

Intensive agriculture reduces soil biodiversity across Europe

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Abstract

Soil biodiversity plays a key role in regulating the processes that underpin the delivery of ecosystem goods and services in terrestrial ecosystems. Agricultural intensification is known to change the diversity of individual groups of soil biota, but less is known about how intensification affects biodiversity of the soil food web as a whole, and whether or not these effects may be generalized across regions. We examined biodiversity in soil food webs from grasslands, extensive, and intensive rotations in four agricultural regions across Europe: in Sweden, the UK, the Czech Republic and Greece. Effects of land-use intensity were quantified based on structure and diversity among functional groups in the soil food web, as well as on community-weighted mean body mass of soil fauna. We also elucidate land-use intensity effects on diversity of taxonomic units within taxonomic groups of soil fauna. We found that between regions soil food web diversity measures were variable, but that increasing land-use intensity caused highly consistent responses. In particular, land-use intensification reduced the complexity in the soil food webs, as well as the community-weighted mean body mass of soil fauna. In all regions across Europe, species richness of earthworms, Collembolans, and oribatid mites was negatively affected by increased land-use intensity. The taxonomic distinctness, which is a measure of taxonomic relatedness of species in a community that is independent of species richness, was also reduced by land-use intensification. We conclude that intensive agriculture reduces soil biodiversity, making soil food webs less diverse and composed of smaller bodied organisms. Land-use intensification results in fewer functional groups of soil biota with fewer and taxonomically more closely related species. We discuss how these changes in soil biodiversity due to land-use intensification may threaten the functioning of soil in agricultural production systems.

Keywords: agricultural intensification, body mass, ecosystem services, functional groups, soil food web, taxonomic breadth, taxonomic distinctness, terrestrial ecosystems

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Introduction

Soil biodiversity plays a key role in regulating processes that underpin the delivery of ecosystem goods and services in terrestrial ecosystems (Barrios, 2007; Eisenhauer *et al.*, 2012; Wall *et al.*, 2012; de Vries *et al.*, 2013; Wagg *et al.*, 2014). Among the threats to soil biodiversity, land-use change due to agricultural intensification and subsequent loss of soil organic matter are considered major drivers (Gardi *et al.*, 2013). Negative effects of intensive agricultural land use on soil biodiversity have been often observed. However, the majority of studies has focused on abundance, species richness, and community structure of single (e.g., Yeates *et al.*, 1999; Sousa *et al.*, 2006; Feijoo *et al.*, 2011) or limited amounts of taxonomic groups of soil biota, or single sites (e.g., Wardle *et al.*, 1999; Postma-Blaauw *et al.*, 2010; Wickings & Grandy, 2013). Alternative approaches have considered soil food webs that aggregate species or taxa to functional groups based on their trophic positions and taxonomy (Moore *et al.*, 1989). Food web approaches can be useful for predicting transfer rates of nutrients, carbon, and energy between the trophic positions and through the community (Hunt *et al.*, 1987; de Ruiter *et al.*, 1993), but the metrics that they provide are more indicative of ecosystem processes and functioning, rather than providing information on soil biodiversity. As most studies are either incidental (too few groups) or too general (food web approaches), or focusing on only one or few sites a good perspective on consequences of global land-use intensification across a variety of regions is still lacking.

The possible consequences of loss of species from food webs due to agricultural intensification have mainly focused on terrestrial above-ground host-parasitoid systems (e.g., Albrecht *et al.*, 2007; Tylanakis *et al.*, 2007; Macfadyen *et al.*, 2009; Lohaus *et al.*, 2013), whereas such knowledge on soil food webs is mainly lacking. Understanding the consequences of agricultural land use on soil biodiversity requires taking into account that biodiversity is a multidimensional concept (Purvis & Hector, 2000). Changes in diversity within one group in the food web can affect diversity of another group through bottom-up or top-down effects (Gessner *et al.*, 2010), thereby affecting food web properties, including food web structure, diversity, or stability (Neutel *et al.*, 2002). Therefore, when analyzing soil biodiversity responses to land-use intensification, various aspects of diversity and ecologically relevant properties, such as body mass, have to be addressed; both for the entire soil food web and its components.

The aim of this study was to test how agricultural intensification can impact on soil biodiversity across agricultural regions that vary in a number of aspects,

including soil types and climatic conditions. We analyzed effects of agricultural intensification on structure and diversity of almost all components of the soil food webs, on diversity of their components (soil faunal taxonomic groups) and on community-weighted mean body mass of soil fauna in four European regions, represented by southern Sweden, southern UK, western Czech Republic, and northern Greece. We have recently shown that land-use intensification in these four regions profoundly changes ecosystem processes (de Vries *et al.*, 2013). In the present study, we also examine how general diversity measures, measures that incorporate information about the taxonomic relatedness of species within soil faunal taxonomic groups, and community-weighted mean body mass of soil fauna as an important trait value of the soil biota are influenced by increased land-use intensity. The latter diversity measures have not yet been explored in soil communities, but can offer a way to measure complementary aspects of species diversity (Gascón *et al.*, 2009), which could indicate functionally important aspects of community composition (Srivastava *et al.*, 2012).

We considered 19 different functional groups of the soil food web, namely bacteria, saprophytic fungi, arbuscular mycorrhizal fungi, amoebae, flagellates, enchytraeids, earthworms, Collembolans (bacterivorous, fungivorous, phytophagous, omnivorous and predaceous), mites (fungivorous and predaceous), as well as nematodes (bacterivorous, fungivorous, plant associated, plant parasitic, and omnivorous/predaceous). Specifically, we quantified effects of agricultural land-use intensity on the average trophic level and the diversity among functional groups in the soil food web, as well as on the diversity within four soil faunal taxonomic groups (earthworms, oribatid mites, Collembolans, and nematodes). In addition, we determined whether changes in diversity among functional groups may be related to changes in diversity within soil faunal taxonomic groups. Finally, we established land-use intensification effects on community-weighted mean body mass of soil fauna, as this is an important trait value of the soil biota.

Materials and methods

Field sites, soil sampling, and analysis

We collected soil samples from farms in southern Sweden (region Scania: SE), southern UK (region Chilterns: UK), western Czech Republic (region České Budějovice: CZ) and northern Greece (region Kria Brisi: GR). The regions and farms were chosen to represent replicating agricultural management types across Europe, irrespective of soil types and climate. The annual mean/min/max temperature at the different sites

are: 7.8/6.6/9.6 °C (SE), 9.5/5.5/13.5 °C (UK), 7.9/3/13 °C (CZ), and 14/4/31 °C (GR). The annual precipitation is 666, 625, 700, and 435 mm, respectively. The dominant soil types are Calcaric Cambisol (SE), Chromic Luvisol, Leptosol (UK), Stagnic Luvisol, Dystric Cambisol (CZ), and Fluvisol (GR).

