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## Intensive agriculture reduces soil biodiversity across Europe

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# 1 **Intensive agriculture reduces soil biodiversity across Europe**

2 **Running head:** Intensive agriculture and soil biodiversity

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41

## 42 **Keywords**

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

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## 46 **Abstract**

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

## 69 **Introduction**

70           Soil biodiversity plays a key role in regulating processes that underpin the delivery of  
71 ecosystem goods and services in terrestrial ecosystems (Barrios, 2007; Eisenhauer *et al.*,  
72 2012; Wall *et al.*, 2012; de Vries *et al.*, 2013, Wagg *et al.*, 2014). Among the threats to soil  
73 biodiversity, land use change due to agricultural intensification and subsequent loss of soil  
74 organic matter are considered major drivers (Gardi *et al.*, 2013). Negative effects of intensive  
75 agricultural land use on soil biodiversity have been often observed. However, the majority of  
76 studies has focused on abundance, species richness, and community structure of single (e.g.  
77 Yeates *et al.*, 1999; Sousa *et al.*, 2006; Feijoo *et al.*, 2011) or limited amounts of taxonomic  
78 groups of soil biota, or single sites (e.g. Wardle *et al.*, 1999; Postma-Blaauw *et al.*, 2010;  
79 Wickings & Grandy, 2013). Alternative approaches have considered soil food webs that  
80 aggregate species or taxa to functional groups based on their trophic positions and taxonomy  
81 (Moore *et al.*, 1989). Food web approaches can be useful for predicting transfer rates of  
82 nutrients, carbon and energy between the trophic positions and through the community (Hunt  
83 *et al.*, 1987; de Ruiter *et al.*, 1993), but the metrics that they provide are more indicative of  
84 ecosystem processes and functioning, rather than providing information on soil biodiversity.  
85 As most studies are either incidental (too few groups) or too general (food web approaches),  
86 or focusing on only one or few sites a good perspective on consequences of global land use  
87 intensification across a variety of regions is still lacking.

88           The possible consequences of loss of species from food webs due to agricultural  
89 intensification have mainly focused on terrestrial above-ground host-parasitoid systems (e.g.  
90 Albrecht *et al.*, 2007; Tylianakis *et al.*, 2007; Macfadyen *et al.*, 2009; Lohaus *et al.*, 2013),  
91 whereas such knowledge on soil food webs is mainly lacking. Understanding the  
92 consequences of agricultural land use on soil biodiversity requires taking into account that  
93 biodiversity is a multidimensional concept (Purvis & Hector, 2000). Changes in diversity

94 within one group in the food web can affect diversity of another group through bottom-up or  
95 top down effects (Gessner *et al.*, 2010), thereby affecting food web properties, including food  
96 web structure, diversity or stability (Neutel *et al.*, 2002). Therefore, when analyzing soil  
97 biodiversity responses to land use intensification, various aspects of diversity and ecologically  
98 relevant properties, such as body mass, have to be addressed; both for the entire soil food web  
99 and its components.

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

115         We considered 19 different functional groups of the soil food web, namely bacteria,  
116 saprophytic fungi, arbuscular mycorrhizal fungi, amoebae, flagellates, enchytraeids,  
117 earthworms, Collembolans (bacterivorous, fungivorous, phytophagous, omnivorous and  
118 predaceous), mites (fungivorous and predaceous), as well as nematodes (bacterivorous,

119 fungivorous, plant associated, plant parasitic and omnivorous/predaceous). Specifically, we  
120 quantified effects of agricultural land use intensity on the average trophic level and the  
121 diversity among functional groups in the soil food web, as well as on the diversity within four  
122 soil faunal taxonomic groups (earthworms, oribatid mites, Collembolans and nematodes). In  
123 addition, we determined whether changes in diversity among functional groups may be related  
124 to changes in diversity within soil faunal taxonomic groups. Finally, we established land use  
125 intensification effects on community-weighted mean body mass of soil fauna, as this is an  
126 important trait value of the soil biota.

