Intensive agriculture reduces soil biodiversity across Europe

Running head: Intensive agriculture and soil biodiversity

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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

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Abstract

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

3

Introduction

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

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

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.

Material and methods

Field sites, soil sampling and analysis

We collected soil samples from farms in southern Sweden (region Scania: SE), southern UK (region Chilterns: UK), western Czech Republic (region České Budějovice: CZ) and northern Greece (region Kria Brisi: GR). The regions and farms were chosen to represent replicating agricultural management types across Europe, irrespective of soil types and climate. The annual mean/min/max temperature at the different sites are: 7.8/6.6/9.6 °C (SE), 9.5/5.5/13.5 °C (UK), 7.9/3/13 °C (CZ) and 14/4/31 °C (GR). The annual precipitation is 666 mm, 625 mm, 700 mm and 435 mm respectively. The dominant soil types are Calcaric Cambisol (SE), Chromic Luvisol, Leptosol (UK), Stagnic Luvisol, Dystric Cambisol (CZ), and Fluvisol (GR).

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

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), Mršic (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

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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 μm^3, and 400 μm^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 *gij* 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 $G = (gij)$ 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: $\dfrac{\left[\sum\sum_{i<j}\omega_{ij}x_ix_j\right]}{\left[\sum\sum_{i<j}x_ix_j\right]}$ 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.

Results

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

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

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

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

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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

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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 then 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).

Discussion

341

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.

Acknowledgements

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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

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

	Source	df	SS	MS	F	P	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: wi^a su^b G, I: NS	I: wi^a su^b G, E: NS	I: wi^a su^b G, E: NS	G, E, I: NS
	Residual	96	11990.45	124.90						
	Total	119	34014.09							
(b) Shannon index (H)	Region	3	8667.71	2889.24	16.16	0.0002	a	b	c	d
	Intensity	8	11851.62	1481.45	8.29	0.0002	$G^a E^a I^b$	$G^a E^b I^b$	$G^a E^b I^a$	$G^a E^b I^c$
	Sampling season	12	4947.67	412.31	2.31	0.0004	E: wi^a su^b G, I: NS	I: wi^a su^b G, E: NS	I: wi^a su^b G, E: NS	G, E, I: NS
	Residual	96	17159.82	178.79						
	Total	119	42626.82							
(c) Av. taxon. distinc. (Δ^*)	Region	3	6726.94	2242.32	11.82	0.0002	a	b	c	c
	Intensity	8	7236.89	904.61	4.77	0.0002	$G^a E^a I^b$	NS	NS	$G^a E^a I^b$
	Sampling season	12	4667.83	388.99	2.05	0.0160	G, E, I: NS	I: wi^a su^b G, E: NS	G, E, I: NS	G, E, I: NS
	Residual	96	18210.19	189.69						
	Total	119	36841.85							
(d) Av. taxon. breadth (Δ^+)	Region	3	6552.58	2184.19	11.70	0.0002	a	b	c	c
	Intensity	8	7157.29	894.66	4.79	0.0002	$G^a E^a I^b$	NS	NS	$G^a E^a I^b$
	Sampling season	12	4547.10	378.10	2.03	0.0170	G, E, I: NS	I: wi^a su^b G, E: NS	G, E, I: NS	G, E, I: NS
	Residual	96	17921.75	186.66						
	Total	119	36179.63							

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

Figures legends

698 **Figure 1.** Average values (± 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 (± 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 (± 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 (± 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.