Soil samples were collected at two occasions: autumn–winter 2008 and spring–summer 2009. The precise date of sampling differed between countries to ensure similar phenological status of the growing crop, i.e.: SE and UK: November 2008, June 2009, GR: December 2008, April 2009, CZ: November 2008, May 2009. At each sampling occasion, in each region sampling was done at five farms, each including three management types. The management types were: low intensity [grasslands (G)]; medium intensity [extensive rotations (E), where a legume or grass is present in a 5 year rotation and kept for at least a year – tilled at most every 2 years]; and high intensity [intensive rotation (I) with annual crops and winter wheat at the time of sampling – annually tilled]. This nested design resulted in 60 sampling sites (4 regions × 5 farms × 3 management types). In each site (i.e., field), two plots of 1 m² each were randomly selected for sampling but were at least 15 m away from the edge of the field and separated from each other by at least 50 m. Duplicate samples (i.e., from the same sampling site) were analyzed separately but data were averaged prior to statistical analyses. Additional details on climate, soil properties and management of sites are given in de Vries *et al.* (2013) (see Tables S4–S7).

For earthworms soil monoliths of 25 × 25 cm length × width and 10 cm depth were taken from each plot. Earthworms were hand sorted, preserved in 5% formalin in the field and transferred after 24 h to 70% ethanol. Earthworms were counted, weighed, and determined to species level using keys of Sims & Gerard (1985), Mršić (1991) and Pižl (2002). For microorganisms, mesofauna, nematodes, protozoa, and enchytraeids 1–3 replicate cores were taken of 3–5 cm diameter and 10 cm depth. Replicate cores were put together to form one composite sample per plot for each group. Samples were kept cool at 4 °C until analysis or extraction. Specific PLFAs were used as markers of bacterial and saprophytic fungal biomass (Frostegård & Bååth, 1996), and NLFAs for arbuscular mycorrhizal fungal (AM) biomass (Olsson *et al.*, 1995). Fatty acids were converted to biomass carbon (C) using the following factors: bacterial biomass 363.6 nmol PLFA = 1 mg carbon (Frostegård & Bååth, 1996), fungal biomass: 11.8 nmol PLFA = 1 mg carbon (Klamer & Bååth, 2004), and AMF biomass: 1.047 nmol NLFA = 1 µg carbon (Olsson *et al.*, 1995).

Soil mesofauna were extracted from undisturbed samples using Tullgren funnels. Collembolans were determined to species level using keys of Gisin (1960), Babenko *et al.* (1994), and Zimbars & Dunger (1994). Mites were sorted to suborders using Krantz & Walter (2009), and oribatid mites were determined to species level using keys of Balogh & Mahunka (1983) and Weigman (2006). Biomass of mesofauna was estimated from body dimensions after Lebrun (1971). Nematodes were extracted using the modified Cobb sieving and decanting method (S'Jacob & Van Bezooijen, 1984), counted and fixed in 4% formaldehyde. 150 randomly chosen individuals were identified to genus level according to Bongers (1994) and

allocated to trophic groups following Yeates *et al.* (1993). Nematode biomass was estimated individually by analyzing digital microscope images with a specially developed software tool by Sgardelis *et al.* (2009). Protozoa numbers were estimated using a modified most probable number method (Rønn *et al.*, 1995).

Biomass was estimated based on assumptions about average body size (biovolumes of flagellates and amoebae: 50 µm³, and 400 µm³ respectively) and dry weight (for both 0.2 pg µm⁻³), following Ekelund *et al.* (2001). Enchytraeids were extracted from intact soil core samples using wet funnels according to O'Connor (1962), and their biomass was estimated according to Makulec (1983). Biomass of soil animals was converted to C (carbon content estimated to 50% of dry mass). Community-weighted mean of body mass was calculated as $CBM = B_{fa} A_{fa}^{-1}$, where B_{fa} is the total biomass and A_{fa} is the total abundance of all soil faunal groups in the sample (bacteria, fungi and AM fungi are not included in the calculation).

Measures of structure and diversity of soil food webs

Soil biota were allocated to 19 different functional groups, namely bacteria, saprophytic fungi, arbuscular mycorrhizal fungi, amebae, flagellates, enchytraeids, earthworms, bacterivorous Collembolans, fungivorous Collembolans, phytophagous Collembolans, omnivorous Collembolans, predaceous Collembolans, fungivorous (oribatid) mites, predaceous mites, bacterivorous nematodes, fungivorous nematodes, plant associated (root hair feeding) nematodes, plant parasitic nematodes, and omnivorous/predaceous nematodes. Biomass of all functional groups was expressed as kg C per m² using the appropriate bulk density values. Carbon flows between functional groups in the food web were estimated to build quantitative food webs based on trophic position following Hunt *et al.* (1987) and de Ruiter *et al.* (1995). The trophic position of functional groups in the food web is defined by the average of the trophic position of the functional group it consumes weighted by the diet fraction this functional group represents as $TL_i = 1 + \sum_{j=1}^{N_{fw}} g_{ij} TL_j$ where TL_i is the trophic level of functional group i and g_{ij} the fraction of the consumer group i 's diet derived from the prey group j and N_{fw} is the number of groups in the food web. These 'flow-based' trophic levels are computed following the method of Levine (1980) and Williams & Martinez (2004). The column vector TL defined as $TL = [(I-G)^{-1}]^T \mathbf{1}$ gives the trophic level of each consumer with I the identity matrix (with dimension $N_{fw} \times N_{fw}$) and $G = (g_{ij})$ with dimension $N_{fw} \times N_{fw}$ and $\mathbf{1}$ a vector filled with ones (with dimension $N_{fw} \times 1$). Values for the coefficients of feeding preferences used are given in de Vries *et al.* (2013).

In the analyses, the following measures describing structure and diversity of the entire food web were calculated: (i) average trophic level (\overline{TL}) calculated as average of all values of group trophic level in the food web as $\overline{TL} = \frac{1}{N_{fw}} (TL)^T \mathbf{1}$ (ii) richness, expressed as the number of functional groups in the food web (N_{fw}); and (iii) Shannon index (H') calculated as $\prod_{i=1}^{N_{fw}} \left(\frac{B_i}{B_{tot}} \right)^{-\frac{B_i}{B_{tot}}}$ with B_i the biomass of the functional group i and B_{tot} the total food web biomass.