## 127 **Material and methods**

### 128 *Field sites, soil sampling and analysis*

129 We collected soil samples from farms in southern Sweden (region Scania: SE), southern  
130 UK (region Chilterns: UK), western Czech Republic (region České Budějovice: CZ) and  
131 northern Greece (region Kria Brisi: GR). The regions and farms were chosen to represent  
132 replicating agricultural management types across Europe, irrespective of soil types and  
133 climate. The annual mean/min/max temperature at the different sites are: 7.8/6.6/9.6 °C (SE),  
134 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  
135 mm, 625 mm, 700 mm and 435 mm respectively. The dominant soil types are Calcaric  
136 Cambisol (SE), Chromic Luvisol, Leptosol (UK), Stagnic Luvisol, Dystric Cambisol (CZ),  
137 and Fluvisol (GR).

138 Soil samples were collected at two occasions: autumn-winter 2008 and spring-summer  
139 2009. The precise date of sampling differed between countries to ensure similar phenological  
140 status of the growing crop, i.e: SE and UK: November 2008, June 2009, GR: December 2008,  
141 April 2009, CZ: November 2008, May 2009. At each sampling occasion, in each region  
142 sampling was done at five farms, each including three management types. The management  
143 types were: low intensity (grasslands (G)); medium intensity (extensive rotations (E), where a  
144 legume or grass is present in a 5 year rotation and kept for at least a year - tilled at most every  
145 two years); and high intensity (intensive rotation (I) with annual crops and winter wheat at the  
146 time of sampling - annually tilled). This nested design resulted in 60 sampling sites (4 regions  
147 × 5 farms × 3 management types). In each site (i.e. field), two plots of 1 m<sup>2</sup> each were  
148 randomly selected for sampling but were at least 15 m away from the edge of the field and  
149 separated from each other by at least 50 m. Duplicate samples (i.e from the same sampling  
150 site) were analyzed separately but data were averaged prior to statistical analyses. Additional



151 details on climate, soil properties and management of sites are given in de Vries *et al.* (2013)  
152 (see SI, Tables S4-S7).

153 For earthworms soil monoliths of 25 x 25 cm length x width and 10 cm depth were taken  
154 from each plot. Earthworms were hand sorted, preserved in 5% formalin in the field and  
155 transferred after 24h to 70 % ethanol. Earthworms were counted, weighed and determined to  
156 species level using keys of Sims & Gerard (1985), Mršić (1991) and Pižl (2002). For  
157 microorganisms, mesofauna, nematodes, protozoa and enchytraeids 1-3 replicate cores were  
158 taken of 3-5cm diameter and 10cm depth. Replicate cores were but together to form one  
159 composite sample per plot for each group. Samples were kept cool at 4°C until analysis or  
160 extraction. Specific PLFAs were used as markers of bacterial and saprophytic fungal biomass  
161 (Frostegård & Bååth, 1996), and NLFAs for arbuscular mycorrhizal fungal (AM) biomass  
162 (Olsson *et al.*, 1995). Fatty acids were converted to biomass carbon (C) using the following  
163 factors: bacterial biomass 363.6 nmol PLFA = 1 mg carbon (Frostegård & Bååth, 1996),  
164 fungal biomass: 11.8 nmol PLFA = 1 mg carbon (Klamer & Bååth, 2004), and AMF biomass:  
165 1.047 nmol NLFA = 1 µg carbon (Olsson *et al.*, 1995).

166 Soil mesofauna were extracted from undisturbed samples using Tullgren funnels.  
167 Collembolans were determined to species level using keys of Gisin (1960), Babenko *et al.*  
168 (1994), and Zimbars & Dunger (1994). Mites were sorted to suborders using Krantz & Walter  
169 (2009), and oribatid mites were determined to species level using keys of Balogh & Mahunka  
170 (1983) and Weigman (2006). Biomass of mesofauna was estimated from body dimensions  
171 after Lebrun (1971). Nematodes were extracted using the modified Cobb sieving and  
172 decanting method (s'Jacob & Van Bezooijen, 1984), counted and fixed in 4% formaldehyde.  
173 150 randomly chosen individuals were identified to genus level according to Bongers (1994)  
174 and allocated to trophic groups following Yeates *et al.* (1993). Nematode biomass was  
175 estimated individually by analyzing digital microscope images with a specially developed

176 software tool by Sgardelis *et al.* (2009). Protozoa numbers were estimated using a modified  
177 most probable number method (Rønn *et al.*, 1995).

