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Land-use intensification reduces soil macrofauna biomass at the community but not individual level
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Title: Land-use intensification reduces soil macrofauna biomass at the community but not individual level

Author names: Rui Yin[1,2,3,*] (rui.yin@ufz.de), Paul Kardol[4] (Paul.Kardol@slu.se), Nico Eisenhauer[2,3] (nico.eisenhauer@idiv.de), Martin Schädler[1,2] (martin.schaedler@ufz.de)

Affiliations:

[1]Helmholtz-Centre for Environmental Research-UFZ, Department of Community Ecology, Theodor-Lieder-Strasse 4, 06110 Halle (Saale), Germany

[2]German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Puschstrasse 4, 04103 Leipzig, Germany

[3]Institute for Biology, Leipzig University, Puschstrasse 4, 04103 Leipzig, Germany

[4]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, 901-83, Umeå, Sweden

[*]Corresponding author: Rui Yin, email: rui.yin@ufz.de

Abstract

Land-use intensification and climate change are main threats to the abundance and diversity of soil macrofauna. However, little is known about their biomass in response to these concurrent drivers. Here, we investigated the biomass responses of soil macrofauna along a land-use intensity gradient of five land-use regimes (i.e., from extensively-used grassland to conventional cropland) under two climate scenarios (ambient *vs.* future). We found that land-use intensification (but not climate change) significantly reduced soil macrofauna biomass at the community rather than individual level. Further, the community structure of soil macrofauna based on total biomass data varied with land-use type (i.e., grasslands *vs.* croplands). Collectively, our findings suggest that land-use intensification can negatively shift the community biomass patterns of soil macrofauna consistently under both ambient and future climates in agroecosystems.

Keywords: Agroecosystem; Body mass; Climate change; Community biomass; Intensive land use; Soil invertebrate

Introduction

Soil macrofauna account for the majority of soil fauna biomass across many terrestrial ecosystems, and contribute substantially to ecosystem functions (Gongalsky, 2021). For example, 'litter transformers' (e.g., Julida, Isopoda) fragment coarse organic debris and promote microbial decomposition (David, 2014). 'Ecosystem engineers' (e.g., earthworms) incorporate large amounts of organic fragments into the mineral soil horizon to facilitate nutrient cycling and primary production (Blouin et al., 2013) and form the environment for other species in the soil (Eisenhauer, 2010).

Larger soil fauna may be more affected by environmental changes than smaller fauna represented by *r*-strategists (e.g., Briones, 2014; Tsiafouli et al., 2015; Phillips et al., 2019). However, soil macrofauna attract much less attention, compared with other groups of soil organisms (e.g., microbes, microfauna, and mesofauna) (Basturk et al., 2021). Additionally, previous macrofauna studies focused more on the responses of their abundance and diversity to global changes (Franco et al., 2016; Phillips et al., 2019; Yin et al., 2019), but less on their biomass responses.

Body mass, as one of the most important physio-morphological traits, largely determines the food intake and metabolic rate of invertebrates (Eklöf et al., 2017). Moreover, the resource utilization and allocation capacity of a community is often reflected by the total biomass of co-occurring species within that community (Post and Pedersen, 2008). Changes in biomass pattern of macrofauna community may directly influence the energy fluxes in soil food webs, therefore biomass may be even more important to ecosystem functioning than their abundance and diversity (Basturk et al., 2021).

As soil fauna are thermosensitive, their biomass patterns could be shifted by climate change (Xu et al., 2017). For instance, Vestergård et al. (2015) found that the total biomass of mesofauna communities was reduced by warming, especially when combined with drought. Warming speeds up individual metabolism (Scheffers et al., 2016), resulting body size/mass reduction of soil mesofauna (Yin et al., 2020). Additionally, land-use intensification have been reported to cause abundance and diversity loss of soil fauna (especially for macrofauna, Postma-Blaauw et al., 2012), and simultaneously reduce the complexity of their community structure (Decaëns et al. 1994; Tsiafouli et al. 2015). But less is known about how these two global change drivers individually and collectively influence soil macrofauna biomass, at the both individual and community levels.

Here, we address this question in the framework of the 'Global Change Experimental Facility' (GCEF) in Germany. Specifically, we performed a two-year study in a full-factorial combination of climate (ambient *vs.* future, i.e., increased temperature and altered precipitations) and land use (from low to high land-use intensity: extensively-used meadow → extensively-used pasture → intensively-used meadow → organic cropland → conventional cropland). We tested two hypotheses: (1) climate change and land-use intensification will reduce soil macrofauna biomass at the both individual and community levels; (2) interactions between climate and land use will be significant on soil macrofauna biomass. More precisely, land-use intensification will exacerbate the detrimental effects of climate change on soil macrofauna biomass; whilst extensive land use will alleviate these climate change effects.

Materials and Methods

Our study was conducted at the ‘Global Change Experimental Facility’ (GCEF) in Bad Lauchstädt, Germany (51° 23' 30" N, 11° 52' 49" E, 116 m a.s.l.). This study site is characterized by a subcontinental climate with a mean annual temperature and precipitation of 8.9°C and 498 mm, respectively. The soil type is Haplic Chernozem, the contents of total carbon and nitrogen within the upper soil (15 cm) varied between 1.71–2.09% and 0.15–0.18%, respectively (Schädler et al., 2019).

The GCEF was established in late 2012, and consists total 50 plots arranged into 10 blocks (Fig. S1A). Half of these plots (25/50) are under five ambient climate blocks, and the other half (25/50) are subjected to five future climate blocks (i.e., increased temperature by ~0.55 °C, and changed precipitation patterns with ~20% reduction in summer and ~10% increment in spring/autumn), which is a projection of the climate of Central Germany for the years of 2070-2100 based on several models, i.e., COSMO-CLM (Rockel et al., 2008), REMO (Jacob and Podzun, 1997), and RCAO (Döscher et al., 2002). Using a split-plot design, each five land-use regimes are randomly arranged into either ambient or future climate block (Fig. S1B). Descriptions of these five land-use regimes are provided in Figure S2.