Measures of diversity within soil faunal taxonomic groups

For the four key soil faunal taxonomic groups (earthworms, Collembolans, oribatid mites and nematodes) that comprise in total 12 functional groups in the food web we considered both commonly used diversity measures, such as richness and Shannon index, as well as measures that incorporate information about the taxonomic relatedness of species, such as average taxonomic distinctness and breadth (for definition see below). These measures were based on abundance data of species or genera in the taxonomic groups and were independent from the measures concerning the entire soil food web that were based on functional group biomass data.

The following diversity measures were estimated: (i) Richness (N) as number (ln transformed) of species of earthworms (N_E), Collembolans (N_C), oribatid mites (N_O) and genera of nematodes (N_N); (ii) Shannon index (H) for earthworms (H_E), Collembolans (H_C), oribatid mites (H_O) and nematodes (H_N), (iii) average taxonomic distinctness (Δ^*) for earthworms (Δ^*_E), Collembolans (Δ^*_C), oribatid mites (Δ^*_O) and nematodes (Δ^*_N), and (iv) average taxonomic breadth (Δ^+) for earthworms (Δ^+_E), Collembolans (Δ^+_C), oribatid mites (Δ^+_O) and nematodes (Δ^+_N). For the nematode taxonomic group, which includes five abundantly represented functional groups, the four diversity measures were estimated also for each group separately.

Average taxonomic distinctness (Δ^*) was calculated according to Warwick & Clarke (1995) between all species/genera in a community at each sample as:
$$\frac{|\sum_{i < j} \omega_{ij} x_i x_j|}{|\sum_{i < j} x_i x_j|}$$
 where ω_{ij} is

the path length between the two species i and j that show the greatest taxonomic (phylogenetic) distance between them in a Linnaean classification tree including all species of a community and a maximum distance set to 100, and x_i and x_j are the number of individuals of species i and j , respectively. This index provides an estimate of the expected taxonomic distance between two randomly chosen individuals from a sample and is independent of sample size (Clarke & Warwick, 2001). Average taxonomic breadth (Δ^+) was computed analogously to the average taxonomic distinctness, but is based on presence/absence, instead of abundance data for species and therefore provides the average taxonomic distance between all pairs of species in a community. Communities with several closely related species can be considered less diverse than communities with the same number, but with more distantly related species (Clarke & Warwick, 1998) as diversity is measured in terms of features accumulated over evolutionary history (Schweiger *et al.*, 2008). Taxonomic trees were built according to information about suborder, family, genus, and species level for Collembolans; superfamily, family, genus, and species level for Oribatida; class, order, superfamily, family, and genus level for Nematoda; and family, genus, and species level for earthworms. All taxonomic information was derived from the Fauna Europaea Database (de Jong, 2013).

Statistical analysis

We used permutational analyses of variance to evaluate the effects of land-use intensity in the different regions while

accounting for sampling season during these analyses (PERMANOVA; Anderson, 2005) with $\log(x + 1)$ transformed data for the analysis. Data were transformed to weight down the effect of numerically dominant taxa in analyses. All PERMANOVA analyses were performed with region (SE, UK, CZ, GR) as fixed factor, land-use intensity levels (G, E, I) nested within region and sampling season (autumn–winter 2008, spring–summer 2009) nested within the factors region and land-use intensity. The distance measure to generate dissimilarity matrices for data was the deviance of dissimilarities, and 4999 permutations were used in all cases. Pair-wise *a posteriori* tests were performed among levels of factor: (i) 'region', (ii) 'land-use intensity' within factor 'region' and (iii) 'sampling season' within factor 'land-use intensity' within factor 'region'. We used the Fortran software PERMANOVA (Anderson, 2005) for these analyses.

The following sets of variables were analyzed with PERMANOVA: (i) Measures describing the entire food web: N_{fw} , F_H , and TL ; (ii) Richness within the four soil faunal taxonomic groups: N_E , N_C , N_O , and N_N ; (iii) Shannon index within the four soil faunal taxonomic groups: H_E , H_C , H_O , and H_N ; (iv) average taxonomic distinctness within the four soil faunal taxonomic groups: Δ^*_E , Δ^*_C , Δ^*_O , and Δ^*_N ; and (v) average taxonomic breadth within the four soil faunal taxonomic groups: Δ^+_E , Δ^+_C , Δ^+_O , and Δ^+_N . In addition, permutational univariate analyses of variance were used for each of the individual response variables mentioned and furthermore, for the community-weighted mean body mass of soil fauna (CBM) and for the four measures concerning diversity within the five nematode functional groups separately.

Pearson correlation tests were used for simple bivariate testing of relationships between measures regarding diversity within the four soil faunal taxonomic groups and measures regarding diversity among functional groups in the soil food web. For this analysis we used the SPSS v19 software package.

Results*Land-use intensity influence on structure and diversity among functional groups in the soil food web*

The overall diversity and structure of soil food webs differed significantly with land-use intensity and region after statistically accounting for seasonal effects (Table 1). This overall effect (multivariate) was primarily a result of the significant differences between intensive rotations (I) and grasslands (G). These differences were unanimous for all regions. The extensive rotations (E) were more variable and were not different from intensive rotations and grasslands in SE, UK, and GR, and from grasslands in CZ (for pair-wise *a posteriori* comparisons see Table 1).