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

### 186 *Measures of structure and diversity of soil food webs*

187 Soil biota were allocated to 19 different functional groups, namely bacteria, saprophytic  
188 fungi, arbuscular mycorrhizal fungi, amoebae, flagellates, enchytraeids, earthworms,  
189 bacterivorous Collembolans, fungivorous Collembolans, phytophagous Collembolans,  
190 omnivorous Collembolans, predaceous Collembolans, fungivorous (oribatid) mites,  
191 predaceous mites, bacterivorous nematodes, fungivorous nematodes, plant associated (root  
192 hair feeding) nematodes, plant parasitic nematodes, and omnivorous/predaceous nematodes.  
193 Biomass of all functional groups was expressed as kg C per  $\text{m}^2$  using the appropriate bulk  
194 density values. Carbon flows between functional groups in the food web were estimated in  
195 order to build quantitative food webs based on trophic position following Hunt *et al.* (1987)  
196 and de Ruiter *et al.* (1995). The trophic position of functional groups in the food web is  
197 defined by the average of the trophic position of the functional group it consumes weighted by  
198 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  
199 trophic level of functional group  $i$  and  $g_{ij}$  the fraction of the consumer group  $i$ 's diet derived  
200 from the prey group  $j$  and  $N_{fw}$  is the number of groups in the food web. These "flow-based"

201 trophic levels are computed following the method of Levine (1980) and Williams & Martinez  
 202 (2004). The column vector  $TL$  defined as  $TL = ((I - G)^{-1})^T \mathbf{1}$  gives the trophic level of each  
 203 consumer with  $I$  the identity matrix (with dimension  $N_{fw} \times N_{fw}$ ) and  $G = (g_{ij})$  with  
 204 dimension  $N_{fw} \times N_{fw}$  and  $\mathbf{1}$  a vector filled with ones (with dimension  $N_{fw} \times 1$ ). Values for  
 205 the coefficients of feeding preferences used are given in de Vries *et al.* (2013).

206 In the analyses, the following measures describing structure and diversity of the entire food  
 207 web were calculated: i) average trophic level ( $\overline{TL}$ ) calculated as average of all values of group  
 208 trophic level in the food web as  $\overline{TL} = \frac{1}{N_{fw}} (TL)^T \mathbf{1}$ ; ii) richness, expressed as the number of  
 209 functional groups in the food web ( $N_{fw}$ ); and iii) Shannon index ( $F_H$ ) calculated as  $F_H =$   
 210  $\prod_{i=1}^{N_{fw}} \left( \frac{B_i}{B_{tot}} \right)^{-\frac{B_i}{B_{tot}}}$  with  $B_i$  the biomass of the functional group  $i$  and  $B_{tot}$  the total food web  
 211 biomass.

### 212 *Measures of diversity within soil faunal taxonomic groups*

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

221 The following diversity measures were estimated: i) Richness ( $N$ ) as number (ln  
 222 transformed) of species of earthworms ( $N_E$ ), Collembolans ( $N_C$ ), oribatid mites ( $N_O$ ) and  
 223 genera of nematodes ( $N_N$ ); ii) Shannon index ( $H$ ) for earthworms ( $H_E$ ), Collembolans ( $H_C$ ),  
 224 oribatid mites ( $H_O$ ) and nematodes ( $H_N$ ), iii) average taxonomic distinctness ( $\Delta^*$ ) for

225 earthworms ( $\Delta^*_{E}$ ), Collembolans ( $\Delta^*_{C}$ ), oribatid mites ( $\Delta^*_{O}$ ) and nematodes ( $\Delta^*_{N}$ ), and iv)  
226 average taxonomic breadth ( $\Delta^+$ ) for earthworms ( $\Delta^+_{E}$ ), Collembolans ( $\Delta^+_{C}$ ), oribatid mites  
227 ( $\Delta^+_{O}$ ) and nematodes ( $\Delta^+_{N}$ ). For the nematode taxonomic group, which includes five  
228 abundantly represented functional groups, the four diversity measures were estimated also for  
229 each group separately.