We sampled totally 200 soil cores (Ø 16 cm, 10 cm depth) during a two-year study period for autumn season: in 26.10.2015 and 25.10.2016. Specifically, two soil cores per plot were taken and gathered into one sample at each sampling period to extract soil macrofauna using a Kempson extraction method (Kempson et al., 1963). Using a digital microscope (VHX-600, Keyence Corp., Osaka, Japan), the extracted macrofauna (body length > 3 mm) were determined to some specific taxa, i.e., Araneae, Chilopoda, Coleoptera, Diplura, Diptera, Formicidae, Gastropoda, Isopoda, Julida, Lumbricidae, Psocoptera, Symphyla, and Thysanoptera. For all taxa, we divided the number of individuals in each sample by the surface area (0.04 m^2) of the two soil cores to calculate density, and measured the body size (length, μm) of each individual. The body mass (M, μg) of each taxon was calculated by a body size assessment method based on taxon-specific formulas (Table S1). For each plot, the total biomass and mean body mass of macrofauna communities were represented by mean ± se.

Linear mixed models (LMMs) were conducted using the '*lme4*' package (Bates et al., 2011) to assess the effects of climate (as mainplot factor level; ambient *vs.* future), land use (as subplot factor level; extensively-used meadow *vs.* extensively-used pasture *vs.* intensively-used meadow *vs.* organic farming *vs.* conventional farming), date (2015 autumn and 2016 autumn), and their interactions on the total biomass and mean body mass of soil macrofauna. Land use was nested into mainplot, and mainplot was served as a random effect. Data was tested for assumptions of normality and homogeneity of variances using the Shapiro-Wilk and Levene's tests. The post-hoc comparisons of means among groups were applied using the '*emmeans*' package (Lenth et al., 2019). To visualize how climate, land use, and their interaction influence community structure of soil macrofauna (based on total biomass data), permutational multivariate analysis of variance (PERMANOVA) and pairwise comparison were conducted using '*adonis*' and '*pairwise.adonis*' functions with the '*bray*' method and 999 permutations fitted to non-metric multidimensional scaling (NMDS) ordination in R '*vegan*' package (Martinez Arbizu, 2020; Oksanen et al., 2013). All statistical analyses were conducted using R version 4.0.3 (R Core Team, 2021).

Results and Discussion

In this study, climate change did not significantly affect the biomass patterns of soil macrofauna (Table S2). The same experiment showed that climate change significantly reduced the total biomass of soil mesofauna (Yin et al., 2020). However, the total biomass of soil macrofauna remained unchanged under future climate (Fig. 1A; Table S2), possibly because soil macrofauna are more resistant to the variations in climate than soil mesofauna (Bokhorst et al., 2012). Therefore, the responses of macrofauna biomass to climate change may take longer to manifest.

Additionally, we found no evidence of body mass reduction in soil macrofauna under future climate (Fig. 1 B; Table S2), despite climate change has been reported to shrink the body size and mass of many organisms (Gardner et al., 2011). However, soil fauna body mass has been reported to decrease from mesic to arid conditions; the aridity is an environmental filter especially for large-bodied fauna (Andriuzzi et al., 2020). We sampled in two consecutive autumn years (2015/2016), the wetter autumn conditions in our future climate plots may mitigate the detrimental warming effects.

Detrimental effects of land-use intensification are prevalent in soil biota, especially in large-bodied fauna (Postma-Blaauw et al., 2010). We found that land-use intensification significantly reduced the total biomass but not the mean body mass of soil macrofauna across all plots and dates (Fig. 1A-B; Table S2). These findings indicate that agricultural intensification threatens macrofauna biomass at the community but not individual level.

Further, the significant effects of land use on macrofauna total biomass were taxon-specific (Table S3). For example, the total biomass of Coleoptera and Chilopoda was significantly higher in extensively-used pasture than that in croplands (Fig. 1C-D); whereas the total biomass of Julida in intensively-used meadow and Diplura in extensively-used meadow was significantly higher than that in croplands, respectively (Fig. 1E-F). In general, grazing (along with livestock trampling) may cause soil compaction and reduction in porosity, as well as the formation of local anoxic conditions (Schrama et al., 2013), and these effects are expected to be detrimental to soil macrofauna. In turn, livestock dung is an attractive food resource for Coleoptera (Galante et al., 1995), and low to moderate grazing intensity may facilitate their total biomass (Tonelli et al., 2018). Further, agricultural extensification can increase the complexity of soil food webs, and the mean body mass of soil fauna (Postma-Blaauw et al., 2010), but may also cause the increased predation (Flohre et al., 2011). As the top predators of soil food webs, Chilopoda are highly mobile and prefer to dwell at the soil surface when the soil porosity is low and when hypoxic conditions are prevalent. In our pastures, therefore, the increase of total biomass of Coleoptera may accordingly increase the total biomass of predators (e.g., Chilopoda) through a bottom-up trophic cascade (Wu et al., 2011).

In the context of land-use intensification, the reduced total biomass of soil fauna might be due to their decreased density (Yin et al., 2020). Indeed, a generally positive correlation was detected between total biomass of soil macrofauna and their density; Strikingly, this pattern was significant only in croplands, but not in grasslands (Fig. 2A).

By contrast, there was no significant correlation between their mean body mass and density (Fig. 2B). Furthermore, the community structure of soil macrofauna (based on total biomass data) was significantly affected by land-use (but not climate) treatment (Fig. 2C; Table S4A), and these significant effects were driven by the two land-use types (i.e., grasslands vs. croplands) (Table S4B). As partially supported by other studies (Guan et al., 2021; Yin et al., 2019), land-use type conversion is the foremost driving force of shifts in the community composition or food web structure of soil fauna.

Collectively, our results partially support our 1st hypothesis, showing that land-use intensification shifted the biomass patterns of soil macrofauna with a significant reduction in total biomass; however, we did not find any evidence of significant interactions between climate and land use on soil macrofauna biomass to support our 2nd hypothesis, suggesting that the effects of land use were consistent under the both ambient and future climate scenarios.