Land-use intensity significantly affected all the individual measures of food web diversity and structure, i.e., the number of functional groups (N_{fw}), Shannon index (F_H), and the average trophic level

Table 1 Results of a PERMANOVA for the overall effect of region, land-use intensity (nested in region) and sampling season (nested in region and land-use intensity) on all measures of the soil food web. Pair-wise *a posteriori* comparisons: regions, land-use intensity levels, and sampling seasons not sharing the same letter are significantly different. Codes for regions: Sweden (SE), United Kingdom (UK), Czech Republic (CZ), and Greece (GR). Codes for land-use intensity levels: grassland (G), extensive rotation (E), and intensive rotation (I). Codes for sampling seasons: autumn–winter 2008 (wi), spring–summer 2009 (su)

Source	df	SS	MS	F	P	<i>a posteriori</i> comparisons			
						SE	UK	CZ	GR
Region	3	45.23	15.08	11.31	0.0002	a	b	c	cb
Intensity	8	57.59	7.20	5.40	0.0002	G ^a E ^{ab} I ^b	G ^a E ^{ab} I ^b	G ^a E ^a I ^b	G ^a E ^{ab} I ^b
Sampling season	12	44.78	3.73	2.80	0.0002	G, E: wi ^a su ^b I: NS	G, I: wi ^a su ^b E: NS	G, E, I: NS	G, E, I: NS
Residual	96	128.01	1.33						
Total	119	275.60							

(TL) (permutational univariate analysis of variance, Fig. 1). In each region, at least one of these variables had a significantly higher value in grassland compared to intensive rotation. This indicates that soil food webs are less complex in soils from intensive rotations than in soil from grasslands. The number of functional groups, the Shannon index and the average trophic level in the soil food web varied significantly among regions (Fig. 1). The average trophic level was higher in soil food webs from CZ compared to the other regions, while the Shannon index was higher in food webs from SE. This can be explained by the total biomass of almost all functional groups in the food webs that varied accordingly among the regions.

Land-use intensity influence on community-weighted mean body mass of soil fauna

Land-use intensity significantly affected the community-weighted mean body mass of soil fauna (CBM) (permutational univariate analysis of variance, Fig. 2). In all regions except United Kingdom, the CBM was significantly lower in the intensive rotation compared to the grassland. This indicates that soil animals under intensive rotation are generally smaller; larger animals appear more prone to be reduced by land-use intensification.

Land-use intensity and diversity within soil faunal taxonomic groups

Across all sites, we identified a total of 20 earthworm, 72 Collembolan and 48 oribatid mite species, as well as 75 nematode genera. All four sets of diversity measures of faunal taxonomic groups differed significantly among land-use intensities and regions when accounting for seasonal effects (Table 2). These overall effects (multivariate) resulted mainly from the significant

differences between intensive rotations and grasslands of all diversity measures in all regions, except for average taxonomic distinctness and breadth in CZ and United Kingdom. The diversity within faunal taxonomic groups in extensive rotations did not differ from the intensive rotations or the grasslands, depending on region (for pair-wise *a posteriori* comparisons see Table 2).

In most faunal groups the measures Richness (*N*), Shannon index (*H*), average taxonomic distinctness (Δ^*), and breadth (Δ^+) showed lower levels of diversity with increasing agricultural intensity (permutational univariate analysis of variance, Figs 3 and 4). Earthworm communities in SE and GR, and Collembolan and oribatid mite communities in all regions except in CZ had fewer numbers of species in the intensively managed fields compared to grasslands and those species were also taxonomically more closely related to each other. In contrast, the diversity of the nematode community was not negatively affected by land-use intensity, and in some regions the Shannon index was higher in fields with intensive rotation than those with extensive rotation. The diversity of the nematode functional groups (bacterivorous, fungivorous, plant associated, and omnivorous/predaceous) was not significantly affected by increasing agricultural intensity ($P > 0.05$ in all cases). Occasionally, the diversity of plant parasitic nematodes was negatively affected by increasing management intensity, as was observed for richness in CZ and SE ($P < 0.0008$), Shannon index in CZ and UK ($P < 0.001$), average taxonomic distinctness in CZ ($P < 0.0266$) and average taxonomic breadth in CZ and UK ($P < 0.0234$).

Several measures of diversity within the taxonomic groups differed significantly between regions (Table 2). Earthworm diversity was lower in GR than in SE. Collembolan diversity was generally higher in CZ than in the other regions and oribatid mite diversity was higher in GR and CZ than in SE and UK (Figs 3 and 4).

