

This is the accepted manuscript version of the contribution published as:

Yin, R., Kardol, P., Thakur, M.P., **Gruss, I.**, Wu, G.-L., Eisenhauer, N., **Schädler, M.**
(2020):

Soil functional biodiversity and biological quality under threat: Intensive land use outweighs
climate change

Soil Biol. Biochem. **147** , art. 107847

The publisher's version is available at:

<http://dx.doi.org/10.1016/j.soilbio.2020.107847>

Article type: Research Article

Soil functional biodiversity and biological quality under threat: intensive land use outweighs climate change

Rui Yin^{1,2,3,4} (rui.yin@ufz.de), Paul Kardol⁵ (Paul.Kardol@slu.se), Madhav P. Thakur⁶ (M.Thakur@nioo.knaw.nl), Iwona Gruss^{2,7} (iwona.gruss@upwr.edu.pl), Gao-Lin Wu^{1,8*} (wugaolin@nwsuaf.edu.cn), Nico Eisenhauer^{3,4,¶} (nico.eisenhauer@idiv.de), Martin Schädler^{2,3,¶} (martin.schaedler@ufz.de)

Running head: Intensive land use threaten functional biodiversity and biological quality of soils

Affiliations:

¹ State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A & F University, Yangling, Shaanxi 712100, China

² Helmholtz-Centre for Environmental Research-UFZ, Department of Community Ecology, Theodor-Lieser-Strasse 4, 06110 Halle (Saale), Germany

³ German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

⁴ Institute for Biology, Leipzig University, Deutscher Platz 5e, 04103 Leipzig, Germany

⁵ Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, 901-83 Umeå, Sweden

⁶ Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, Netherlands

⁷ Wrocław University of Environmental and Life Sciences, Department of Plant Protection,
Plac Grunwaldzki 24 A, 50363 Wrocław, Poland

⁸ CAS Center for Excellence in Quaternary Science and Global Change, Xi'an, 710061, China

¶ Shared senior authorship: Nico Eisenhauer & Martin Schädler

* Corresponding author: Gao-Lin Wu

E-mail address: wugaolin@nwsuaf.edu.cn

Address: State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau,
Institute of Soil and Water Conservation, Northwest A & F University, Yangling, Shaanxi
712100, China

Abstract

Climate change and land-use intensification are the two most common global change drivers of biodiversity loss. Changes in functional diversity and functional composition of ecological communities are likely to threaten ecosystem functioning. However, the functional responses of soil communities to the interactive effects of climate and land use are still poorly known. Here, we investigated the functional responses of Collembola, one of the most abundant and ecologically important groups of soil invertebrates. This study was conducted at the Global Change Experimental Facility (GCEF) in central Germany, where we tested the effects of climate (ambient vs. ‘future’ as projected for this region for the years between 2070 and 2100), land use (conventional farming, organic farming, intensively-used meadow, extensively-used meadow, and extensively-used pasture), and their interactions on the functional diversity (FD), community-weighted mean (CWM) traits (life-history, morphology), and functional composition of Collembola, as well as the Soil Biological Quality-Collembola (QBS-c) index. We found that land use was the overwhelmingly

dominant driver of shifts in functional diversity, functional traits, and functional composition of Collembola, and of shifts in soil biological quality. These significant land-use effects were mainly due to the differences between the two main land-use types, i.e. cropland vs. grasslands. Specifically, Collembola functional biodiversity and soil biological quality were significantly lower in croplands, compared to that in grasslands. However, no significant interactive effects of climate and land use were found in this study, suggesting that land use effects on Collembola were independent of the climate change scenario. Overall, our study shows that functional responses of Collembola are highly vulnerable to land-use intensification under both climate scenarios. These findings are important as reduced functional biodiversity and biological quality of soils may threaten the functioning and service-provisioning of terrestrial ecosystems.

Keywords

Community-weighted mean; functional composition; functional traits; global change; land-use intensification; soil fauna

1. Introduction

Global environmental changes are threatening the biodiversity of terrestrial ecosystems both above and below the ground (Bellard et al., 2012; Newbold et al., 2015). Of all global changes, land-use intensification is one of the strongest drivers of soil biodiversity loss (Sala et al., 2000; Tsiafouli et al., 2015). It has been reported that soil biota are negatively affected by increased agricultural practices in crop fields and meadows (Ponge et al., 2013). Moreover, these land-use effects can be climate-dependent (e.g., Blankinship et al., 2011; Phillips et al., 2019). Changes in soil biodiversity have mostly been assessed using classical taxonomic indices (Vandewalle et al., 2010). As species differ in their responses to environmental change as well as in their effects on ecosystem functions (Mouchet et al., 2010), the

limitations of taxonomic methods are obvious and calls have been made to supplement taxonomy-based approaches with trait-based approaches (Moretti et al., 2017). Trait-based approaches have already been shown to advance our mechanistic understanding and predictive capabilities of the links between species traits and community responses, and thereby ecosystem processes (Laliberte and Shipley, 2011; Violle et al., 2007). So far, trait-based approaches have been mostly used in plant ecological researches, but in recent years, they have also been applied to soil communities (Dou et al., 2019; Hedde et al., 2012; Makkonen et al., 2011; Pey et al., 2014; Vandewalle et al., 2010; Wan Hussin et al., 2012) and future research priorities, i.e., utilizing functional traits to interpret soil community responses and ecosystem effects, have been identified (Eisenhauer and Powell, 2017).

Functional diversity (FD) is defined as a set of functional traits in a given community (de Bello et al., 2010). Generally, functional diversity can be represented by three main components: 1) functional richness (FRic), also known as functional biodiversity, indicates the amount of niche space occupied by the species in the community; 2) functional evenness (FEve) indicates the evenness of abundance distribution in occupied niche space; and 3) functional divergence (FDiv) indicates the degree to which the abundance distribution in functional niche space enhances divergence in functional traits within the community (Mason et al., 2005; Sechi et al., 2018; Villéger et al., 2008). These functional diversity indices are of great value in predicting the impacts of biodiversity on ecosystem functioning (Flynn et al., 2011; Reiss et al., 2009). Given the severity and rates of land degradation, the European Commission has called for actions to manage soils sustainability through protecting soil biodiversity loss (European Commission, 2006).

In this study, the functional responses of soil fauna communities to climate change and land-use intensification were studied using Collembola as our focal taxon. As Collembola are functionally diverse and one of the most abundant and widespread taxon across almost all terrestrial ecosystems (Hopkin, 1997). They are known indicators of soil disturbance, and are

often used in soil biodiversity monitoring programs (Reis et al., 2016). Also, as is reported that the taxonomic diversity of Collembola declined in response to climate change (Makkonen et al., 2011). Moreover, climate effects are likely to interact with land use effects to show an interaction effects, which may intensify or diminish their individual effects, on soil communities (Siebert et al., 2019; Yin et al., 2019a). Previous studies have been investigated the responses of Collembola traits to climate change (Makkonen et al., 2011; Thakur et al., 2018), but it still remains unclear how their traits respond to future climate in the context of land-use change (Martins da Silva et al., 2016; Winck et al., 2017).

Functional traits of soil fauna are closely related to their morphology, physiology, or phenology (Pey et al., 2014), and reflect species-specific ecological preferences or environmental tolerances (de Bello et al., 2010; Moretti et al., 2017). For example, habitat types are tightly related to morphological traits, such as body size, furca size and ocelli number (Christiansen, 1963; Rusek, 2007). Euedaphic species have a high proportion of parthenogenesis, whereas epedaphic and hemiedaphic species have a prevalence of sexual reproduction (Pollierer and Scheu, 2017; Scheu and Drossel, 2007). Besides, euedaphic species have a weaker dispersal ability than epedaphic and hemiedaphic species (Hopkin, 1997). Such traits or trait syndromes may play critical roles in the fate of Collembola under environmental change, as they determine how a species or community responds to environmental change and how these responses may influence ecosystem functioning (Holmstrup et al., 2018; Parisi et al., 2005). Linking traits to functions can be achieved using an easy-to-interpret index – Soil Biological Quality (Qualità Biologica del Suolo: QBS) (Parisi et al., 2005). This index has been developed to combine two important aspects of soil arthropods: (1) their presence in the soil, as a proxy for biodiversity, and (2) their capability to adapt to changing soil conditions, as a proxy for vulnerability (Menta et al., 2018b). In particular, the QBS approach has been applied to a range of land uses to evaluate the effects of land-use degradation (Menta et al., 2018a; Parisi et al., 2005). On that basis, the Soil

Biological Quality-Collembola (QBS-c) index has been proposed for the analysis of Collembola communities (Gruss et al., 2019; Menta et al., 2014; Parisi, 2001; Pinto et al., 2017). It has, for example, been shown that the values of QBS-c significantly decreased from extensive to intensive land management (Joimel et al., 2017; Martins da Silva et al., 2016; Menta et al., 2014; Twardowski et al., 2016). However, the QBS-c approach has not yet been applied in projects on land-use under different climate scenarios.