Conclusion

Land-use intensification was a more severe immediate threat than climate change to soil macrofauna biomass. Our findings provide strong experimental evidence that land-use change from cropland to grassland could shift the community structure of soil macrofauna from a higher to a lower total biomass community. Despite no significant effects of climate change on soil macrofauna biomass were found approximately three years after the establishment of the GCEF experimental platform, long-term observation is needed to determine if the current response pattern will be consistent or change over time. Furthermore, these detrimental effects of land-use intensification on total biomass of soil macrofauna may have far-reaching consequences for the provision of ecosystem functions and energy fluxes, e.g., litter decomposition, nutrient turnover, and productivity of agricultural ecosystems (Taylor et al., 2010). In order to better understand and predict the potential effects of soil fauna biomass loss and community changes on related ecosystem functions in this changing world, we call for future research to explore these functional links and elucidate the mechanisms.

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Conflict of Interest

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

Authors Contributions

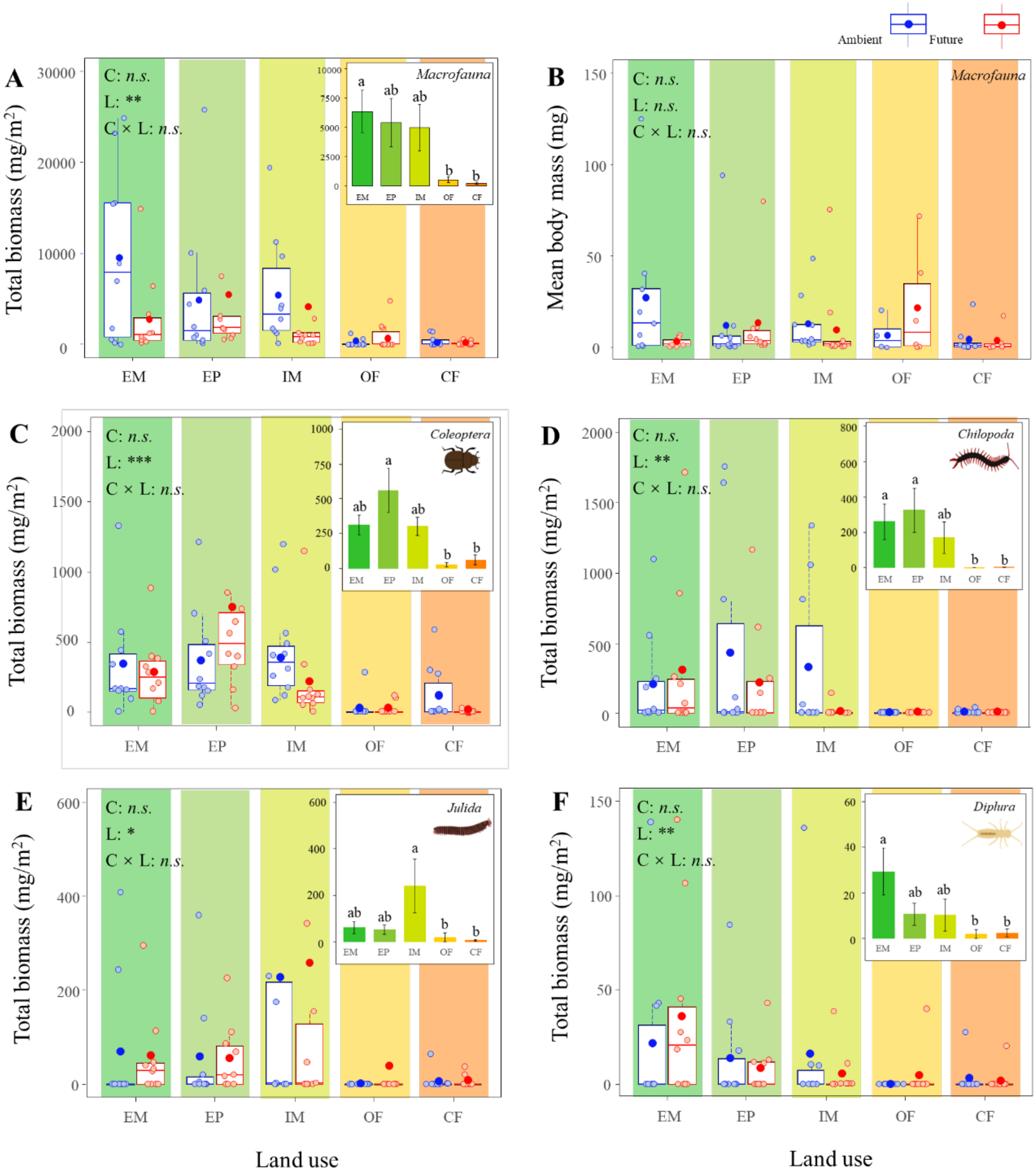
MS is part of the GCEF steering committee that developed the experimental platform; MS and NE conceived this study; RY and MS conducted the field and lab work; R.Y. analyzed the data and wrote the first draft; P.K. offered advices on writing structure. All authors greatly contributed to revising of this paper.