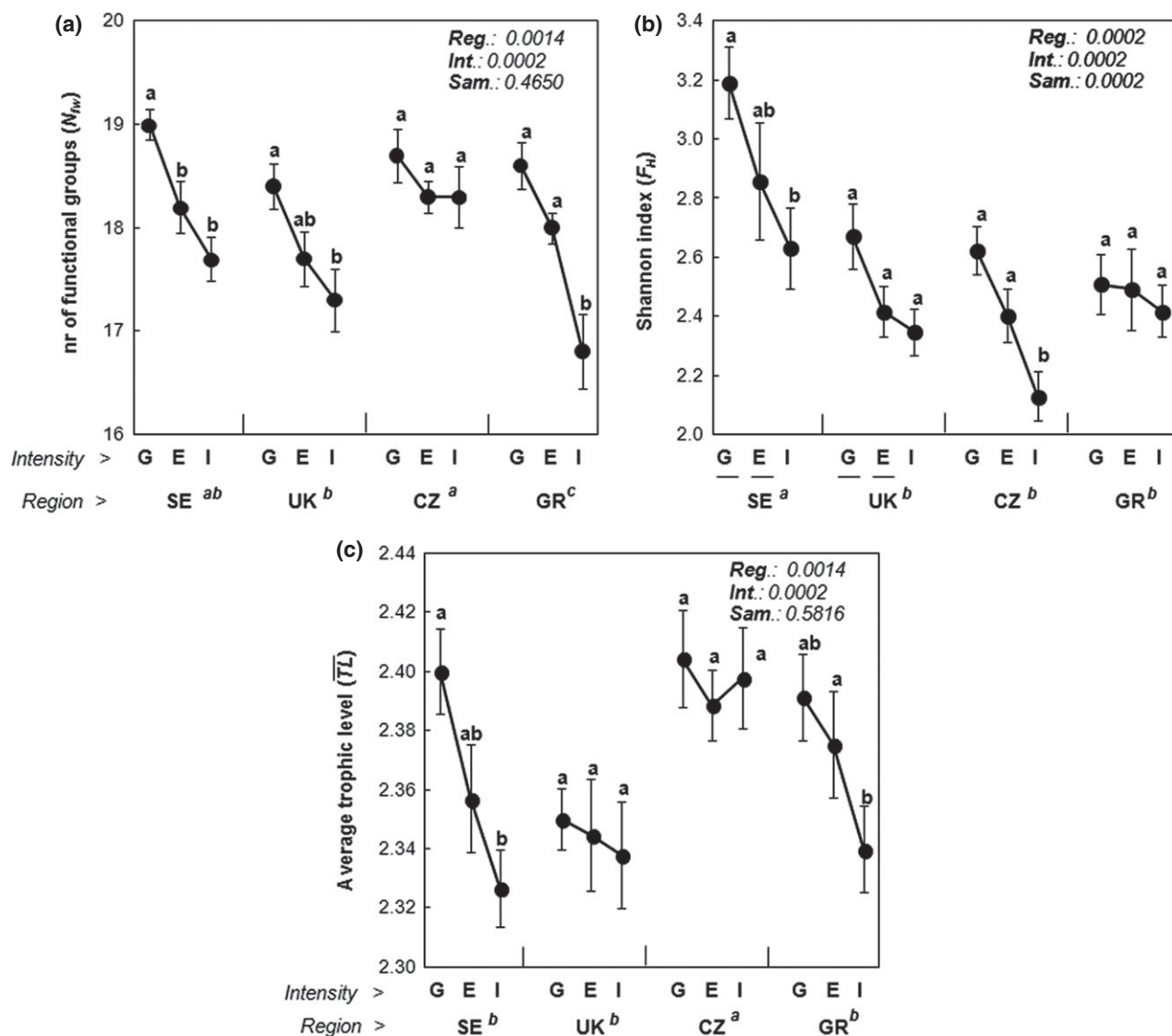


Fig. 1 Average values (\pm SE) of: (a) number of functional groups (N_{fw}), (b) Shannon index (F_H) and (c) average trophic level (\overline{TL}) in the soil food web at the three land-use intensity levels in the four regions across Europe. Data from both sampling seasons are pooled. Significance effects (P -values) of region (Reg.), land-use intensity level (Int.) and sampling season (Sam.) as determined by permutational univariate analysis of variance are given for each measure. Regions (indicated below horizontal axis) and land-use intensity levels for each region not sharing the same letter are significantly different according to pair-wise *a posteriori* comparisons. Underlined land-use intensity levels denote significantly different values between sampling seasons. Codes are depicted in Table 1.

Relationships between diversity among functional groups in the soil food web and diversity within soil faunal taxonomic groups

The diversity measures within soil faunal groups were significantly correlated with those among functional groups (Table 3), suggesting that agricultural intensification consistently affects most soil food web components and reduces soil biodiversity. More specifically, the diversity measures for earthworms, Collembolans and oribatid mites, as well as average taxonomic

breadth of nematodes, were significantly and positively correlated with the number of functional groups in the food web (N_{fw}). Earthworm diversity measures also showed a significant positive correlation with the Shannon index (F_H) of the functional groups in the food web (Table 3).

Discussion

In this study, we show that agricultural intensification affects various aspects of diversity in a consistent

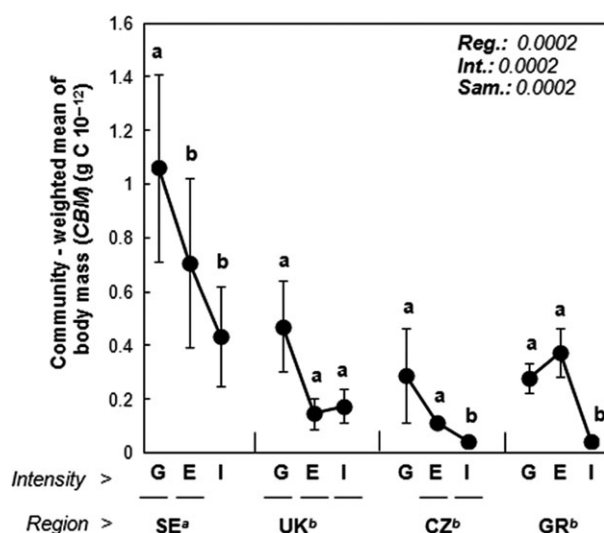


Fig. 2 Average values (\pm SE) of the community-weighted mean body mass of soil fauna (CBM) at the three land-use intensity levels in the four regions across Europe. Data from both sampling seasons are pooled. Significance effects (P -values) of region (Reg.), land-use intensity level (Int.) and sampling season (Sam.) as determined by permutational univariate analysis of variance are given for each measure. Regions (indicated below horizontal axis) and land-use intensity levels for each region not sharing the same letter are significantly different according to pair-wise *a posteriori* comparisons. Underlined land-use intensity levels denote significantly different values between sampling seasons. Codes are depicted in Table 1.

negative way in four agricultural regions across Europe with contrasting soil and climatic conditions. Specifically, increasing land-use intensity decreases diversity within soil faunal taxonomic groups, diversity among functional groups, as well as the average trophic level in the soil food web. The reductions of diversity at the soil food web level were due to a decrease in biomass of functional groups with larger body sizes, especially earthworms, enchytraeids, Collembolans, and oribatid mites, or a decrease in biomass of groups at higher trophic levels, especially predaceous mites, as reported in de Vries *et al.* (2013). As a result, the community-weighted mean body mass of soil fauna was significantly decreased by land-use intensification. Hence at high land-use intensity, food webs contain fewer trophic levels and fewer species with large body mass.

The effect of land use was so intense that in some cases, one or more functional groups were entirely missing. In Greece, for example, earthworms and predaceous Collembolans were absent from intensive rotations, whereas in Sweden, fungivorous mites and predaceous Collembolans were missing. These groups of organisms are characterized by relatively low growth

rates and are known to be sensitive to disturbance, with populations often needing decades to recover after tillage (Siepel, 1996; Maraun & Scheu, 2000; Adl *et al.*, 2006). The presence of a functional group can be related to certain functions, as e.g., earthworms are related to processes of C and N cycling (de Vries *et al.*, 2013), and its biomass is indicative of the magnitude of those functions (*sensu* Hughes & Roughgarden, 2000; Thébaud & Loreau, 2006; Berg & Bengtsson, 2007). Hence, the loss or decrease in biomass of these functional groups from the soil food webs will likely result in a long-term reduction in soil functioning in intensive agricultural production systems.

Our study shows that changes in the biomass of functional or taxonomic groups are accompanied by changes in their diversity and that they occur across latitudinal positions and soil types as sampled within Europe. The biomass of e.g., earthworms, Collembolans, and oribatid mites were significantly reduced by agricultural intensification (de Vries *et al.*, 2013) as also the diversity, which confirms other case-specific studies (e.g., Pizl, 1999; Caruso *et al.*, 2007; Smith *et al.*, 2008; Dahms *et al.*, 2010). Our data also point out that a decrease in diversity within faunal taxonomic groups was related to a decrease in diversity among functional groups. This indicates that agricultural intensification has a consistent negative effect across most soil food web components and is not limited to specific groups of soil biota, such as arbuscular mycorrhizal fungi (Helgason *et al.*, 1998). Agricultural intensification not only reduced richness and Shannon index of faunal groups but also the average taxonomic distinctness and average taxonomic breadth, which means that the loss of species was consistently related to the loss of taxonomically more distantly related species. Thus, agricultural intensification also caused a loss of taxonomic diversity, which is known to relate positively to functioning (Heemsbergen *et al.*, 2004).