We used the unique Global Change Experimental Facility (GCEF, see Schädler et al. 2019) to test the following hypotheses: climate change and intensive land use will 1) decrease Collembola functional diversity; 2) shift functional composition of Collembola communities; and 3) decrease the soil biological quality, i.e., QBS-c values. Furthermore, 4) climate change will intensify the effects of land-use intensification on Collembola functional diversity and soil biological quality.

2. Materials and methods

2.1. Experimental platform

This study was conducted at the Global Change Experimental Facility (GCEF) (51° 23' 30N, 11° 52' 49E, 116 m a.s.l. in Bad Lauchstädt, Saxony-Anhalt, Germany) of the Helmholtz-Centre for Environmental Research (UFZ) (Schädler et al. 2019). This area is characterized by a temperate, slightly continental climate with an average temperature of 9.7°C (1993–2013) and a mean annual precipitation of 525 mm (1993–2013). The soil type is a humus and nutrient-rich Haplic Chernozem (Altermann et al., 2005; WRB, 2007).

A detailed description of the GCEF and the experimental treatments is given in Schädler et al. (2019). In brief, the GCEF includes 50 sub-plots (24 × 16 m) which are arranged in ten main-plots, whereby five main-plots are subjected to the ambient climate whilst the other five to the future climate. Ambient climate treatment refers to the actual and non-manipulated

climate in terms of precipitation and temperature at the field site whilst the future climate treatment refers to a consensus scenario across different regional projections for the period 2070-2100 with an increased temperature and a changed precipitation pattern with reduced precipitation in summer and increased precipitation in spring and autumn. The use of automated roofs and side panels to passively increase night temperatures results in an average increase in daily mean temperature of 0.55°C especially caused by a stronger increase in minimum temperatures (1.14°C on average) and an increase in growing degree days by 5.2%. This set-up further allows a reduction in summer precipitation by ~20% and an increase in rainfall in spring and autumn by ~10% in line with future climate projections superimposed on the ambient variation in precipitation.

The five different land-use regimes include 1) the cropland type ‘conventional farming’ (CF) with a typical regional crop rotation consisting of winter rape, winter wheat and winter barley, mineral fertilizers and; 2) the cropland type ‘organic farming’ (OF) characterized by legumes replacing the rape in the crop rotation, mechanical weed control, non-stained seeds and a restricted use of pesticides; 3) the grassland type ‘intensively-used meadow’ (IM) with a commercially used mixture of forage grasses, and by moderate fertilization and frequent mowing (3-4 times per year); 4) the grassland type ‘extensively-used meadow’ (EM) consisting of a diverse mixture of more than 50 regionally typical plant species, moderate mowing (2times per year); 5) the grassland type ‘extensively-used pasture’ (EP) with the same set of species as EM but managed by 2-3 grazing events per year. All treatments are described in detail in Schädler et al. (2019).

2.2. Collembola sampling, extraction, and identification

Two soil cores (16 cm diameter, and 5 cm length) were sampled from each sub-plot in fall (October) 2016. Based on previous work in the GCEF (e.g., Siebert et al., 2019), it proved that samplings in fall were considered to be most representative of the treatment effects. A

Kempson heat extraction apparatus (Kempson et al., 1963) were used to extract Collembola in polyethylene glycol. Subsequently, we transferred the extracted Collembola individuals to 70% ethanol to preserve to be determined. For each sample, Collembola were counted and determined to species by placing on constant slides in the Faure medium based on the keys of Fjellberg (2007a; 2017b) and Hopkin (2007).

2.3. Trait-based approaches for Collembola

Based on previous study (Moretti et al., 2017), nine traits of Collembola were collected, which might be responsive to changes in climate and land use, including life-history traits (habitat, reproductive mode and dispersal ability) and morphological traits (furca, ocelli, pigmentation, hair, body size, and antenna). Each trait was scored from 0 to 4 (Table S1), and these trait values were obtained from existing data bases, and (Gruss et al., 2019; Malmström, 2012; Vandewalle et al., 2010). Higher scores indicate better adaptation to environment changes; for example, soil surface-dwelling species, sexual productive mode, fast dispersal ability, present (and long) furca, high number of ocelli, present (with patterns) pigmentation, the presence and abundance of hairs, large body size, and high ratio of antenna to body length. The QBS-c (biological quality index based on Collembola species) was calculated as the sum of trait values of each species for each sub-plot (Table S2). Higher values of QBS-c indicate higher soil biological quality. Community-weighted mean (CWM) traits for each sub-plot were calculated according to Garnier et al. (2004):

$$CWM = \sum_{i=1}^n P_i \times X_i$$

Where P_i is the relative abundance of the i^{th} species, X_i is the trait value of the i^{th} species, and n is the number of species in the community.

2.4. Calculations and statistical analyses

All statistical analyses were performed using the R statistical software (R Core Team, 2017). For each sub-plot, we calculated functional diversity based on CWM traits using the FD package (Laliberté et al., 2014). This package uses Principal Co-ordinates Analysis (PCoA) to return axes that are then used as ‘traits’ to compute functional diversity indices, including functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) (Villéger et al., 2008).

All FD indices, CWM traits, and the QBS-c index were analyzed using split-plot linear mixed models (LMMs) to assess the interactive effects of climate and land use. Post-hoc Tukey’s HSD tests were carried out to reveal significant differences among the respective levels within factors.

Mean values of nine traits for each sub-plot were used in multivariate analysis, and a non-parametric multivariate analysis of variance (PERMANOVA) was applied to analyze the effects of climate, land use and their interaction on functional composition of Collembola communities fitted to non-metric multidimensional scaling (NMDS) ordination. Analysis of similarities (ANOSIM) based on Bray-Curtis distances were conducted using PAST (Hammer et al., 2001) and the Vegan package (Oksanen et al., 2013) to test the significance within different land-use regimes. Visualization of 2D-NMDS was performed using the packages ‘scatterplot 2D’ and rgl (Ligges and Mächler, 2003).

Correlation graphs were produced using the PerformanceAnalytics package (Peterson et al., 2015) to show Pairwise Pearson's correlations of Collembola functional diversity, with functional composition and soil biological quality.

3. Results

3.1. Effects of climate and land use on functional diversity indices

The responses of functional diversity indices to climate change and land use differed in direction and magnitude (Table 1). Specifically, functional richness (FRic) was lower in

croplands than in grasslands across climate scenarios (Figure 1a), while functional evenness (FEve) was higher in croplands than in grasslands across climate scenarios (Figure 1b). FRic was negatively correlated with FEve (Figure S1). Functional diversity (FDiv) was not affected by any of treatments (Table 1).

3.2. Effects of climate and land use on community weighted mean (CWM) traits

All CWM traits of Collembola were significantly influenced by land use, but not by climate change, and by the interactive effects of climate and land use (Table 2). Generally, the CWM traits values were significantly higher in the three grasslands than in the two croplands across climate scenarios (Figure 2a-f). Among these traits, the CWM of hairs was significantly higher in extensively-used grasslands (meadows and pastures) than in croplands and intensively-used meadows (Figure 2g). Similarly, the CWM of body size decreased significantly from extensively-used pastures to conventional farming (Figure 2h). However, the CWM of antenna length was highest in intensively-used meadows compared to the other land-use regimes (Figure 2i).

