology and global change. Ecology 75, 1861–1876.

Walter, J., Hein, R., Beierkuhnlein, C., Hammerl, V., Jentsch, A., Schädler, M., Schuerings, J., Kreyling, J., 2013. Combined effects of multifactor climate change and land-use on decomposition in temperate grassland. Soil Biol. Biochem. 60, 10–18.

Wardle, D., Bonner, K., Barker, G., 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. Funct. Ecol. 16, 585–595.

Wood, S., Scheipl, F., 2017. gamm4: Generalized Additive Mixed Models using 'mgcv' and 'lme4'. R package version 0.2-5.

Wright, A.J., Ebeling, A., De Kroon, H., Roscher, C., Weigelt, A., Buchmann, N., Buchmann, T., Fischer, C., Hacker, N., Hildebrandt, A., 2015. Flooding disturbances increase resource availability and productivity but reduce stability in diverse plant communities. Nat. Commun. 6, 6092.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc. Natl. Acad. Sci. 96, 1463–1468.