Figure legends

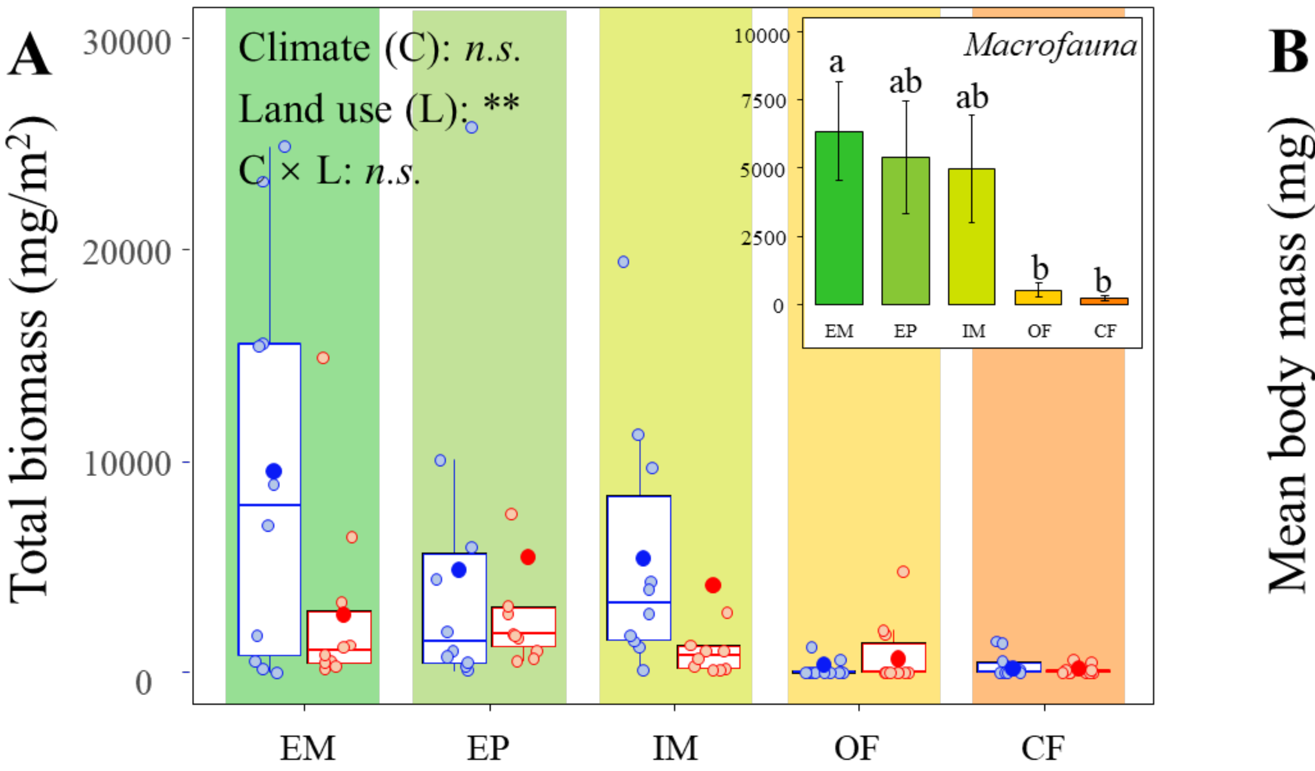
Fig. 1 Interaction effects of climate and land use on total biomass (**A**) and mean body mass (**B**) of soil macrofauna, as well as total biomass of Coleoptera (**C**), Chilopoda (**D**), Julida (**E**), and Diplura (**F**). Boxplots show the mean (the solid dot), the median (the horizontal line), the first and third quartile (the rectangle), and the 1.5 × interquartile range (the whiskers). Jitter points around the boxplot represent sample numbers for each climate (ambient climate in blue, future climate in red). The histogram on the upper right (**A**) shows the effects of land use on total biomass of soil macrofauna (mean ± se). Different lowercase letters represent significant differences among land-use regimes at $P < 0.05$ based on the post-hoc Tukey's HSD tests. Abbreviation: EM (in lawn green): extensively-used meadow, EP (in olive drab): extensively-used pasture, IM (in lime green): intensively-used meadow, OF (in yellow): organic farming, and CF (in orange): conventional farming.

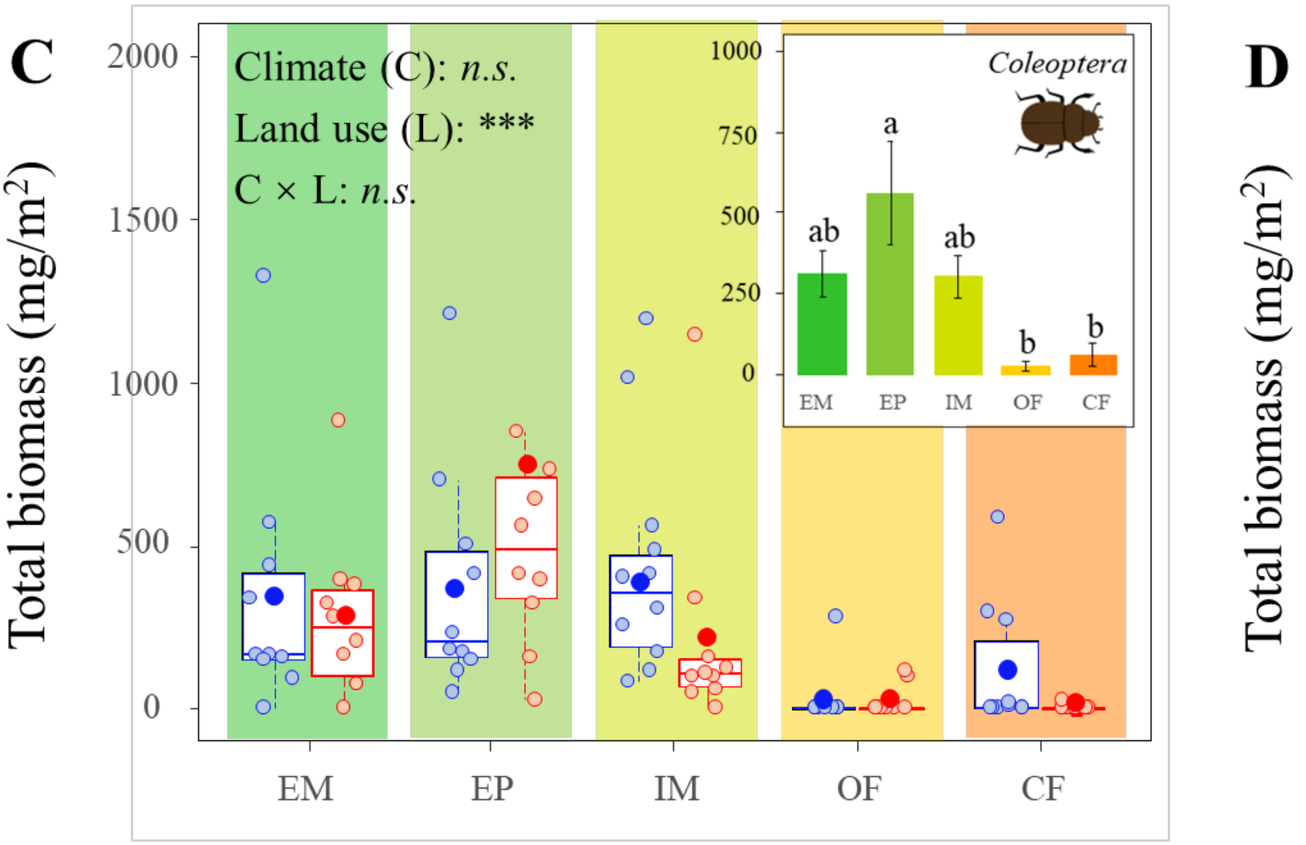
Fig. 2 Linear correlations between density and total biomass of soil macrofauna (**A**), as well as between density and mean body mass of soil macrofauna (**B**). Shown are the fitted regression lines with 95% confidence intervals, and dots for all individual samples for extensively-used meadow (EM, in lawn green), extensively-used pasture (EP, in olive drab), intensively-used meadow (IM, in lime green), organic farming (OF, in yellow), and conventional farming (CF, in orange). When $P < 0.05$, $R = 0.2 \sim 0.4$ and $0.7 \sim 0.9$ represents low and high correlation, respectively. Effects of climate and land use on community structure of soil macrofauna based on total biomass data (**C**). Non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis distances visualizes community differences between climate scenarios represented by dots (ambient), and triangles (future), and among land-use regimes (EM, with lawn green symbols; EP, with olive drab symbols; IM, with lime green symbols; OF, with yellow symbols; CF, with orange symbols). Ellipses represent 95% confidence estimates for mean NMDS scores of five land-use regimes.