3.3. Effects of climate and land use on functional composition

The functional composition of Collembola communities was significantly influenced by land use, but not by the interactive effects of climate and land use (Table 3; Figure 3). Further, ANOSIM analyses showed that the significant effects of land use were derived from the differences between the two main land-use types, i.e., croplands vs. grasslands, but not from management intensities within each of these two land-use types (Figure 3). Additionally, Collembola functional composition was correlated with their functional biodiversity (FRic) (Figure S1).

3.4. Effects of climate and land use on soil biological quality

In line with our findings of functional diversity and trait values, the QBS-c index was significantly decreased by intensive land use, showing decreased QBS-c values from grasslands to croplands across climate scenarios (Table 2; Figure 4). The QBS-c values were positively correlated to functional biodiversity (FRic) and functional composition (Figure S1).

4. Discussion

The responses of soil biota to global change are non-random as they depend on the traits of species. In this study, we used trait-based approaches revealing the functional responses of Collembola communities to the interactive effects of climate change and land-use intensification. Partially supported as our first three hypotheses, our results revealed that intensive land use but not climate change (i) decreased Collembola functional biodiversity, (ii) shifted their functional traits and composition, and (iii) degraded the soil biological quality. These findings partly support our first three hypotheses. Contrary to our last hypothesis, no significant interactive effects of climate and land use were found on these variables. Taken together, these findings indicate that intensive land use reduces soil functional biodiversity and biological quality independent of climate change

4.1. Land-use intensification decreased functional biodiversity

Functional diversity is receiving increased attention as an important component of biodiversity (Cadotte et al., 2011; Flynn et al., 2011; Gallé et al., 2019; Wieczynski et al., 2019), as it can often better relate community structure with ecosystem functioning compared to taxonomic diversity (Fontana et al., 2016; Tilman et al., 1997). In this study, we highlight how a set of functional diversity indices, i.e., functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) of Collembola respond to climate change and land-use intensification. We found that Collembola functional richness was decreased by land-use intensification, but not by climate change. Furthermore, these significant effects of land-use

intensification were due to the differences between land-use types (croplands vs. grasslands) but not due to the distinct management intensities within the same land-use type. This finding corroborates the notion that land-use type and intensity differentially filter traits in belowground fauna communities with strong negative effects of specific land-use types on functional diversity and much smaller effects of variation in intensity within land-use types (Birkhofer et al., 2017). Similarly, Chauvat et al., (2007) also found that Collembola taxonomic diversity decreased in responses to land-use type conversion (from arable lands to grasslands) within the same landscape.

Contrary to functional richness, the functional evenness of Collembola communities was higher in croplands than in grasslands, and we also found a significantly negative correlation between functional richness and evenness. This is partially supported by Mason et al. (2005), who argued that functional richness and evenness are the same entities (i.e., to species), orthogonal but independent of each other; whereas functional divergence reflects mechanisms of ecological niche differentiation. For example, habitat heterogeneity has been shown to increase functional divergence (*via* trait-divergence) of aboveground organisms, which promote the co-occurrence of species with different ecological requirements (Pacala and Tilman, 1994). Accordingly, we expected that the functional divergence of Collembola would be higher in grasslands (more heterogeneous land type) than in croplands (more homogeneous land type). However, our results showed that Collembola functional traits were equally divergent between the two main land-use types, suggesting that land use alone might not be a main driver of functional divergence for belowground fauna.

4.2. Land-use intensification shifted trait composition, and threatened soil biology quality

Our results showed that functional traits and functional composition were shifted by land-use intensification, but not by climate change. Specifically, from grasslands to croplands, the

dominance of soil surface-dwelling species with sexual reproduction and fast dispersal shifted to a community dominated by soil-dwelling species with parthenogenetic reproduction and slow dispersal. This change was accompanied by morphological trait shifts, such as smaller body size and furca, as well as fewer ocelli. Such shifts in functional traits may result in unexpected responses of individual performance and community assembly, and thereby ecosystem functioning in a changing world. For example, the decreased mean body sizes of soil fauna may lead to a reduction in their community biomass, and thereby affect litter decomposition and nutrient cycling. Our findings are partially supported by another study (Martins da Silva et al., 2016), which showed that the responses of Collembola functional traits differed among land-use types, i.e., the proportion of soil dwelling species was higher in natural sites than in arable sites, but soil surface-dwelling species showed the opposite pattern. In the present study, we also found that land-use intensification shifted the functional composition of Collembola communities, and decreased the values of Soil Biological Quality index (QBS). Similarly, Ponge et al., (2013) using a comparable score (termed as ‘the composite index’) to estimate the effects of land uses and agricultural practice on the functional (i.e., morphological) traits of soil animals in French Brittany showed that land-use intensification also exerted unfavorable effects on soil biology quality. Besides, some other studies showed that land-use change shifted Collembola community structure through changing their community traits (Salmon et al., 2014; Salmon and Ponge, 2012). Our findings therefore suggest that land-use intensification is the main factor determining the dominance of single functional traits, thereby influencing the Collembola functional composition pattern and soil biological quality.

4.3. Negligible climate change effects on Collembola functional response variables

Our previous study suggests that Collembola (abundance) are rather vulnerable to our projected future climate scenario (Yin et al., 2019b). Additionally, climate change may shift

the functional traits and functional composition of soil biota (Makkonen et al., 2011; Thakur et al., 2017; Wallenstein and Hall, 2012). However, in this study, we did not find any significant effects of climate change on Collembola functional response variables. These findings are in line with Holmstrup et al. (2018), who found that functional responses of Collembola communities were significantly affected by short-term warming to 10°C above ambient, while no effects were found under lower, and more realistic levels of climate warming in field conditions. This indicates that the functional diversity of Collembola communities is largely resistant to minor temperature increase, with little effects of simulated realistic climate change particularly so in field settings. This could further be related to potentially greater buffering of temperature in the soil given its highly compact three dimensional structure (Thakur et al., 2019). Furthermore, effects of small but realistic temperature changes may simply take longer to develop, resulting in strong(er) effects in the longer-term. Instead of testing soil community responses under highly controlled conditions, our study simulated a realistic future climate scenario with natural variability for Central Germany in the years of 2070 – 2100 (i.e., +0.6 °C above ambient) (Schädler et al., 2019).

4.4. No interactive effects of climate and land use on Collembola functional response variables

To determine the consequences of global change for terrestrial ecosystems, it is important to understand how the interplay of climate and land use constrains biodiversity and ecosystem functions (Oliver et al., 2016; Peters et al., 2019). We therefore hypothesized that the functional responses of Collembola would depend on interactive effects of climate change and land-use intensification. However, we did not find any interactive effects. This finding is counter-intuitive, since intensively-used lands, as characterized by higher levels of disturbance and lower biodiversity, are generally more vulnerable to climate change (Isbell et al., 2017). By contrast, extensively-used lands with less disturbance and higher biodiversity

potentially mitigate these detrimental effects of climate change (Oliver et al., 2016). In previous studies, we found that climate change did not alter land-use effects on the ecosystem function (i.e., litter decomposition) of soil detritivores (Yin et al., 2019c). All these findings suggest that predicted climate change may not intensify effects of land-use change. However, we do expect that increasing frequency and magnitude of extreme climatic events may intensify land-use effects on soil communities and recommend such experiments as a priority for future global change studies.

5. Conclusion

We conclude that the functional responses of Collembola are particularly vulnerable to land-use intensification but lesser so to climate change scenarios used in our study. Specifically, intensive land use decreased the functional biodiversity and shifted community traits, and thereby the functional composition of Collembola. Further, our findings show that these significant land-use effects were determined by the differences between the two main land-use types (croplands vs. grasslands), rather than by the different management intensities within the same land-use type. However, no interactive effects of climate and land use were detected in this study, suggesting that the functional responses of Collembola to land-use intensification were consistent under both climate scenarios. Based on these findings, we suggest that reduced Collembola functional biodiversity and soil biological quality may threaten the functions and services of intensively-managed ecosystems. Moreover, trait-based approaches were proven useful tools in this study in evaluating the functional responses of Collembola to environmental change. However, we still do not know the relationships between Collembola and other soil biota under long-term environmental change.