It has been argued that functional redundancy in soil communities can be high, due to generalized feeding habits among most soil biota (Setälä *et al.*, 2005). An explanation for the perceived low degree of specificity can be that our tools to detect specialized interactions between cryptic species have been too coarse. With tools to resolve genetic patterns in organisms, specialized trophic interactions are more common than previously thought (Jørgensen *et al.*, 2005; Jørgensen & Hedlund, 2013). Here, we have focused on the trophic role of species, e.g., fungivorous Collembolans, ignoring that two species may both feed on fungi but that their preference for fungal species can differ. Functional differentiation may play an important role in determining how a functional group actually

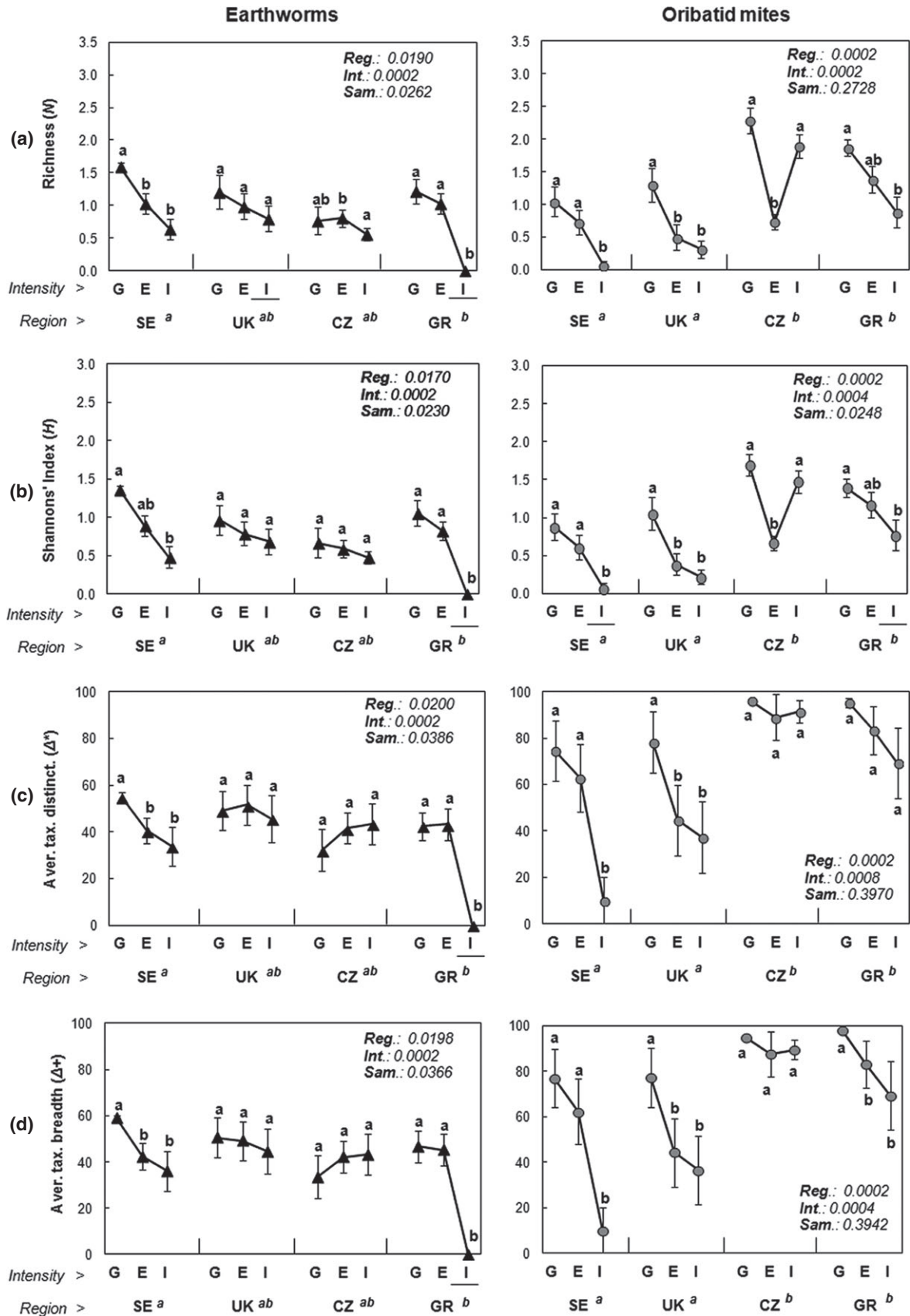
Table 2 Results of PERMANOVAS for the effect of region, land-use intensity (nested in region) and sampling season (nested in region and land-use intensity) on the diversity of earthworms, Collembolans, oribatid mites, and nematodes for the following sets of diversity measures: (a) richness, (b) Shannon index, (c) average taxonomic distinctness, and (d) average taxonomic breadth. Pair-wise *a posteriori* comparisons: regions, land-use intensity levels, and sampling seasons not sharing the same letter are significantly different. Codes are depicted in Table 1