Fig. 1



Ambient
Future
A
Total biomass (mg/m^2)
C: n.s.
L: **
C × L: n.s.
Macrofauna
EM
EP
IM
OF
CF
B
Mean body mass (mg)
C: n.s.
L: n.s.
C × L: n.s.
Macrofauna
C
Total biomass (mg/m^2)
C: n.s.
L: ***
C × L: n.s.
Coleoptera
D
Total biomass (mg/m^2)
C: n.s.
L: **
C × L: n.s.
Chilopoda
E
Total biomass (mg/m^2)
C: n.s.
L: *
C × L: n.s.
Julida
F
Total biomass (mg/m^2)
C: n.s.
L: **
C × L: n.s.
Diplura
Land use
Land use


A
Total biomass (mg/m2)
30000
20000
10000
0
Climate (C): n.s.
Land use (L): **
C × L: n.s.
EM
EP
IM
OF
CF
Macrofauna
10000
7500
5000
2500
0
a
ab
ab
b
b
B
Mean body mass (mg)


C
Total biomass (mg/m2)
2000
1500
1000
500
0
Climate (C): n.s.
Land use (L): ***
C × L: n.s.
EM
EP
IM
OF
CF
Coleoptera
1000
750
500
250
0
ab
a
ab
b
b
D
Total biomass (mg/m2)

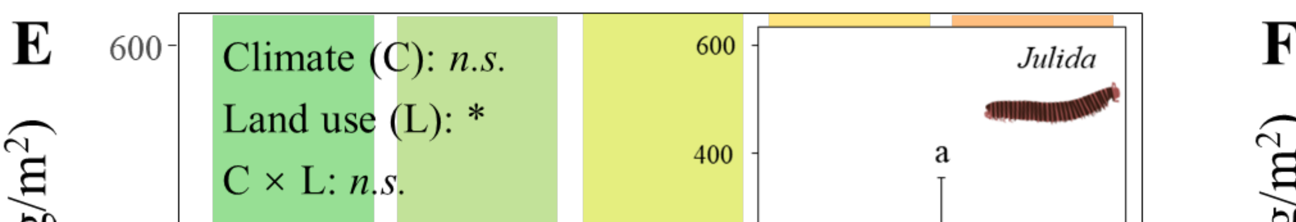
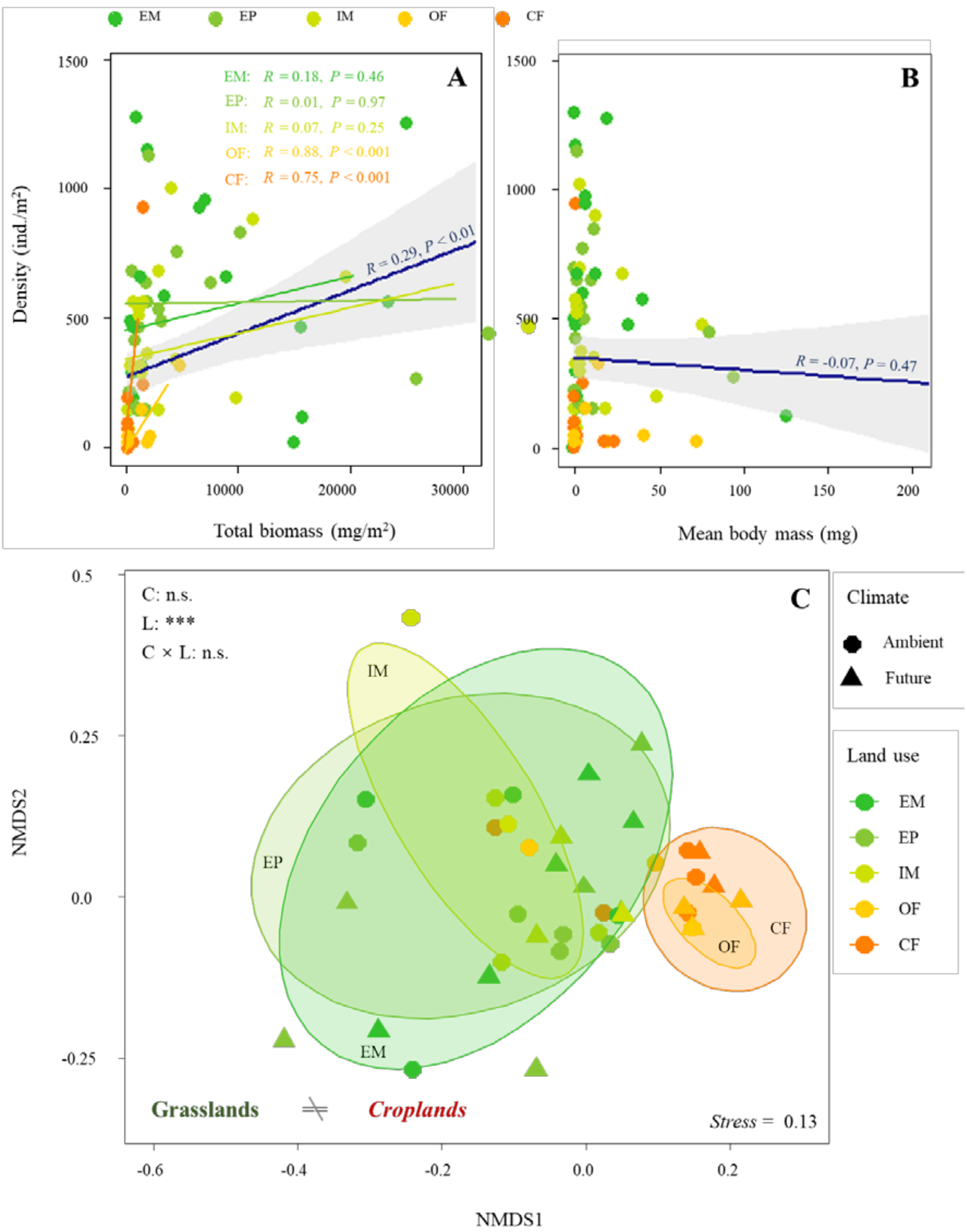