In a soil food web context, Collembola responses may depend on direct effects of environmental change, but also on bottom-up effects (i.e., through changes in their food sources) and top-down effects (i.e., through changes in predators). We further suggest future

studies to investigate functional responses of soil communities to multiple types of environmental change (Rillig et al., 2019), and explore the potential links between species traits and community structure. Moreover, it will be important to explicitly link changes in the functional composition of soil communities to ecosystem functioning, to better understand the ecological consequences of belowground functional shifts in a changing world.

Acknowledgments

We thank the Helmholtz Association, Federal Ministry of Education and Research, the State Ministry of Science and Economy of Saxony-Anhalt and the State Ministry for Higher Education, Research and the Arts Saxony to fund the Global Change Experimental Facility (GCEF) project. We further acknowledge funding from the National Natural Science Foundation of China (NSFC 41722107, 41977063 to G.L.W.), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB40020302 to G.L.W.), the China Scholarship Council (CSC No. 201406910015 to R.Y.), and the German Research Foundation (TH 2307/1-1 to M.P.T.). This project also received support from the European Research Council under the European Union's Horizon 2020 research and innovation program (grant agreement No. 677232 to N.E.). Further support came from the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the DFG (FZT 118). We also thank the staff of the Bad Lauchstädt Experimental Research Station, especially Ines Merbach and Konrad Kirsch, for their hard work in maintaining the GCEF, as well as Stefan Klotz, François Buscot and Thomas Reitz for their roles in setting up the GCEF.

Conflict of interest

The authors declare no conflict of interest.

Authors' contributions

R.Y., N.E., and M.S. conceived the idea and designed the study; R.Y., I.G. and M.S. performed the experiment and collected the data; R.Y., and M.P.T analyzed the data; R.Y. and G.L.W led the writing of the manuscript with substantial help of P.K. All authors contributed critically to the draft and gave final approval for publication.

References

- Altermann, M., Rinklebe, J., Merbach, I., Körschens, M., Langer, U., Hofmann, B., 2005. Chernozem - Soil of the Year 2005. *Journal of Plant Nutrition and Soil Science*. doi:10.1002/jpln.200521814
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters*. doi:10.1111/j.1461-0248.2011.01736.x
- Birkhofer, K., Gossner, M.M., Diekötter, T., Drees, C., Ferlian, O., Maraun, M., Scheu, S., Weisser, W.W., Wolters, V., Wurst, S., Zaitsev, A.S., Smith, H.G., 2017. Land-use type and intensity differentially filter traits in above- and below-ground arthropod communities. *Journal of Animal Ecology* 86, 511–520. doi:10.1111/1365-2656.12641
- Blankinship, J.C., Niklaus, P.A., Hungate, B.A., 2011. A meta-analysis of responses of soil biota to global change. *Oecologia*. doi:10.1007/s00442-011-1909-0
- Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*. doi:10.1111/j.1365-2664.2011.02048.x
- Chauvat, M., Wolters, V., Dauber, J., 2007. Response of collembolan communities to land-use change and grassland succession. *Ecography* 30, 183–192. doi:10.1111/j.2007.0906-7590.04888.x
- Christiansen, K., 1963. Bionomics of collembola. *Annual Review of Entomology* 9, 147–178. doi:10.1146/annurev.en.09.010164.001051

- de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., da Silva, P.M., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A., Harrison, P.A., 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation* 19, 2873–2893. doi:10.1007/s10531-010-9850-9
- Dou, Y., Zhang, B., Sun, X., Chang, L., Wu, D., 2019. Marshland restoration benefits *Collembola* recruitment: a long-term chronosequence study in Sanjiang mire marshland, China. *PeerJ* 7, e7198. doi:10.7717/peerj.7198
- Eisenhauer, N., Powell, J.R., 2017. Plant trait effects on soil organisms and functions. *Pedobiologia*. doi:10.1016/j.pedobi.2017.11.001
- European Commission, 2006. Thematic strategy for soil protection, Com (2006).
- Fjellberg, A., 2007a. The *Collembola* of Fennoscandia and Denmark - Part II: Entomobryomorpha and Symphypleona, Brill. doi:10.1163/ej.9789004157705.i-265
- Fjellberg, A., 2007b. The *Collembola* of Fennoscandia and Denmark: Part II: Entomobryomorpha and symphypleona. *Fauna Entomologica Scandinavica* 42, 1–270.
- Flynn, D.F.B., Mirotchnick, N., Jain, M., Palmer, M.I., Naeem, S., 2011. Functional and phylogenetic diversity as predictors of biodiversity- Ecosystem-function relationships. *Ecology* 92, 1573–1581. doi:10.1890/10-1245.1
- Fontana, S., Petchey, O.L., Pomati, F., 2016. Individual-level trait diversity concepts and indices to comprehensively describe community change in multidimensional trait space. *Functional Ecology* 30, 808–818. doi:10.1111/1365-2435.12551
- Gallé, R., Happe, A.K., Baillod, A.B., Tschardtke, T., Batáry, P., 2019. Landscape configuration, organic management, and within-field position drive functional diversity of spiders and carabids. *Journal of Applied Ecology* 56, 63–72. doi:10.1111/1365-2664.13257

464 Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G.,
 465 Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.P., 2004. Plant functional
 466 markers capture ecosystem properties during secondary succession. *Ecology* 85, 2630–
 467 2637. doi:10.1890/03-0799

468 Gruss, I., Twardowski, J.P., Latawiec, A., Królczyk, J., Medyńska-Juraszek, A., 2019. The
 469 Effect of Biochar Used as Soil Amendment on Morphological Diversity of Collembola.
 470 *Sustainability* 11, 5126. doi:10.3390/su11185126

471 Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. Past: Paleontological statistics software
 472 package for education and data analysis. *Palaeontologia Electronica* 4.

473 Hedde, M., Pey, B., Auclerc, A., Capowiez, Y., 2012. BETSI, a complete framework for
 474 studying soil invertebrate functional traits. 16th International Colloquium on Soil
 475 Zoology, Coimbra, P. doi:10.13140/2.1.1286.6888

476 Holmstrup, M., Ehlers, B.K., Slotsbo, S., Ilieva-Makulec, K., Sigurdsson, B.D., Leblans,
 477 N.I.W., Ellers, J., Berg, M.P., 2018. Functional diversity of Collembola is reduced in
 478 soils subjected to short-term, but not long-term, geothermal warming. *Functional*
 479 *Ecology* 1304–1316. doi:10.1111/1365-2435.13058

480 Hopkin, S.P., 1997. *The Biology of the Collembola (Springtails): The Most Abundant Insects*
 481 *in the World*, Oxford University Press.

482 Isbell, F., Adler, P.R., Eisenhauer, N., Fornara, D., Kimmel, K., Kremen, C., Letourneau,
 483 D.K., Liebman, M., Polley, H.W., Quijas, S., Scherer-Lorenzen, M., 2017. Benefits of
 484 increasing plant diversity in sustainable agroecosystems. *Journal of Ecology*.
 485 doi:10.1111/1365-2745.12789

486 Joimel, S., Schwartz, C., Hedde, M., Kiyota, S., Krogh, P.H., Nahmani, J., Pérès, G., Vergnes,
 487 A., Cortet, J., 2017. Urban and industrial land uses have a higher soil biological quality
 488 than expected from physicochemical quality. *Science of the Total Environment* 584,
 489 614–621. doi:10.1016/j.scitotenv.2017.01.086

490 Kempson, D., Lloyd, M., Ghelardi, R., 1963. A new extractor for woodland litter.
 491 *Pedobiologia* 1–30.

492 Laliberte, E., Shipley, B., 2011. Measuring functional diversity (FD) from multiple traits, and
 493 other tools for functional ecology. *R Help*.

