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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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42 **Keywords**

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

45 **Paper type:** Primary Research Article

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 m² 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 pg
180 μm^{-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 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 (Δ^*) for

225 earthworms (Δ^*_{E}), Collembolans (Δ^*_{C}), oribatid mites (Δ^*_{O}) and nematodes (Δ^*_{N}), and iv)
226 average taxonomic breadth (Δ^+) for earthworms (Δ^+_{E}), Collembolans (Δ^+_{C}), oribatid mites
227 (Δ^+_{O}) and nematodes (Δ^+_{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 (Δ^*) 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 ω_{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 (Δ^+) 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: Δ^*_E , Δ^*_C , Δ^*_O and Δ^*_N ; and v) average taxonomic breadth within the four
266 soil faunal taxonomic groups: Δ^+_E , Δ^+_C , Δ^+_O and Δ^+_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 (Δ^*) and breadth (Δ^+) 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 ^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							

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 ^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: w ⁱ ^a s ^u ^b G, I: NS	I: w ⁱ ^a s ^u ^b G, E: NS	I: w ⁱ ^a s ^u ^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: w ⁱ ^a s ^u ^b G, I: NS	I: w ⁱ ^a s ^u ^b G, E: NS	I: w ⁱ ^a s ^u ^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: w ⁱ ^a s ^u ^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: w ⁱ ^a s ^u ^b 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. (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

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 (Δ^*) and (d) average taxonomic breadth (Δ^+) 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 (Δ^*) and (d) average taxonomic breadth (Δ^+) 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.