	Source	df	SS	MS	F	P	<i>a posteriori</i> comparisons			
							SE	UK	CZ	GR
(a) Richness (N)	Region	3	9049.10	3016.37	24.15	0.0002	a	b	c	d
	Intensity	8	9580.97	1197.62	9.59	0.0002	G ^a E ^b I ^c	G ^a E ^b I ^b	G ^a E ^b I ^c	G ^a E ^a I ^b
	Sampling season	12	3393.57	282.80	2.26	0.0010	E: wi ^a su ^b G, I: NS	I: wi ^a su ^b G, E: NS	I: wi ^a su ^b G, E: NS	G, E, I: NS
	Residual	96	11990.45	124.90						
	Total	119	34014.09							
(b) Shannon index (H)	Region	3	8667.71	2889.24	16.16	0.0002	a	b	c	d
	Intensity	8	11851.62	1481.45	8.29	0.0002	G ^a E ^a I ^b	G ^a E ^b I ^b	G ^a E ^b I ^a	G ^a E ^b I ^c
	Sampling season	12	4947.67	412.31	2.31	0.0004	E: wi ^a su ^b G, I: NS	I: wi ^a su ^b G, E: NS	I: wi ^a su ^b G, E: NS	G, E, I: NS
	Residual	96	17159.82	178.79						
	Total	119	42626.82							
(c) Av. taxon. distinct. (Δ^*)	Region	3	6726.94	2242.32	11.82	0.0002	a	b	c	c
	Intensity	8	7236.89	904.61	4.77	0.0002	G ^a E ^a I ^b	NS	NS	G ^a E ^a I ^b
	Sampling season	12	4667.83	388.99	2.05	0.0160	G, E, I: NS	I: wi ^a su ^b G, E: NS	G, E, I: NS	G, E, I: NS
	Residual	96	18210.19	189.69						
	Total	119	36841.85							
(d) Av. taxon. breadth (Δ^+)	Region	3	6552.58	2184.19	11.70	0.0002	a	b	c	c
	Intensity	8	7157.29	894.66	4.79	0.0002	G ^a E ^a I ^b	NS	NS	G ^a E ^a I ^b
	Sampling season	12	4547.10	378.10	2.03	0.0170	G, E, I: NS	I: wi ^a su ^b G, E: NS	G, E, I: NS	G, E, I: NS
	Residual	96	17921.75	186.66						
	Total	119	36179.63							

performs, and in the absence of functionally similar species in the community, one species may have a crucial role in affecting a particular ecosystem process (Wardle, 1999) especially in soil ecosystems with low diversity (Barrett *et al.*, 2008). Specific functions such as burrowing by anecic and endogeic earthworms can have substantial effects on soil structure, as these species are sensitive to intensified land management (Gormsen *et al.*, 2004). In Sweden and Greece, intensive rotations had on average only two earthworm

species less than grasslands. However, the average taxonomic distinctness was significantly reduced in these regions, which may be expected to have important implications for functioning. Given that average taxonomic distinctness serves as a valid proxy for functional differentiation in the community (Gascón *et al.*, 2009; Birkhofer *et al.*, 2014), and that earthworms play an important role in C and N cycling (Lubbers *et al.*, 2013), this decrease in taxonomic differentiation can significantly affect the outcome or the rates of

Fig. 3 Average values (\pm SE) of: (a) richness (N), (b) Shannon index (H'), (c) average taxonomic distinctness (Δ^*) and (d) average taxonomic breadth (Δ^+) for earthworms and oribatid mites at the three land-use intensity levels in the four regions across Europe. Data from both sampling seasons are pooled. Significance effects (*P*-values) of region (Reg.), land-use intensity level (Int.) and sampling season (Sam.) as determined by permutational univariate analysis of variance are given for each combination of soil faunal group and diversity measure. Regions (indicated below horizontal axis) and land-use intensity levels for each region not sharing the same letter are significantly different according to pair-wise *a posteriori* comparisons. Underlined land-use intensity levels denote significantly different values between sampling seasons. Codes are depicted in Table 1.



these processes. The declined diversity may reduce ecosystem processes, but previous modeling work using the same dataset has shown that different ecosystem processes relate to loss of specific (or combinations of) species groups (de Vries *et al.*, 2013), which shows that care should be taken with generalizations as that soil biodiversity loss would mean general loss of ecosystem functions.

Our results confirm other studies showing that soil animals with larger body sizes, such as earthworms and predaceous Collembolans and mites, are sensitive to intensive agriculture (Mulder *et al.*, 2005; Smith *et al.*, 2008; Postma-Blaauw *et al.*, 2010). Oribatid mites that mainly feed on fungi (e.g., Maraun *et al.*, 1998) and have relatively small size, may suffer from disturbance associated with increasing intensity of agricultural management as well (Sgardelis & Usher, 1994). A decline of diversity within soil faunal groups due to intensive land use is most probably related to frequent tillage, which affects soil physical properties (Roger-Estrade *et al.*, 2010) to the disadvantage of many soil organisms (van Capelle *et al.*, 2012). Tillage alters soil microhabitats and interrupts life cycles, and it is expected that organisms with relatively long life spans are particularly sensitive, such as Collembolans (e.g., Brennan *et al.*, 2006), oribatid mites (e.g., Franchini & Rockett, 1996) and earthworms (e.g., Eriksen-Hamel *et al.*, 2009). In the sites under extensive rotations, less frequent tillage promoted diversity of soil faunal groups such as oribatid mites in Sweden, earthworms in Czech Republic and Greece, and Collembolans in Sweden and Greece.

While most soil diversity measures were consistently and negatively affected by intensive agriculture for three faunal groups, diversity of the nematode taxonomic group and the nematode functional groups was hardly affected. This also applies to the biomass of the various nematode functional groups (de Vries *et al.*, 2013). Microbivorous nematodes, are reported to be affected by intensively managed systems (Tsiafouli *et al.*, 2006; Birkhofer *et al.*, 2012), while other studies find no evidence for this (Sánchez-Moreno *et al.*, 2011). This suggests that these nematodes might be affected by specific agricultural practices such as tillage, fertil-

ization, pesticide application, or the application of organic amendments (Tsiafouli *et al.*, 2007; Zhao & Neher, 2013), rather than by land-use intensity in general. Omnivorous and predaceous nematodes are generally considered sensitive to disturbance (Bongers & Ferris, 1999). Their persistence under increasing land-use intensity could be explained by either the higher availability of prey, since other predaceous groups are declining, or by an increase in suitable food resources for omnivorous species (Postma-Blaauw *et al.*, 2010; Mills & Adl, 2011). In any case, our data show that when the diversity of other taxonomic groups are depleted under intensive agriculture the functional role of nematodes becomes more important.

We conclude that the negative effect of intensive agriculture on soil biodiversity was consistent across regions with widely contrasting climate and soil conditions. Overall, agricultural intensification from grassland to extensive and intensive rotation appears to systematically simplify soil food web diversity, with potential consequences for functioning. The community-weighted mean body mass of soil fauna, the average trophic level and diversity among functional groups in the food web decreased, while some functional groups were lost entirely under intensive land use. Furthermore, soil faunal communities had fewer and taxonomically more closely related species, which suggests that agricultural intensification can threaten the divergent functions that may be provided by taxonomically distant species. Given that the loss of soil biodiversity is ultimately linked to a loss of soil functions that underpin ecosystem services (de Vries *et al.*, 2013; Wagg *et al.*, 2014), we propose that future agricultural policies need to consider how to halt and/or reverse this loss of soil biodiversity. Our finding that the relationship between management regimes and soil biota is fairly stable across regions supports the notion that land-use intensification may lead to the same responses of soil biodiversity at continental scales. Future studies need to be targeted at promoting and evaluating innovative management practices for conserving and/or increasing soil biodiversity and the functioning of soil while maintaining sufficient levels of agricultural production.