494 Laliberté, E., Legendre, P., Shipley, B., & Laliberté, M.E., 2014. Package ‘FD’. Measuring
 495 functional diversity from multiple traits, and other tools for functional ecology.

496 Ligges, U., Mächler, M., 2003. Scatterplot3d - An R package for visualizing multivariate data.
 497 *Journal of Statistical Software* 8, 1–20.

498 Makkonen, M., Berg, M.P., van Hal, J.R., Callaghan, T. V., Press, M.C., Aerts, R., 2011.
 499 Traits explain the responses of a sub-arctic Collembola community to climate
 500 manipulation. *Soil Biology and Biochemistry* 43, 377–384.
 501 doi:10.1016/j.soilbio.2010.11.004

502 Malmström, A., 2012. Life-history traits predict recovery patterns in Collembola species after
 503 fire: A 10 year study. *Applied Soil Ecology* 56, 35–42. doi:10.1016/j.apsoil.2012.02.007

504 Martins da Silva, P., Carvalho, F., Dirilgen, T., Stone, D., Creamer, R., Bolger, T., Sousa,
 505 J.P., 2016. Traits of collembolan life-form indicate land use types and soil properties
 506 across an European transect. *Applied Soil Ecology* 97, 69–77.
 507 doi:10.1016/j.apsoil.2015.07.018

508 Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional
 509 evenness and functional divergence: The primary components of functional diversity.
 510 *Oikos* 111, 112–118. doi:10.1111/j.0030-1299.2005.13886.x

511 Menta, C., Conti, F.D., Pinto, S., 2018a. Microarthropods biodiversity in natural, seminatural
 512 and cultivated soils—QBS-ar approach. *Applied Soil Ecology* 123, 740–743.
 513 doi:10.1016/j.apsoil.2017.05.020

514 Menta, C., Conti, F.D., Pinto, S., Bodini, A., 2018b. Soil Biological Quality index (QBS-ar):
515 15 years of application at global scale. Ecological Indicators.
516 doi:10.1016/j.ecolind.2017.11.030

517 Menta, C., García-Montero, L.G., Pinto, S., Conti, F.D., Baroni, G., Maresi, M., 2014. Does
518 the natural “microcosm” created by *Tuber aestivum* affect soil microarthropods? A new
519 hypothesis based on Collembola in truffle culture. Applied Soil Ecology 84, 31–37.
520 doi:10.1016/j.apsoil.2014.06.012

521 Moretti, M., Dias, A.T.C., de Bello, F., Altermatt, F., Chown, S.L., Azcárate, F.M., Bell, J.R.,
522 Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J.P., Ellers, J., Berg,
523 M.P., 2017. Handbook of protocols for standardized measurement of terrestrial
524 invertebrate functional traits. Functional Ecology 31, 558–567. doi:10.1111/1365-
525 2435.12776

526 Mouchet, M.A., Villéger, S., Mason, N.W.H., Mouillot, D., 2010. Functional diversity
527 measures: An overview of their redundancy and their ability to discriminate community
528 assembly rules. Functional Ecology 24, 867–876. doi:10.1111/j.1365-2435.2010.01695.x

529 Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L.,
530 Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-
531 Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T.,
532 Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia,
533 D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W.,
534 Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., MacE,
535 G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local
536 terrestrial biodiversity. Nature 520, 45–50. doi:10.1038/nature14324

537 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., 2013. Package ‘vegan’ R
538 Packag

539 Oliver, I., Dorrough, J., Doherty, H., Andrew, N.R., 2016. Additive and synergistic effects of
 540 land cover, land use and climate on insect biodiversity. *Landscape Ecology* 31, 2415–
 541 2431. doi:10.1007/s10980-016-0411-9

542 Pacala, S.W., Tilman, D., 1994. Limiting similarity in mechanistic and spatial models of plant
 543 competition in heterogeneous environments. *American Naturalist* 143, 222–257.
 544 doi:10.1086/285602

545 Parisi, V., 2001. The biological quality of soil. A method based on microarthropods | La
 546 qualità biologica del suolo. Un metodo basato sui microartropodi. *Acta Naturalia de*
 547 *l'Ateneo Parmense* 37, 105–114.

548 Parisi, V., Menta, C., Gardi, C., Jacomini, C., Mozzanica, E., 2005. Microarthropod
 549 communities as a tool to assess soil quality and biodiversity: A new approach in Italy.
 550 *Agriculture, Ecosystems and Environment* 105, 323–333.
 551 doi:10.1016/j.agee.2004.02.002

552 Peters, M.K., Hemp, A., Appelhans, T., Becker, J.N., Behler, C., Classen, A., Detsch, F.,
 553 Ensslin, A., Ferger, S.W., Frederiksen, S.B., Gebert, F., Gerschlauser, F., Gütlein, A.,
 554 Helbig-Bonitz, M., Hemp, C., Kindeketa, W.J., Kühnel, A., Mayr, A. V., Mwangomo,
 555 E., Ngereza, C., Njovu, H.K., Otte, I., Pabst, H., Renner, M., Röder, J., Rutten, G.,
 556 Schellenberger Costa, D., Sierra-Cornejo, N., Vollstädt, M.G.R., Dulle, H.I., Eardley,
 557 C.D., Howell, K.M., Keller, A., Peters, R.S., Ssymank, A., Kakengi, V., Zhang, J.,
 558 Bogner, C., Böhning-Gaese, K., Brandl, R., Hertel, D., Huwe, B., Kiese, R., Kleyer, M.,
 559 Kuzyakov, Y., Nauss, T., Schleuning, M., Tschapka, M., Fischer, M., Steffan-Dewenter,
 560 I., 2019. Climate–land-use interactions shape tropical mountain biodiversity and
 561 ecosystem functions. *Nature*. doi:10.1038/s41586-019-1048-z

562 Peterson, B., Carl, P., Boudt, K., Bennett, R., Ulrich, J., Zivot, E., Lestel, M., Balkissoon, K.,
 563 Wuertz, D., 2015. Package “PerformanceAnalytics.” R Documentation.

564 Pey, B., Nahmani, J., Auclerc, A., Capowiez, Y., Cluzeau, D., Cortet, J.Ô., Decaëns, T.,
 565 Deharveng, L., Dubs, F., Joimel, S., Briard, C., Grumiaux, F., Laporte, M.A., Pasquet,
 566 A., Pelosi, C., Pernin, C., Ponge, J.F., Salmon, S., Santorufo, L., Hedde, M., 2014.
 567 Current use of and future needs for soil invertebrate functional traits in community
 568 ecology. *Basic and Applied Ecology* 15, 194–206. doi:10.1016/j.baae.2014.03.007
 569 Phillips, H., Beaumelle, L., Tyndall, K., Burton, V., Cameron, E., Eisenhauer, N., Ferlian, O.,
 570 2019. The effects of global change on soil faunal communities: a meta-analytic
 571 approach. *Research Ideas and Outcomes* 5. doi:10.3897/rio.5.e36427
 572 Pinto, S., Gatti, F., García-Montero, L.G., Menta, C., 2017. Does soil fauna like truffles just
 573 as humans do? One-year study of biodiversity in natural brûlés of *Tuber aestivum* Vittad.
 574 *Science of the Total Environment* 584, 1175–1184. doi:10.1016/j.scitotenv.2017.01.181
 575 Pollierer, M.M., Scheu, S., 2017. Driving factors and temporal fluctuation of Collembola
 576 communities and reproductive mode across forest types and regions. *Ecology and*
 577 *Evolution* 7, 4390–4403. doi:10.1002/ece3.3035
 578 Ponge, J.F., Pérès, G., Guernion, M., Ruiz-Camacho, N., Cortet, J.Ô., Pernin, C., Villenave,
 579 C., Chaussod, R., Martin-Laurent, F., Bispo, A., Cluzeau, D., 2013. The impact of
 580 agricultural practices on soil biota: A regional study. *Soil Biology and Biochemistry* 67,
 581 271–284. doi:10.1016/j.soilbio.2013.08.026
 582 R Core Team, 2017. R: A language and environment for statistical computing. [http://www.R-](http://www.R-project.org/)
 583 [project.org/](http://www.R-project.org/). [WWW Document]. R Foundation for Statistical Computing, Vienna,
 584 Austria. doi:10.1007/978-3-540-74686-7
 585 Reis, F., Carvalho, F., Martins Da Silva, P., Mendes, S., Santos, S.A.P., Sousa, J.P., 2016.
 586 The use of a functional approach as surrogate of Collembola species richness in
 587 European perennial crops and forests. *Ecological Indicators* 61, 676–682.
 588 doi:10.1016/j.ecolind.2015.10.019