230 Average taxonomic distinctness ( $\Delta^*$ ) was calculated according to Warwick & Clarke  
231 (1995) between all species/genera in a community at each sample as:  $\frac{[\sum\sum_{i<j}\omega_{ij}x_i x_j]}{[\sum\sum_{i<j}x_i x_j]}$  where  $\omega_{ij}$   
232 is the path length between the two species  $i$  and  $j$  that show the greatest taxonomic  
233 (phylogenetic) distance between them in a Linnaean classification tree including all species of  
234 a community and a maximum distance set to 100, and  $x_i$  and  $x_j$  are the number of individuals  
235 of species  $i$  and  $j$ , respectively. This index provides an estimate of the expected taxonomic  
236 distance between two randomly chosen individuals from a sample and is independent of  
237 sample size (Clarke & Warwick, 2001). Average taxonomic breadth ( $\Delta^+$ ) was computed  
238 analogously to the average taxonomic distinctness, but is based on presence/absence, instead  
239 of abundance data for species and therefore provides the average taxonomic distance between  
240 all pairs of species in a community. Communities with several closely related species can be  
241 considered less diverse than communities with the same number, but with more distantly  
242 related species (Clarke & Warwick, 1998) as diversity is measured in terms of features  
243 accumulated over evolutionary history (Schweiger *et al.*, 2008). Taxonomic trees were built  
244 according to information about suborder, family, genus and species level for Collembolans;  
245 superfamily, family, genus and species level for Oribatida; class, order, superfamily, family  
246 and genus level for Nematoda; and family, genus and species level for earthworms. All  
247 taxonomic information was derived from the Fauna Europaea Database (de Jong, 2013).

248 *Statistical analysis*

249 We used permutational analyses of variance to evaluate the effects of land use  
250 intensity in the different regions while accounting for sampling season during these analyses  
251 (PERMANOVA; Anderson, 2005) with  $\log(x+1)$  transformed data for the analysis. Data were  
252 transformed to weight down the effect of numerically dominant taxa in analyses. All  
253 PERMANOVA analyses were performed with region (SE, UK, CZ, GR) as fixed factor, land  
254 use intensity levels (G, E, I,) nested within region and sampling season (autumn-winter 2008,  
255 spring-summer 2009) nested within the factors region and land use intensity. The distance  
256 measure to generate dissimilarity matrices for data was the deviance of dissimilarities, and  
257 4999 permutations were used in all cases. Pair-wise *a posteriori* tests were performed among  
258 levels of factor: a) “region”, b) “land use intensity” within factor “region” and c) “sampling  
259 season” within factor “land use intensity” within factor “region”. We used the Fortran  
260 software PERMANOVA (Anderson, 2005) for these analyses.

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

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

## 274 **Results**

### 275 *Land use intensity influence on structure and diversity among functional groups* 276 *in the soil food web*

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

284 Land use intensity significantly affected all the individual measures of food web diversity  
285 and structure, i.e. the number of functional groups ( $N_{fw}$ ), Shannon index ( $F_H$ ), and the average  
286 trophic level ( $\overline{TL}$ ) (permutational univariate analysis of variance, Fig. 1). In each region, at  
287 least one of these variables had a significantly higher value in grassland compared to intensive  
288 rotation. This indicates that soil food webs are less complex in soils from intensive rotations  
289 than in soil from grasslands. The number of functional groups, the Shannon index and the  
290 average trophic level in the soil food web varied significantly among regions (Fig. 1). The  
291 average trophic level was higher in soil food webs from CZ compared to the other regions,  
292 while the Shannon index was higher in food webs from SE. This can be explained by the total  
293 biomass of almost all functional groups in the food webs that varied accordingly among the  
294 regions.

### 295 *Land use intensity influence on community-weighted mean body mass of soil* 296 *fauna*

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

### 302 *Land use intensity and diversity within soil faunal taxonomic groups*

303 Across all sites, we identified a total of 20 earthworm, 72 Collembolan and 48 oribatid  
304 mite species, as well as 75 nematode genera. All four sets of diversity measures of faunal  
305 taxonomic groups differed significantly among land use intensities and regions when  
306 accounting for seasonal effects (Table 2). These overall effects (multivariate) resulted mainly  
307 from the significant differences between intensive rotations and grasslands of all diversity  
308 measures in all regions, except for average taxonomic distinctness and breadth in CZ and UK.  
309 The diversity within faunal taxonomic groups in extensive rotations did not differ from the  
310 intensive rotations or the grasslands, depending on region (for pair-wise a posteriori  
311 comparisons see Table 2).