Fig. 4 Average values (\pm SE) of: (a) richness (N), (b) Shannon index (H'), (c) average taxonomic distinctness (Δ^*) and (d) average taxonomic breadth (Δ^+) for Collembolans and nematodes at the three land-use intensity levels in the four regions across Europe. Data from both sampling seasons are pooled. Significance effects (P -values) of region (Reg.), land-use intensity level (Int.) and sampling season (Sam.) as determined by permutational univariate analysis of variance are given for each combination of soil faunal group and diversity measure. Regions (indicated below horizontal axis) and land-use intensity levels for each region not sharing the same letter are significantly different according to pair-wise *a posteriori* comparisons. Underlined land-use intensity levels denote significantly different values between sampling seasons. Codes are depicted in Table 1.

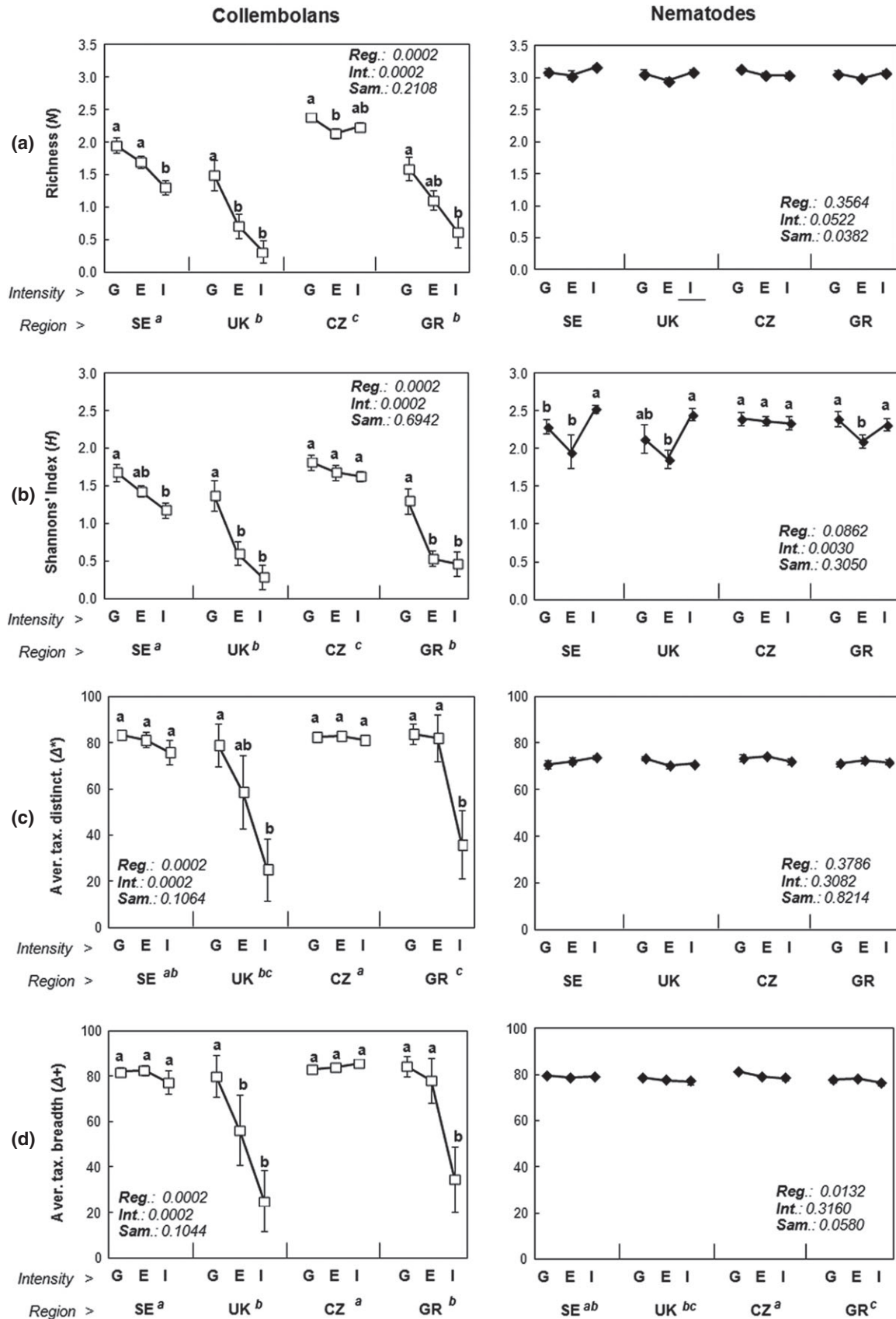


Table 3 Pearson correlation coefficients ($n = 120$) of diversity measures within soil faunal taxonomic groups toward diversity measures among functional groups in the food web, indicated with number of groups (N_{fw}) and the Shannon index (F_H) (* $P < 0.05$, ** $P < 0.001$)

Diversity of taxonomic groups	No of functional groups (N_{fw})	Shannon index (F_H)
Earthworms		
Richness (N_E)	0.41**	0.47**
Shannon index (H_E)	0.42**	0.43**
Aver. taxon. distinctn. (Δ^*_E)	0.35**	0.26*
Aver. tax. breadth (Δ^+_E)	0.37**	0.30**
Collembolans		
Richness (N_C)	0.60**	0.09
Shannon index (H_C)	0.57**	0.17
Aver. taxon. distinctn. (Δ^*_C)	0.46**	0.01
Aver. tax. breadth (Δ^+_C)	0.47**	0.02
Oribatid mites		
Richness (N_O)	0.34**	0.08
Shannon index (H_O)	0.33**	0.08
Aver. taxon. distinctn. (Δ^*_O)	0.20*	0.09
Aver. taxon. breadth (Δ^+_O)	0.21*	0.09
Nematodes		
Richness (N_N)	0.17	0.01
Shannon index (H_N)	0.07	-0.05
Aver. taxon. distinctn. (Δ^*_N)	0.03	-0.03
Aver. taxon. breadth (Δ^+_N)	0.27*	0.10

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