589 Reiss, J., Bridle, J.R., Montoya, J.M., Woodward, G., 2009. Emerging horizons in
590 biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution*.
591 doi:10.1016/j.tree.2009.03.018

592 Rillig, M.C., Ryo, M., Lehmann, A., Aguilar-Trigueros, C.A., Buchert, S., Wulf, A., Iwasaki,
593 A., Roy, J., Yang, G., 2019. The role of multiple global change factors in driving soil
594 functions and microbial biodiversity. *Science (New York, N.Y.)* 366, 886–890.
595 doi:10.1126/science.aay2832

596 Rusek, J., 2007. A new classification of Collembola and Protura life forms. *Contributions to*
597 *Soil Zoology in Central Europe II* 109–115.

598 Sala, O.E., Stuart, F., Iii, C., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-
599 Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M.,
600 Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall,
601 D.H., 2000. Global Biodiversity Scenarios for the Year 2100. *Science* 287, 1770–1774.
602 doi:10.1126/science.287.5459.1770

603 Salmon, S., Ponge, J.F., 2012. Species traits and habitats in springtail communities: A
604 regional scale study. *Pedobiologia* 55, 295–301. doi:10.1016/j.pedobi.2012.05.003

605 Salmon, S., Ponge, J.F., Gachet, S., Deharveng, L., Lefebvre, N., Delabrosse, F., 2014.
606 Linking species, traits and habitat characteristics of Collembola at European scale. *Soil*
607 *Biology and Biochemistry* 75, 73–85. doi:10.1016/j.soilbio.2014.04.002

608 Schädler, M., Buscot, F., Klotz, S., Reitz, T., Durka, W., Bumberger, J., Merbach, I.,
609 Michalski, S.G., Kirsch, K., Remmler, P., Schulz, E., Auge, H., 2019. Investigating the
610 consequences of climate change under different land-use regimes: a novel experimental
611 infrastructure. *Ecosphere* 10, e02635. doi:10.1002/ecs2.2635

612 Scheu, S., Drossel, B., 2007. Sexual reproduction prevails in a world of structured resources
613 in short supply. *Proceedings of the Royal Society B: Biological Sciences* 274, 1225–
614 1231. doi:10.1098/rspb.2007.0040

615 Sechi, V., De Goede, R.G.M., Rutgers, M., Brussaard, L., Mulder, C., 2018. Functional
616 diversity in nematode communities across terrestrial ecosystems. *Basic and Applied*
617 *Ecology* 30, 76–86. doi:10.1016/j.baae.2018.05.004

618 Siebert, J., Thakur, M.P., Reitz, T., Schädler, M., Schulz, E., Yin, R., Weigelt, A., Eisenhauer,
619 N., 2019. Extensive grassland-use sustains high levels of soil biological activity, but does
620 not alleviate detrimental climate change effects, *Advances in Ecological Research* 60,
621 25–58. doi:10.1016/bs.aecr.2019.02.002

622 Thakur, M.P., Griffin, J.N., Künne, T., Dunker, S., Fanesi, A., Eisenhauer, N., 2018.
623 Temperature effects on prey and basal resources exceed that of predators in an
624 experimental community. *Ecology and Evolution* 8, 12670–12680.
625 doi:10.1002/ece3.4695

626 Thakur, M.P., Künne, T., Griffin, J.N., Eisenhauer, N., 2017. Warming magnifies predation
627 and reduces prey coexistence in a model litter arthropod system. *Proceedings of the*
628 *Royal Society B: Biological Sciences* 284. doi:10.1098/rspb.2016.2570

629 Thakur, M.P., Phillips, H.R.P., Brose, U., De Vries, F.T., Lavelle, P., Loreau, M., Mathieu, J.,
630 Mulder, C., Van der Putten, W.H., Rillig, M.C., Wardle, D.A., Bach, E.M., Bartz,
631 M.L.C., Bennett, J.M., Briones, M.J.I., Brown, G., Decaëns, T., Eisenhauer, N., Ferlian,
632 O., Guerra, C.A., König- Ries, B., Orgiazzi, A., Ramirez, K.S., Russell, D.J., Rutgers,
633 M., Wall, D.H., Cameron, E.K., 2019. Towards an integrative understanding of soil
634 biodiversity. *Biological Reviews* brv.12567. doi:10.1111/brv.12567

635 Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of
636 functional diversity and composition on ecosystem processes. *Science* 277, 1300–1302.
637 doi:10.1126/science.277.5330.1300

638 Tsiafouli, M.A., Thébault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H.,
639 Birkhofer, K., Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., Bjornlund, L.,
640 Jørgensen, H.B., Christensen, S., Hertefeldt, T.D., Hotes, S., Gera Hol, W.H., Frouz, J.,

- Liiri, M., Mortimer, S.R., Setälä, H., Tzanopoulos, J., Uteseny, K., Pižl, V., Stary, J.,
Wolters, V., Hedlund, K., 2015. Intensive agriculture reduces soil biodiversity across
Europe. *Global Change Biology* 21, 973–985. doi:10.1111/gcb.12752
- Twardowski, J.P., Hurej, M., Gruss, I., 2016. Diversity and abundance of springtails
(Hexapoda: Collembola) in soil under 90-year potato monoculture in relation to crop
rotation. *Archives of Agronomy and Soil Science* 62, 1158–1168.
doi:10.1080/03650340.2015.1131270
- Vandewalle, M., de Bello, F., Berg, M.P., Bolger, T., Dolédec, S., Dubs, F., Feld, C.K.,
Harrington, R., Harrison, P.A., Lavorel, S., da Silva, P.M., Moretti, M., Niemelä, J.,
Santos, P., Sattler, T., Sousa, J.P., Sykes, M.T., Vanbergen, A.J., Woodcock, B.A., 2010.
Functional traits as indicators of biodiversity response to land use changes across
ecosystems and organisms. *Biodiversity and Conservation* 19, 2921–2947.
doi:10.1007/s10531-010-9798-9
- Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity
indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301.
doi:10.1890/07-1206.1
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007.
Let the concept of trait be functional! *Oikos*. doi:10.1111/j.0030-1299.2007.15559.x
- Wallenstein, M.D., Hall, E.K., 2012. A trait-based framework for predicting when and where
microbial adaptation to climate change will affect ecosystem functioning.
Biogeochemistry 109, 35–47. doi:10.1007/s10533-011-9641-8
- Wan Hussin, W.M.R., Cooper, K.M., Froján, C.R.S.B., Defew, E.C., Paterson, D.M., 2012.
Impacts of physical disturbance on the recovery of a macrofaunal community: A
comparative analysis using traditional and novel approaches. *Ecological Indicators* 12,
37–45. doi:10.1016/j.ecolind.2011.03.016