E
600
Climate (C): n.s.
Land use (L): *
C × L: n.s.
Julida
600
400
a
F

Fig. 2



EM
EP
IM
OF
CF
A
EM: R = 0.18, P = 0.46
EP: R = 0.01, P = 0.97
IM: R = 0.07, P = 0.25
OF: R = 0.88, P < 0.001
CF: R = 0.75, P < 0.001
R = 0.29, P < 0.01
Density (ind./m²)
Total biomass (mg/m²)
B
R = -0.07, P = 0.47
Mean body mass (mg)
C
C: n.s.
L: ***
C × L: n.s.
IM
EP
EM
OF
CF
Grasslands
Croplands
Stress = 0.13
NMDS1
NMDS2
Climate
Ambient
Future
Land use
EM
EP
IM
OF
CF

Supplementary materials

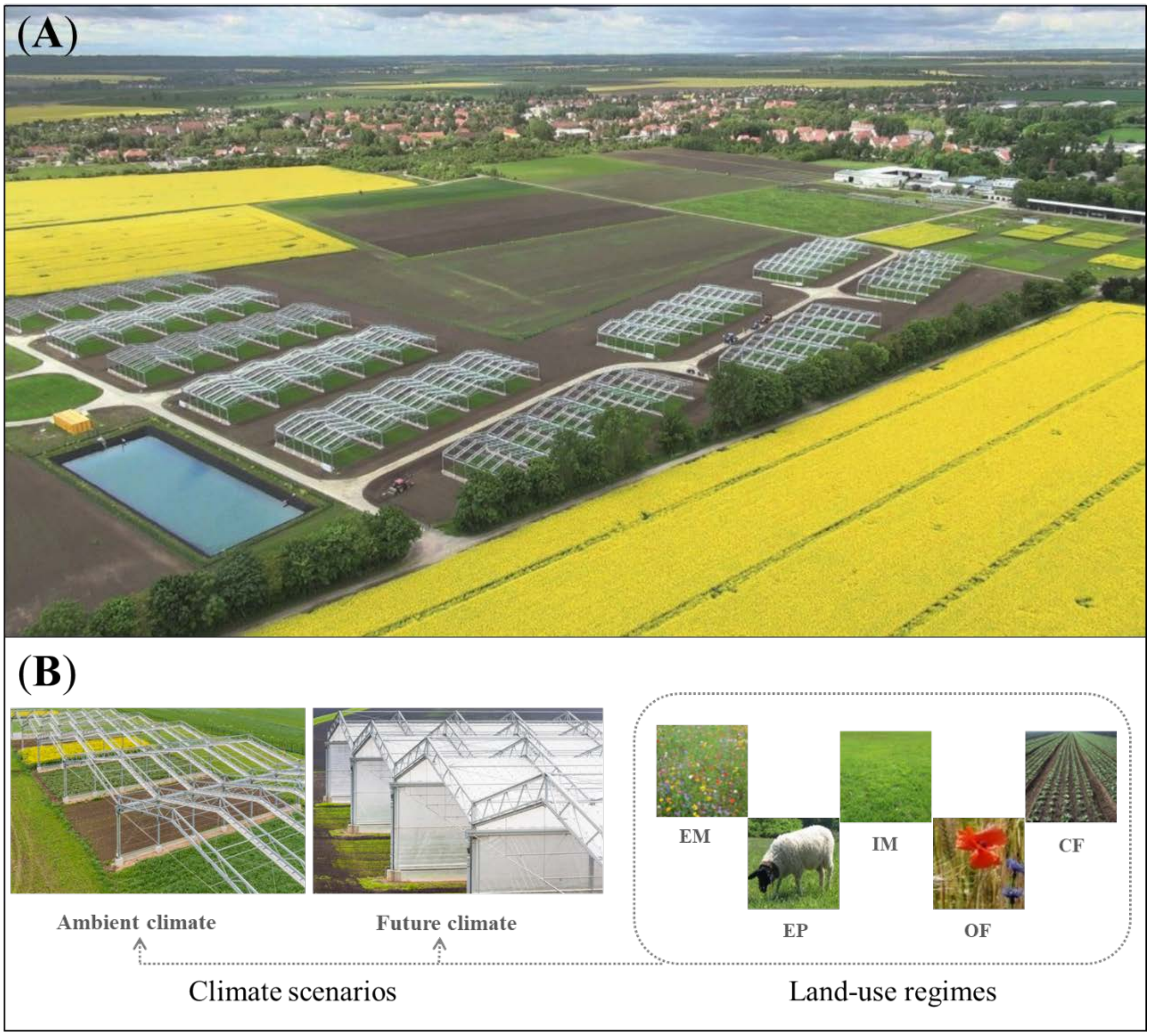
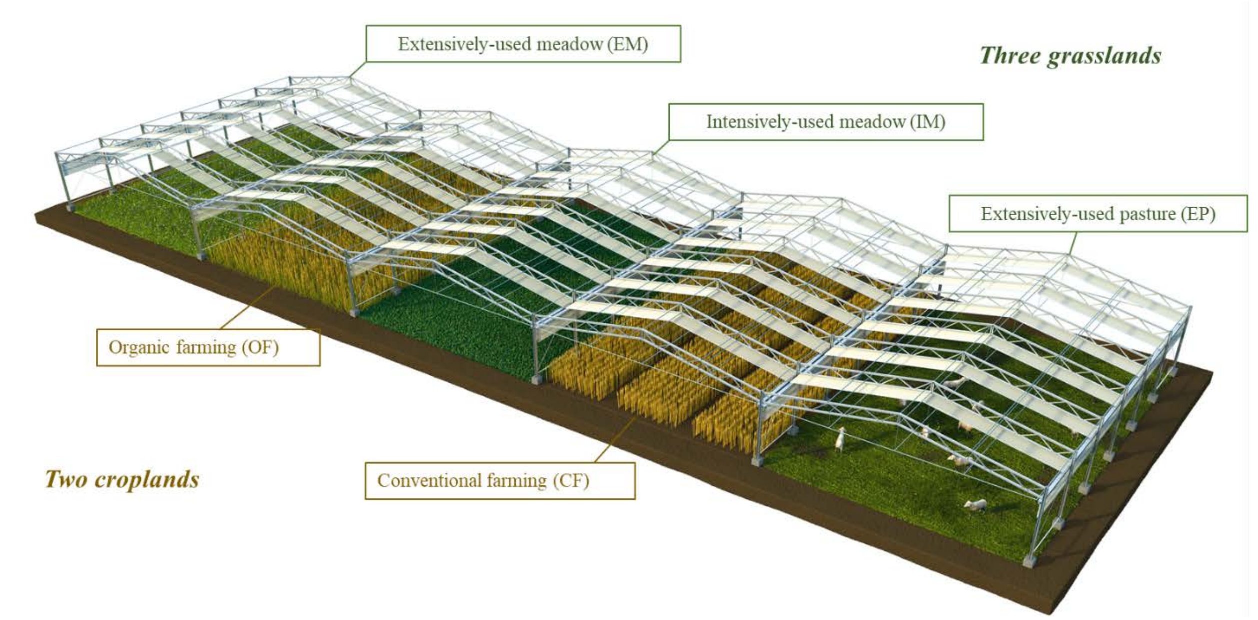


Fig. S1 Global Change Experimental Facility (GCEF). (**A**) Aerial image of GCEF set-up: total 50 plots (24 m × 16 m = 384 m^2 per plot) are arranged into 10 blocks (i.e., 5 plots/block), of which 5 blocks for ambient climate, the other 5 blocks for future climate. Picture: Tricklabor/Service Drone, copyrights: UFZ. (**B**) Climate and land use treatment settings. Climate treatments as main-plot factor have two levels: ambient climate (the control) *vs*. future climate (i.e., the increased temperature by ~0.55 °C, and the altered precipitation by ~20% reduction in summer and ~10% increment in spring/autumn). Picture: Andrè Künzelmann, copyrights: UFZ. Land-use treatments as sub-plot factor have five land-use regimes, i.e., EM = extensive-used meadow; EP = extensive-used pasture; IM = intensive-used meadow; OF = organic farming; CF = conventional farming. Each these five land-use regimes are randomly nested into a block.

Fig. S2 Detailed description of five land-use regimes at the Global Change Experimental Facility (GCEF).



Land-use regime (Abbreviation)	**Descriptions**