312 In most faunal groups the measures Richness (N), Shannon index (H), average taxonomic  
313 distinctness ( $\Delta^*$ ) and breadth ( $\Delta^+$ ) showed lower levels of diversity with increasing agricultural  
314 intensity (permutational univariate analysis of variance, Fig. 3,4). Earthworm communities in  
315 SE and GR, and Collembolan and oribatid mite communities in all regions except in CZ had  
316 fewer numbers of species in the intensively managed fields compared to grasslands and those  
317 species were also taxonomically more closely related to each other. In contrast, the diversity  
318 of the nematode community was not negatively affected by land use intensity, and in some  
319 regions the Shannon index was higher in fields with intensive rotation than those with  
320 extensive rotation. The diversity of the nematode functional groups (bacterivorous,  
321 fungivorous, plant associated and omnivorous/predaceous) was not significantly affected by

322 increasing agricultural intensity ( $P > 0.05$  in all cases). Occasionally, the diversity of plant  
323 parasitic nematodes was negatively affected by increasing management intensity, as was  
324 observed for richness in CZ and SE ( $P < 0.0008$ ), Shannon index in CZ and UK ( $P < 0.001$ ),  
325 average taxonomic distinctness in CZ ( $P < 0.0266$ ) and average taxonomic breadth in CZ and  
326 UK ( $P < 0.0234$ ).

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

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

333 The diversity measures within soil faunal groups were significantly correlated to those  
334 among functional groups (Table 3), suggesting that agricultural intensification consistently  
335 affects most soil food web components and reduces soil biodiversity. More specifically, the  
336 diversity measures for earthworms, Collembolans and oribatid mites, as well as average  
337 taxonomic breadth of nematodes, were significantly and positively correlated to the number of  
338 functional groups in the food web ( $N_{fw}$ ). Earthworm diversity measures also showed a  
339 significant positive correlation to the Shannon index ( $F_H$ ) of the functional groups in the food  
340 web (Table 3).



## 341 **Discussion**

342           In this study, we show that agricultural intensification affects various aspects of  
343 diversity in a consistent negative way in four agricultural regions across Europe with  
344 contrasting soil and climatic conditions. Specifically, increasing land use intensity decreases  
345 diversity within soil faunal taxonomic groups, diversity among functional groups, as well as  
346 the average trophic level in the soil food web. The reductions of diversity at the soil food web  
347 level were due to a decrease in biomass of functional groups with larger body sizes, especially  
348 earthworms, enchytraeids, Collembolans, and oribatid mites, or a decrease in biomass of  
349 groups at higher trophic levels, especially predaceous mites, as reported in de Vries *et al.*  
350 (2013). As a result, the community- weighted mean body mass of soil fauna was significantly  
351 decreased by land use intensification. Hence at high land use intensity food webs contain  
352 fewer trophic levels and fewer species with large body mass.

353           The effect of land use was so intense that in some cases, one or more functional  
354 groups were entirely missing. In Greece, for example, earthworms and predaceous  
355 Collembolans were absent from intensive rotations, whereas in Sweden, fungivorous mites  
356 and predaceous Collembolans were missing. These groups of organisms are characterized by  
357 relatively low growth rates and are known to be sensitive to disturbance, with populations  
358 often needing decades to recover after tillage (Siepel, 1996; Adl. *et al.*, 2006; Maraun &  
359 Scheu, 2000). The presence of a functional group can be related to certain functions, as e.g.  
360 earthworms are related to processes of C and N cycling (de Vries *et al.*, 2013), and its  
361 biomass is indicative of the magnitude of those functions (*sensu* Hughes & Roughgarden,  
362 2000; Thébault & Loreau, 2006; Berg & Bengtsson, 2007). Hence, the loss or decrease in  
363 biomass of these functional groups from the soil food webs will likely result in a long-term  
364 reduction of soil functioning in intensive agricultural production systems.