666 Wieczynski, D.J., Boyle, B., Buzzard, V., Duran, S.M., Henderson, A.N., Hulshof, C.M.,
 667 Kerkhoff, A.J., McCarthy, M.C., Michaletz, S.T., Swenson, N.G., Asner, G.P., Bentley,
 668 L.P., Enquist, B.J., Savage, V.M., 2019. Climate shapes and shifts functional
 669 biodiversity in forests worldwide. *Proceedings of the National Academy of Sciences of*
 670 *the United States of America* 116, 587–592. doi:10.1073/pnas.1813723116
 671 Winck, B.R., Saccol de Sá, E.L., Rigotti, V.M., Chauvat, M., 2017. Relationship between
 672 land-use types and functional diversity of epigeic Collembola in Southern Brazil.
 673 *Applied Soil Ecology* 109, 49–59. doi:10.1016/j.apsoil.2016.09.021
 674 WRB, I.W.G., 2007. World reference base for soil resources 2006, World Soil Resources
 675 Reports.
 676 Yin, R., Gruss, I., Eisenhauer, N., Kardol, P., Thakur, M.P., Schmidt, A., Xu, Z., Siebert, J.,
 677 Zhang, C., Wu, G.-L., Schädler, M., 2019a. Land use modulates the effects of climate
 678 change on density but not community composition of Collembola. *Soil Biology and*
 679 *Biochemistry* 138, 107598. doi:10.1016/j.soilbio.2019.107598
 680 Yin, R., Eisenhauer, N., Schmidt, A., Gruss, I., Purahong, W., Siebert, J., Schädler, M.,
 681 2019b. Climate change does not alter land-use effects on soil fauna communities.
 682 *Applied Soil Ecology*. doi:10.1016/j.apsoil.2019.03.026
 683 Yin, R., Eisenhauer, N., Auge, H., Purahong, W., Schmidt, A., Schädler, M., 2019c. Additive
 684 effects of experimental climate change and land use on faunal contribution to litter
 685 decomposition. *Soil Biology and Biochemistry* 131, 141–148.
 686 doi:10.1016/j.soilbio.2019.01.009
 687

688 **Tables and figures**

689 **Table 1** Effects of climate, land use and their interaction on Collembola functional diversity
 690 (FD) indices: functional richness (FRic), functional evenness (FEve), and functional
 691 divergence (FDiv) using generalized mixed models. Significant effects are indicated in bold
 692 font: *F*-values with ** $P < 0.01$, *** $P < 0.001$.

Effects	<i>Df</i>	FRic	FEve	FDiv
Climate (C)	1,8	1.52	2.91	0.08
Land use (L)	4,32	7.53***	4.7**	1.11
C × L	4,32	0.81	0.44	0.87

693

694 **Table 2** Effects of climate, land use and their interaction on community-weighted mean (CWM) of life-history traits (habitat-vertical stratification,
695 reproductive mode, and dispersal ability), and morphological traits (furca, ocelli, pigmentation, hair, body size, and antenna length), and Soil
696 Biological Quality index based on Collembola species (QBS-c) using generalized mixed models. Significant effects are indicated in bold font: *F*-
697 values with ** = $P < 0.01$, *** = $P < 0.001$.

Effects	<i>Df</i>	Life-history traits			Morphological traits						QBS-c
		Habitat	Reproductive mode	Dispersal ability	Furca	Ocelli	Pigmentation	Hair	Body size	Antenna length	
Climate (C)	1,8	0.36	0.41	0.05	0.7	0.61	0.06	0.34	2.49	4.02	0.29
Land use (L)	4,32	7.15***	7.48***	8.58***	7.18***	8.23***	9.98***	4.3**	2.58*	7.03***	8.6***
C × L	4,32	0.03	1.22	1.31	1.12	1.4	0.71	2.88	1.35	1.63	1.25

698

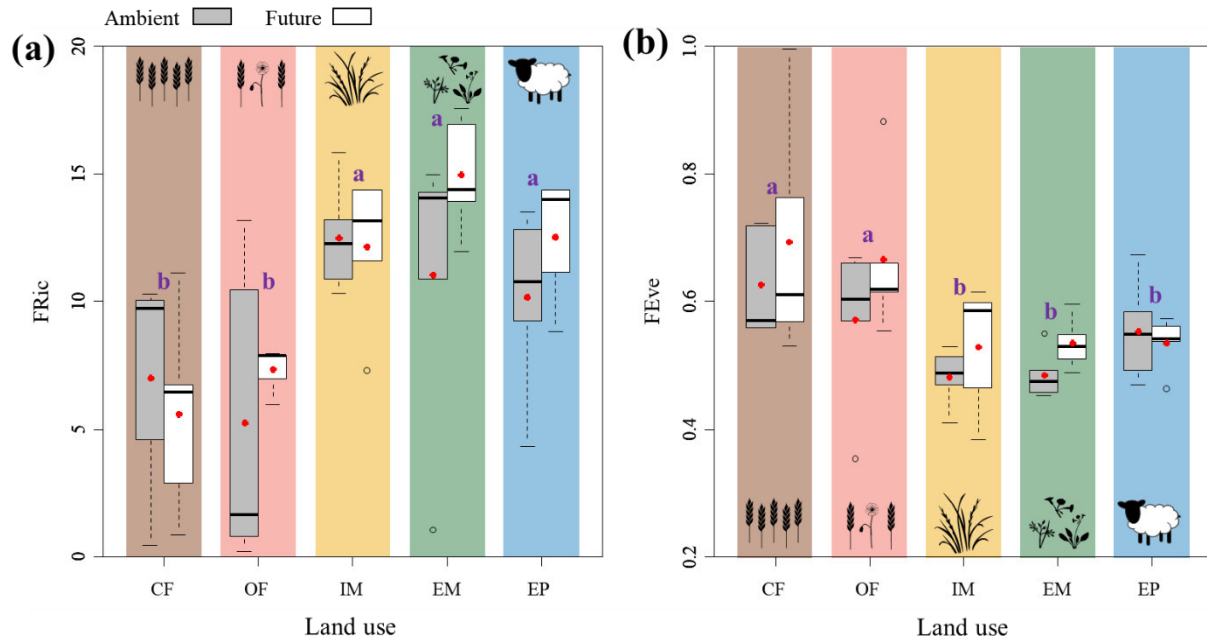


Figure 1 Effects of climate and land use on (a) functional richness (FRic) and (b) functional evenness (FEve) of Collembola. Boxplots show the median (horizontal line), mean (red dot), first and third quartile (rectangle), $1.5 \times$ interquartile range (whiskers), and outliers (isolated black dots). Lowercase letters represent significant differences between land-use regimes (across climate scenarios) by Post-hoc Tukey's HSD tests at $P < 0.05$. Abbreviations for land-use regimes: CF = conventional farming; OF = organic farming; IM = intensively-used meadow; EM = extensively-used meadow; EP = extensively-used pasture. Copyrights of land use icons by Gottschall/Siebert.