Extensively-used meadow (EM)	A wide range of native common grasses, herbs and legumes (totally consisting 50 plant species, for each species seeds were sampled from different local populations to reflect to local gene pool and to introduce genetic variability) with moderate mowing (2-3 times per year) and no fertilization.
Extensively-used pasture (EP)	Plant species composition and land management as the same as extensively used meadows (see above), but with sheep grazing (2-3 grazing periods per year with a group of 20 sheep grazing for 24 hours).
Intensively-used meadow (IM)	Conventional used mixture of forage grasses with moderate fertilization and frequent mowing (3-4 times per year).
Organic farming (OF)	A crop rotation aiming to maintain soil fertility, minimize measures of pest and weed control, and provide an environmentally friendly management of agroecosystems with mechanical weed control, organic fertilization, non-stained seeds and restricted use of pesticides. Crop rotational sequences: 2012-2013: oat (common crop on all subplots to homogenize soil conditions); 2013-2014: horse bean; 2014-2015: winter wheat; 2015-2016: winter barley.
Conventional farming (CF)	A typical regional crop rotation with the application of mineral fertilizers and pesticides. Crop rotational sequences: 2012-2013: oat (common crop on all subplots to homogenize soil conditions); 2013-2014: winter rape; 2014-2015: winter wheat; 2015-2016: winter barley.

Table S1 Taxon-specific formulas for the estimation of body mass (M, μg) for different soil macrofauna taxa based on the body size (L, μm) spectrum method.

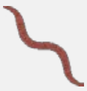
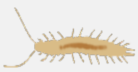
Taxa		Formula	B_0	B_1	Reference
Araneae		$\log M = B_0 + B_1 \times \log L$	-2.42	1.84	Mercer et al., 2001
Chilopoda		$M = e^{(B_0 + B_1 \times \ln(L))}$	-3.29	2.10	Ganihar, 1997
Coleoptera		$M = e^{(B_0 + B_1 \times \ln(L))}$	-3.25	2.49	Sample et al., 1993
Diplura		$M = e^{(B_0 + B_1 \times \ln(L))}$	-3.43	2.59	Ganihar, 1997
Diptera		$M = e^{(B_0 + B_1 \times \ln(L))}$	-3.14	2.59	Ganihar, 1997
Formicidae		$M = e^{(B_0 + B_1 \times \ln(L))}$	-3.14	2.34	Ganihar, 1997
Gastropoda		$M = e^{(B_0 + B_1 \times \ln(L))}$	-2.75	1.59	Wardhaugh, 2013
Isopoda		$M = e^{(B_0 + B_1 \times \ln(L))}$	-4.81	3.44	Wardhaugh, 2013
Julida		$M = e^{(B_0 + B_1 \times \ln(L))}$	-4.59	2.54	Gowing and Recher, 1984
Lumbricidae		$\log M = B_0 + B_1 \times \log L$	0.93	1.09	Mercer et al., 2001
Psocoptera		$M = e^{(B_0 + B_1 \times \ln(L))}$	-3.07	2.30	Ganihar, 1997
Symphyla		$M = e^{(B_0 + B_1 \times \ln(L))}$	-3.07	2.30	Ganihar, 1997
Thysanoptera		$M = e^{(B_0 + B_1 \times \ln(L))}$	-3.07	2.30	Ganihar, 1997

Table S2 Results (*F*-values) of linear mixed effects models (Type III ANOVA with Satterthwaite's method) testing the effects of climate, land use, date, and their interactions on total biomass and mean body mass of soil macrofauna community. *F*-value with ** ($P < 0.01$) representing significant effects is indicated in bold font.

Treatments	Total biomass			Mean body mass		
	$Df_{(num:den)}$	*F*-value	*P*-value	$Df_{(num:den)}$	*F*-value	*P*-value
Climate (C)	1:80	1.09	0.30	1:62	0.37	0.54
Land use (L)	4:80	**3.60**	**< 0.01****	4:62	0.46	0.76
Date (D)	1:80	3.24	0.07	1:62	0.05	0.82
C × L	4:80	1.04	0.39	4:62	1.30	028
C × D	1:80	0.03	0.87	1:62	2.34	0.13
L × D	4:80	0.86	0.49	4:62	1.18	0.33
C × L × D	4:80	0.44	0.78	4:62	0.75	0.56

Table S3 Results (*F*-values) of linear mixed effects models (Type III ANOVA with Satterthwaite's method) testing the effects of climate, land use, date, and their interactions on total biomass of Lumbricidae, Araneae, Coleoptera, Chilopoda, Julida, Diptera, Isopoda, Formicidae, Gastropoda, Diplura, Symphyla, Psocoptera, and Thysanoptera across two samplings. *F*-values with *** (P < 0.001), ** (P < 0.01), * (P < 0.05) representing significant effects are indicated in bold font.

Treatments	*Df*	Araneae	Chilopoda	Coleoptera	Diplura	Diptera	Formicidae	Gastropoda
Climate (C)	1,80	1.16	1.26	0.003	0.00	0.48	1.78	1.69
Land use (L)	4,80	1.09	**4.54****	**6.41*****	**4.29****	1.18	1.01	1.33
Date (D)	1,80	1.14	**21.45*****	0.84	**8.19****	0.33	1.85	3.70
C × L	4,80	1.01	1.49	1.53	0.78	0.36	0.85	0.74
C × D	1,80	0.33	3.04	0.47	0.83	0.49	1.79	1.69
L × D	4,80	1.23	3.95	0.69	1.54	0.91	1.04	1.33
C × L × D	4,80	1.36	1.51	1.32	1.40	0.82	0.99	0.75
Treatments	*Df*	Isopoda	Julida	Lumbricidae	Psocoptera	Symphyla	Thysanoptera	
Climate (C)	1,80	0.13	0.07	0.49	1.02	0.59	0.03	
Land use (L)	4,80	1.18	**3.30***	1.94	0.60	1.97	1.42	

Date (D)	1,80	2.76	**8.93****	1.53	0.43	0.34	**13.23*****
C × L	4,80	0.99	0.04	1.17	0.64	0.09	1.02
C × D	1,80	0.08	0.11	0.27	1.44	2.40	0.08
L × D	4,80	1.14	2.83	0.81	0.98	1.00	1.34
C × L × D	4,80	1.11	0.13	1.22	0.74	0.44	1.10

Table S4 Results (R^2-values) of permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis distances testing the effects of climate and land use, and their interaction on community structure of soil macrofauna using total biomass data (**A**). Pairwise comparisons based on Bray-Curtis dissimilarities showing differences between land-use regimes (**B**). R^2-values with *** ($P < 0.001$), ** ($P < 0.01$) representing significant effects are indicated in bold font.

(**A**) PERMANOVA results			
Treatments	*Df*	R^2-value	*P*-value
Climate (C)	1	0.03	0.16
Land use (L)	4	**0.25**	< **0.001***
C × L	4	0.06	0.52
(**B**) Pairwise comparisons between land-use regimes			
Comparisons	*Df*	R^2	*P*-value
EM *vs.* EP	1	0.05	0.45
EM *vs.* IM	1	0.14	0.88
EM *vs.* OF	1	**0.24**	**0.002** **
EM *vs.* CF	1	**0.20**	**0.006** **
EP *vs.* IM	1	0.06	0.37
EP *vs.* OF	1	**0.33**	< **0.001***
EP *vs.* CF	1	**0.26**	**0.003** **
IM *vs.* OF	1	**0.29**	< **0.001***
IM *vs.* CF	1	**0.24**	**0.003** **
OF *vs.* CF	1	0.03	0.46