365 Our study shows that changes in the biomass of functional or taxonomic groups are  
366 accompanied by changes in their diversity and that they occur across latitudinal positions and  
367 soil types as sampled within Europe. The biomass of e.g. earthworms, Collembolans, and  
368 oribatid mites were significantly reduced by agricultural intensification (de Vries *et al.* 2013)  
369 as also the diversity, which confirms other case-specific studies (e.g. Pižl, 1999; Caruso *et al.*,  
370 2007; Smith *et al.*, 2008; Dahms *et al.*, 2010). Our data also point out that a decrease in  
371 diversity within faunal taxonomic groups was related to a decrease in diversity among  
372 functional groups. This indicates that agricultural intensification has a consistent negative  
373 effect across most soil food web components and is not limited to specific groups of soil  
374 biota, such as arbuscular mycorrhizal fungi (Helgason *et al.*, 1998). Agricultural  
375 intensification not only reduced richness and Shannon index of faunal groups, but also the  
376 average taxonomic distinctness and average taxonomic breadth, which means that the loss of  
377 species was consistently related to the loss of taxonomically more distantly related species.  
378 Thus, agricultural intensification also caused a loss of taxonomic diversity, which is known to  
379 relate positively to functioning (Heemsbergen *et al.*, 2004).

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

390 in affecting a particular ecosystem process (Wardle, 1999) especially in soil ecosystems with  
391 low diversity (Barrett *et al.*, 2008). Specific functions such as burrowing by anecic and  
392 endogeic earthworms can have substantial effects on soil structure, as these species are  
393 sensitive to intensified land management (Gormsen *et al.*, 2004). In Sweden and Greece,  
394 intensive rotations had on average only two earthworm species less than grasslands. However  
395 the average taxonomic distinctness was significantly reduced in these regions, which may be  
396 expected to have important implications for functioning. Given that average taxonomic  
397 distinctness serves as a valid proxy for functional differentiation in the community (Gascón *et*  
398 *al.*, 2009; Birkhofer *et al.*, 2014), and that earthworms play an important role in C and N  
399 cycling (Lubbers *et al.*, 2013), this decrease in taxonomic differentiation can significantly  
400 affect the outcome or the rates of these processes. The declined diversity may reduce  
401 ecosystem processes, but previous modeling work using the same dataset has shown that  
402 different ecosystem processes relate to loss of specific (or combinations of) species groups  
403 (De Vries *et al.*, 2013), which shows that care should be taken with generalizations as that soil  
404 biodiversity loss would mean general loss of ecosystem functions.

405         Our results confirm other studies showing that soil animals with larger body sizes,  
406 such as earthworms and predaceous Collembolans and mites, are sensitive to intensive  
407 agriculture (Mulder *et al.*, 2005; Smith *et al.*, 2008; Postma-Blaauw *et al.*, 2010). Oribatid  
408 mites that mainly feed on fungi (e.g. Maraun *et al.*, 1998) and have relatively small size, may  
409 suffer from disturbance associated with increasing intensity of agricultural management as  
410 well (Sgardelis & Usher, 1994). A decline of diversity within soil faunal groups due to  
411 intensive land use is most probably related to frequent tillage, which affects soil physical  
412 properties (Roger-Estrade *et al.*, 2010) to the disadvantage of many soil organisms (van  
413 Capelle *et al.*, 2012). Tillage alters soil microhabitats and interrupts life cycles, and it is  
414 expected that organisms with relatively long life spans are particularly sensitive, such as

415 Collembolans (e.g. Brennan *et al.*, 2006), oribatid mites (e.g. Franchini & Rockett, 1996) and  
416 earthworms (e.g. Eriksen-Hamel *et al.*, 2009). In the sites under extensive rotations, less  
417 frequent tillage promoted diversity of soil faunal groups such as oribatid mites in Sweden,  
418 earthworms in Czech Republic and Greece, and Collembolans in Sweden and Greece.

419         While most soil diversity measures were consistently and negatively affected by  
420 intensive agriculture for three faunal groups, diversity of the nematode taxonomic group and  
421 the nematode functional groups was hardly affected. This also applies to the biomass of the  
422 various nematode functional groups (de Vries *et al.*, 2013). Microbivorous nematodes, are  
423 reported to be affected by intensively managed systems (Tsiafouli *et al.*, 2006, Birkhofer *et*  
424 *al.*, 2012), while other studies find no evidence for this (Sánchez-Moreno *et al.*, 2011). This  
425 suggests that these nematodes might be affected by specific agricultural practices such as  
426 tillage, fertilization, pesticide application, or the application of organic amendments (Tsiafouli  
427 *et al.*, 2007, Zhao & Neher 2013), rather than by land use intensity in general. Omnivorous  
428 and predaceous nematodes are generally considered sensitive to disturbance (Bongers &  
429 Ferris, 1999). Their persistence under increasing land use intensity could be explained by  
430 either the higher availability of prey, since other predaceous groups are declining, or by an  
431 increase of suitable food resources for omnivorous species (Postma-Blaauw *et al.*, 2010; Mills  
432 & Adl, 2011). In any case our data show that when the diversity of other taxonomic groups  
433 are depleted under intensive agriculture the functional role of nematodes becomes more  
434 important.

435         We conclude that the negative effect of intensive agriculture on soil biodiversity was  
436 consistent across regions with widely contrasting climate and soil conditions. Overall,  
437 agricultural intensification from grassland to extensive and intensive rotation appears to  
438 systematically simplify soil food web diversity, with potential consequences for functioning.  
439 The community-weighted mean body mass of soil fauna, the average trophic level and

440 diversity among functional groups in the food web decreased, while some functional groups  
441 were lost entirely under intensive land use. Furthermore, soil faunal communities had fewer  
442 and taxonomically more closely related species, which suggests that agricultural  
443 intensification can threaten the divergent functions that may be provided by taxonomically  
444 distant species. Given that the loss of soil biodiversity is ultimately linked to a loss of soil  
445 functions that underpin ecosystem services (de Vries *et al.*, 2013; Wagg *et al.*, 2014), we  
446 propose that future agricultural policies need to consider how to halt and/or reverse this loss  
447 of soil biodiversity. Our finding that the relationship between management regimes and soil  
448 biota is fairly stable across regions supports the notion that land use intensification may lead  
449 to the same responses of soil biodiversity at continental scales. Future studies need to be  
450 targeted at promoting and evaluating innovative management practices for conserving and/or  
451 increasing soil biodiversity and the functioning of soil while maintaining sufficient levels of  
452 agricultural production.

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

Source	df	SS	MS	F	P	a posteriori 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 <sup>a</sup> E <sup>ab</sup> I <sup>b</sup>	G <sup>a</sup> E <sup>ab</sup> I <sup>b</sup>	G <sup>a</sup> E <sup>a</sup> I <sup>b</sup>	G <sup>a</sup> E <sup>ab</sup> I <sup>b</sup>
Sampling season	12	44.78	3.73	2.80	0.0002	G, E: wi <sup>a</sup> su <sup>b</sup> I: NS	G, I: wi <sup>a</sup> su <sup>b</sup> E: NS	G, E, I: NS	G, E, I: NS
Residual	96	128.01	1.33						
Total	119	275.60							

685

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

	Source	df	SS	MS	F	P	a posteriori 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 <sup>a</sup> E <sup>b</sup> I <sup>c</sup>	G <sup>a</sup> E <sup>b</sup> I <sup>b</sup>	G <sup>a</sup> E <sup>b</sup> I <sup>c</sup>	G <sup>a</sup> E <sup>a</sup> I <sup>b</sup>
	Sampling season	12	3393.57	282.80	2.26	0.0010	E: w <sup>i</sup> <sup>a</sup> s <sup>u</sup> <sup>b</sup> G, I: NS	I: w <sup>i</sup> <sup>a</sup> s <sup>u</sup> <sup>b</sup> G, E: NS	I: w <sup>i</sup> <sup>a</sup> s <sup>u</sup> <sup>b</sup> 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 <sup>a</sup> E <sup>a</sup> I <sup>b</sup>	G <sup>a</sup> E <sup>b</sup> I <sup>b</sup>	G <sup>a</sup> E <sup>b</sup> I <sup>a</sup>	G <sup>a</sup> E <sup>b</sup> I <sup>c</sup>
	Sampling season	12	4947.67	412.31	2.31	0.0004	E: w <sup>i</sup> <sup>a</sup> s <sup>u</sup> <sup>b</sup> G, I: NS	I: w <sup>i</sup> <sup>a</sup> s <sup>u</sup> <sup>b</sup> G, E: NS	I: w <sup>i</sup> <sup>a</sup> s <sup>u</sup> <sup>b</sup> G, E: NS	G, E, I: NS
	Residual	96	17159.82	178.79						
	Total	119	42626.82							
(c) Av. taxon. distinct. (Δ <sup>*</sup> )	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 <sup>a</sup> E <sup>a</sup> I <sup>b</sup>	NS	NS	G <sup>a</sup> E <sup>a</sup> I <sup>b</sup>
	Sampling season	12	4667.83	388.99	2.05	0.0160	G, E, I: NS	I: w <sup>i</sup> <sup>a</sup> s <sup>u</sup> <sup>b</sup> 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 <sup>+</sup> )	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 <sup>a</sup> E <sup>a</sup> I <sup>b</sup>	NS	NS	G <sup>a</sup> E <sup>a</sup> I <sup>b</sup>
	Sampling season	12	4547.10	378.10	2.03	0.0170	G, E, I: NS	I: w <sup>i</sup> <sup>a</sup> s <sup>u</sup> <sup>b</sup> G, E: NS	G, E, I: NS	G, E, I: NS
	Residual	96	17921.75	186.66						
	Total	119	36179.63							

693 **Table 3.** Pearson correlation coefficients ( $n=120$ ) of diversity measures within soil faunal  
 694 taxonomic groups towards diversity measures among functional groups in the food web,  
 695 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. ( $\Delta^*_E$ )	0.35**	0.26*
Aver. tax. breadth ( $\Delta^+_E$ )	0.37**	0.30**
Collembolans		
Richness ( $N_C$ )	0.60**	0.09
Shannon index ( $H_C$ )	0.57**	0.17
Aver. taxon. distinctn. ( $\Delta^*_C$ )	0.46**	0.01
Aver. tax. breadth ( $\Delta^+_C$ )	0.47**	0.02
Oribatid mites		
Richness ( $N_O$ )	0.34**	0.08
Shannon index ( $H_O$ )	0.33**	0.08
Aver. taxon. distinctn. ( $\Delta^*_O$ )	0.20*	0.09
Aver. taxon. breadth ( $\Delta^+_O$ )	0.21*	0.09
Nematodes		
Richness ( $N_N$ )	0.17	0.01
Shannon index ( $H_N$ )	0.07	-0.05
Aver. taxon. distinctn. ( $\Delta^*_N$ )	0.03	-0.03
Aver. taxon. breadth ( $\Delta^+_N$ )	0.27*	0.10

696

697 **Figures legends**

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

707 **Figure 2.** Average values ( $\pm$  s.e.) of the community-weighted mean body mass of soil fauna  
708 ( $CBM$ ) at the three land use intensity levels in the four regions across Europe. Data from both  
709 sampling seasons are pooled. Significance effects ( $P$ -values) of region (Reg.), land use  
710 intensity level (Int.) and sampling season (Sam.) as determined by permutational univariate  
711 analysis of variance are given for each measure. Regions (indicated below horizontal axis)  
712 and land use intensity levels for each region not sharing the same letter are significantly  
713 different according to pair-wise a posteriori comparisons. Underlined land use intensity levels  
714 denote significantly different values between sampling seasons. Codes are depicted in Table  
715 1.

716 **Figure 3.** Average values ( $\pm$  s.e.) of: (a) richness ( $N$ ), (b) Shannon index ( $H'$ ), (c) average  
717 taxonomic distinctness ( $\Delta^*$ ) and (d) average taxonomic breadth ( $\Delta^+$ ) for earthworms and  
718 oribatid mites at the three land use intensity levels in the four regions across Europe. Data  
719 from both sampling seasons are pooled. Significance effects ( $P$ -values) of region (Reg.), land

720 use intensity level (Int.) and sampling season (Sam.) as determined by permutational  
721 univariate analysis of variance are given for each combination of soil faunal group and  
722 diversity measure. Regions (indicated below horizontal axis) and land use intensity levels for  
723 each region not sharing the same letter are significantly different according to pair-wise a  
724 posteriori comparisons. Underlined land use intensity levels denote significantly different  
725 values between sampling seasons. Codes are depicted in Table 1.

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