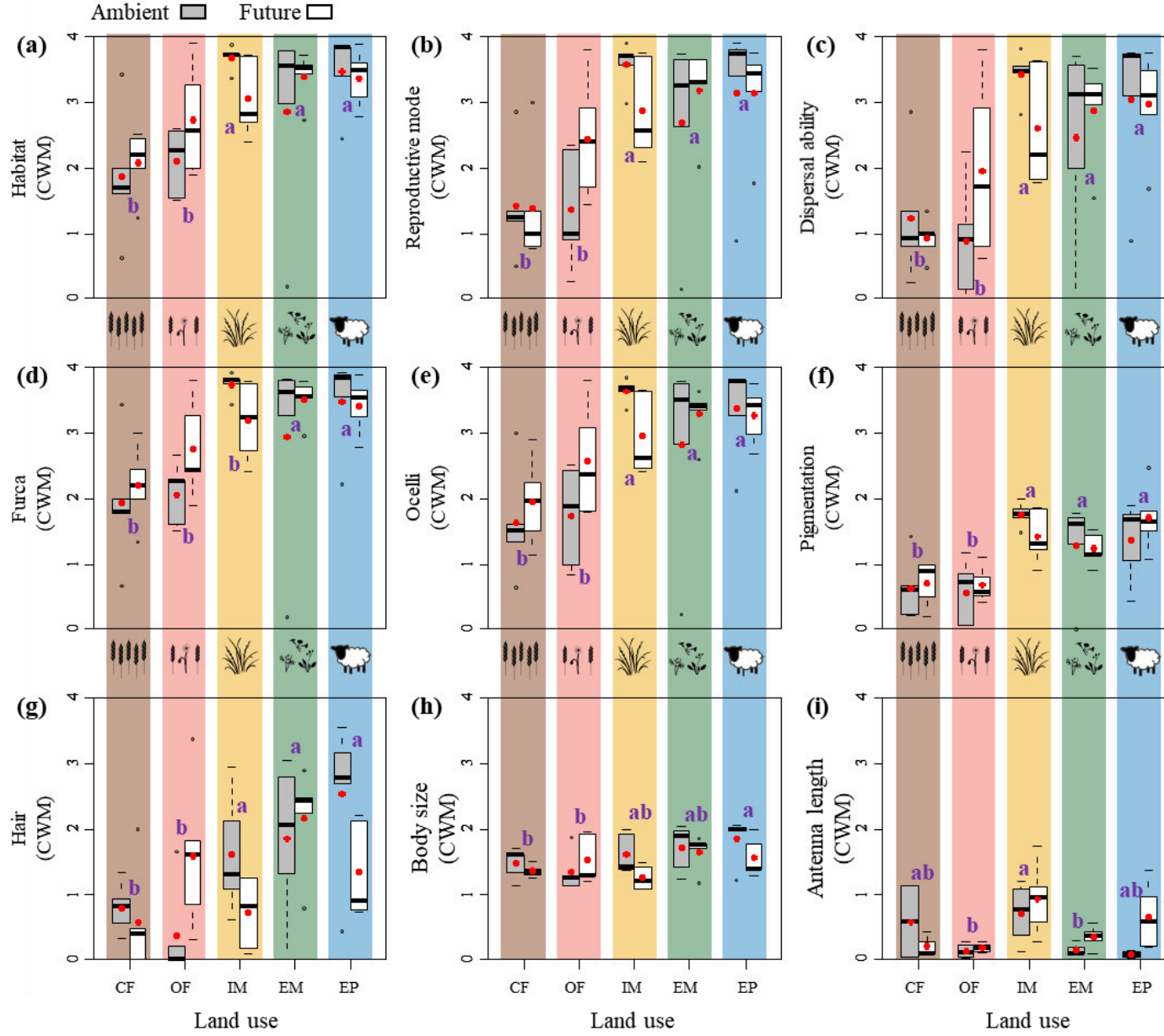


Figure 2 Effects of climate and land use on community-weighted mean (CWM) of Collembola functional traits: (a) habitat – vertical stratification, (b) reproductive mode, (c) dispersal ability, (d) furca, (e) ocelli, (f) pigmentation, (g) hair, (h) body size, and (i) antenna length. Boxplots show the median (horizontal line), mean (red dot), first and third quartile (rectangle), 1.5 × interquartile range (whiskers), and outliers (isolated black dots). Lowercase letters represent significant differences between land-use regimes (across climate scenarios) by Post-hoc Tukey’s HSD tests at $P < 0.05$. Abbreviations for land-use regimes: CF = conventional farming; OF = organic farming; IM = intensively-used meadow; EM = extensively-used meadow; EP = extensively-used pasture. Copyrights of land use icons by Gottschall/Siebert.

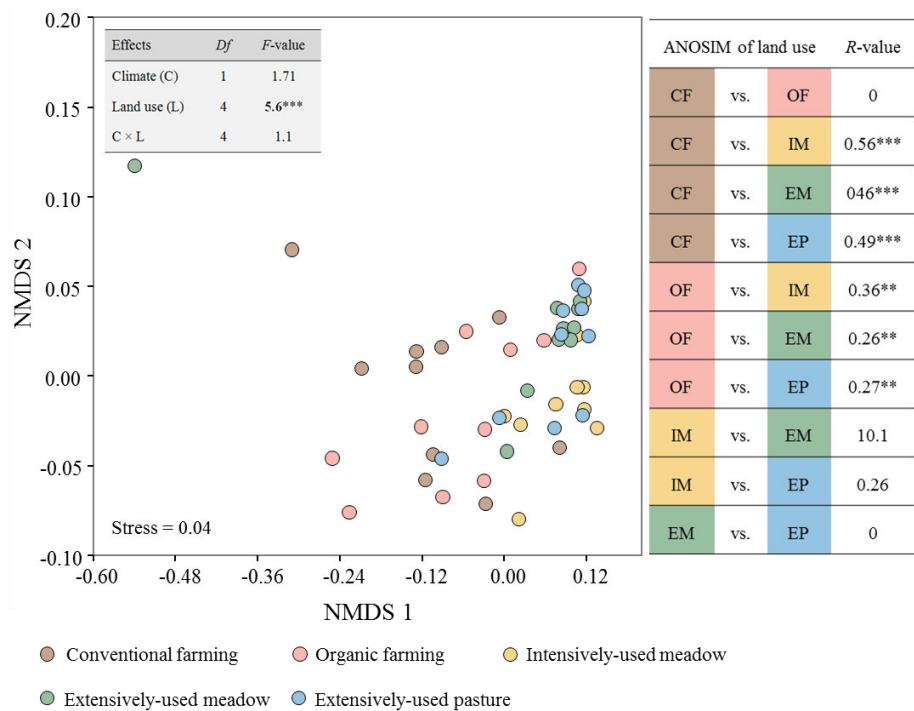


Figure 3 Effects of land use on functional composition of Collembola communities. On the left: Non-metric multidimensional scaling (NMDS) ordination showing similarity of functional composition of Collembola communities among plots under different land use regimes. Effects

of climate, land use, and their interaction were tested by non-parametric multivariate analysis of variance (PERMANOVA). On the right: Analysis of similarity (ANOSIM) of land-use regimes based on Bray-Curtis distance measurement of functional composition revealed a significant separation between the two main land-use types, i.e., croplands vs. grasslands. Significant effects are indicated in bold font: ** = $P < 0.01$, *** = $P < 0.001$.

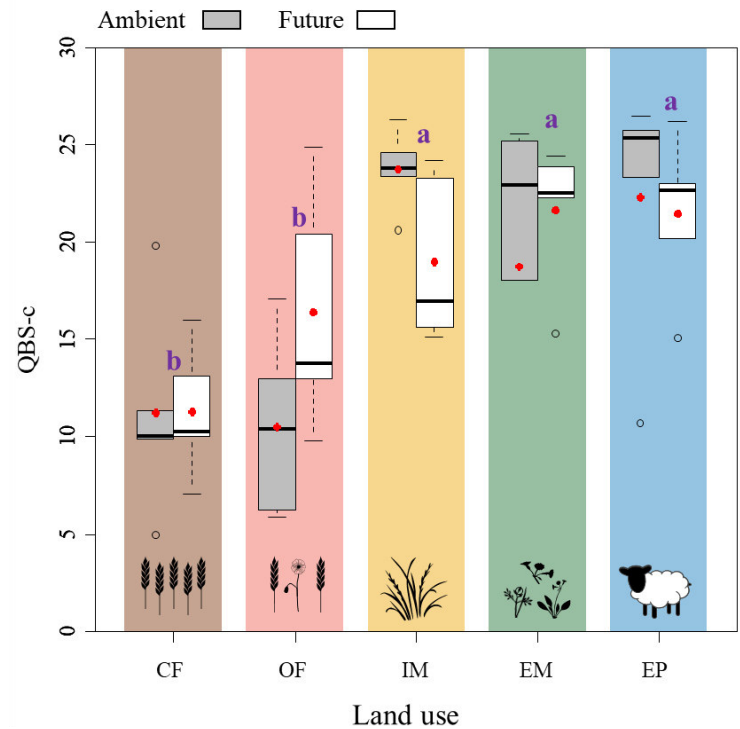


Figure 4 Effects of climate and land use on the soil biology quality (QBS-c). Boxplots show the median (horizontal line), mean (red dot), first and third quartile (rectangle), $1.5 \times$ interquartile range (whiskers), and outliers (isolated black dots). Lowercase letters represent significant differences between land-use regimes (across climate scenarios) by Post-hoc Tukey's HSD tests at $P < 0.05$. Abbreviations for land-use regimes: CF = conventional farming; OF = organic farming; IM = intensively-used meadow; EM = extensively-used meadow; EP = extensively-used pasture. Copyrights of land use icons by Gottschall/Siebert.

Supplementary Material for online publication only

[Click here to download Supplementary Material for online publication only: 2. SUPPLEMENTARY MATERIALS_resubmission.doc](#)

Declaration of interests

☒ 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.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: