



History of land-use intensity can modify the relationship between functional complexity of the soil fauna and soil ecosystem services – A microcosm study

M. Liiri^{a,*}, M. Häsä^b, J. Haimi^b, H. Setälä^a

^a University of Helsinki, Department of Environmental Sciences, Niemenkatu 73, FI-15140 Lahti, Finland

^b University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 Jyväskylä, Finland

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ABSTRACT

Agricultural intensification generally results in the loss of soil organic matter, a decline in soil biodiversity, and the reduced ability of soils to retain nutrients. Intensified land-use can bring about legacy effects in soil ecosystem services that may last for hundreds of years after the cessation of agricultural practises. We studied, in a laboratory pot experiment, whether legacy effects due to intensive land/soil management (intensively managed wheat field) can be alleviated by restoring the disturbed soil with soil fauna typical of less managed soils (grassland soil). We also compared the effects of functional complexity of the soil fauna (microfauna, microfauna + mesofauna (enchytraeids), microfauna + macrofauna (earthworms, *Aporrectodea caliginosa*), all groups together) on the ability of wheat fields and grassland soils to retain nitrogen, carbon, the herbicide metribuzin and wheat biomass production, and whether these effects are a result of the land-use type. Our results showed that even after homogenising the soils in terms of soil macrostructure and faunal community composition, the legacy of land-use remained and affected the rates of soil processes. For example, wheat biomass production and the retention of nitrogen and carbon were higher but the retention of metribuzin was lower in the wheat field than in the grassland soil. The impacts of functional complexity of the fauna were mostly similar between the two soils: the retention of metribuzin and carbon (measured as dissolved organic carbon leaching) was impaired by the most complex faunal community and plant performance was improved by the presence of earthworms. However, impact of the fauna on soil organic matter dynamics was different in the two soils: in the grassland soil, meso- and macrofauna retarded whereas in the wheat field these fauna stimulated soil organic matter loss. We conclude that land-use history affects the level of ecosystem services provided by soils, and that restoring functionally complex faunal communities cannot alleviate the legacies of land-use in the short-term.

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1. Introduction

The intensification of food and biofuel production has led to the conversion of grasslands into intensively managed agricultural lands with a concomitant increase in trade-offs between different ecosystem services provided by soils (DeFries et al., 2004; Rodríguez et al., 2006). For example, agricultural practises such as fertilisation, pesticide application and tillage aim to maximise crop production in the short-term, but also impair the ability of soils to provide other essential ecosystems services (such as nutrient retention and pest control), and reduce soil sustainability in the long-term. For instance, when natural ecosystems are converted to agricultural systems, the aggregate structure of the soil is disrupted (Ladd et al., 1993; Beare et al., 1994) and soil organic matter (SOM)

content is reduced (Lal, 2008; Smith, 2008; Mishra et al., 2010). This can lead to reduced crop yields and stability (Pan et al., 2009), impaired water regulation (e.g. Bot and Benites, 2005) and a lowered ability of soils to retain nutrients (Barrett and Burke, 2000). Such soils may also have a reduced ability to retain and/or degrade pesticides (Jenks et al., 1998; Kah et al., 2007).

The intensification of land-use also results in a decline in soil biodiversity (Mäder et al., 2002; Culman et al., 2010; Postma-Blaauw et al., 2010). However, soil biodiversity is central when the functioning of soils and consequently ecosystem services provided by the soil are considered (Barríos, 2007). The intensification of land-use can have a disproportionate impact on the soil biota and a decline in biodiversity may not be uniform across all taxa. First, large-sized soil organisms, such as earthworms and enchytraeids are more severely affected by intense land-use than smaller sized organisms, such as nematodes and protozoa (Wardle, 1995; Postma-Blaauw et al., 2010). As both earthworms (e.g. Edwards, 2004; Eriksen-Hamel and Whalen, 2007) and enchytraeids (Didden,

* Corresponding author. Tel.: +358 40 805 3883, fax: +358 14 260 2321.

E-mail addresses: mira.liiri@helsinki.fi (M. Liiri), miko.hasa@jyu.fi (M. Häsä), jari.m.haimi@jyu.fi (J. Haimi), heikki.setala@helsinki.fi (H. Setälä).

Table 1
Characteristics of the experimental soils at the beginning of the study. Values in parentheses are SE.

Soil	LOI (%)	pH (H ₂ O)	C (%)	N (%)	C:N	Ca (mg l ⁻¹)	P (mg l ⁻¹)	K (mg l ⁻¹)	Mg (mg l ⁻¹)	S (mg l ⁻¹)
Grassland soil	8.6 (0.001)	8.4 (0.0)	11.5 (1.5)	0.46 (0.11)	25 (3)	>20,000	14	260	190	31
Wheat field soil	7.4 (0.002)	8.3 (0.03)	9.7 (0.4)	0.27 (0.02)	36 (1)	>20,000	28	170	170	30

1990, 1993; Topoliantz et al., 2000; Liiri et al., 2001) are known to contribute to the formation of soil aggregates and the stimulation of soil fertility and plant growth, a loss or decrease of these taxa can have a direct impact on the ability of soils to provide ecosystem services (Bradford et al., 2007). Second, land-use intensification affects the structure of the soil microbial community so that bacteria are favoured over fungi (Bardgett and McAlister, 1999; de Vries et al., 2006). Since bacterial-dominated soils have less conservative nutrient dynamics than fungal-dominated soils, the ability of these soils to retain nutrients is impaired. This can lead to an increased risk of nutrient leaching from the system (Bardgett et al., 2003; de Vries et al., 2006; Vauramo and Setälä, 2010). Shifts in the microbial community structure to a bacterial-dominated community can also impair the capability of soils to stabilise carbon (Six et al., 2006), and even affect the biodegradation of pesticides (Levanon, 1993).

Due to altered nutrient and carbon dynamics (McLaughlan, 2006), intensive land-use can have a long lasting effect on soils. For example, soil ecosystem services can be affected for hundreds of years after the cessation of agricultural practises (Foster et al., 2003). With this in mind, a laboratory microcosm study was established to assess whether the legacies of intensive wheat cultivation can be alleviated and ecosystem services restored to levels found in extensively managed grassland soils. We attempted to achieve this by re-establishing soils with fauna that generally suffer or become locally extinct due to intensive land-use. We also studied whether the impact of increasing functional complexity of soil faunal community differs between soils of contrasting land-use history. As our intention was not to study the effects of land-use intensity per se, but the legacy of land-use on the soil, the soils were sieved to homogenise their macrostructure. Then the two soils were inoculated with comparable soil fauna of various functional groups according to their body size. In general, the body size of an organism correlates with its metabolic rate, lifetime, population density and selection of prey (Peters, 1983). As an indication of the ability of the systems to provide ecosystem services, we measured the ability of soils to retain nitrogen, carbon and a pesticide (herbicide metribuzin), and plant biomass production and nitrogen acquisition. We hypothesised that the legacy of land-use determines the level of ecosystem services provided by the soils. We expected the grassland soil with a fungal-dominated soil food web and higher SOM content to better retain nutrients and the herbicide than the wheat field soil, but retention of carbon is lower due to higher C availability. Plant biomass production in the grassland soil was expected to be lower due to a lack of plant available nutrients. We also hypothesised that the impact of soil faunal complexity on soil processes is relatively less pronounced in the fungal-dominated grassland soil than in the bacterial-dominated wheat field soil because, (i) less nitrogen is liberated per consumed biomass by fungal feeders than by bacterial feeders (Chen and Ferris, 2000), and (ii) the impact of soil fauna in the grassland soil can be masked due to legacies brought about by earlier soil macrofaunal activities (Villenave et al., 1999).

2. Materials and methods

2.1. Experimental design

The soils used in the experiment originated from southern England (51°32'N 1°04'W) from an extensively managed grassland and

an adjacent intensively managed wheat field. The grassland had not been fertilised in the past but was infrequently grazed. The dominant plant species in the grassland were *Festuca ovina*, *Holcus lanatus*, *Dactylis glomerata* and *Arrhenarium elatius*. The wheat field had a crop rotation of wheat–wheat–winter oil seed rape, with winter oil seed rape in 2008 and winter wheat in 2009. The wheat field was fertilised with 184 kg N, 12 kg Mg, 65 kg SO₃ and 100 kg K₂O ha⁻¹ in 2008 and with 181 kg N and 30 kg SO₃ ha⁻¹ in 2009 (for soil characteristics see Table 1). The soil type in both fields was calcareous loam. The soils were collected in September 2009 and kept cool (+5 °C) until the establishment of the microcosms in December 2009.

Before added to the experimental pots (hereafter referred to as microcosms), soils were defaunated by freezing (twice at –20 °C; this method is known to effectively eliminate the soil meso- and macrofauna while having little effect on soil microbes (Bruckner et al., 1995; Koponen et al., 2006)) and then sieved through a 2 mm sieve. Sieving equalised the physical structure between the two soils. Forty microcosms were constructed by filling 20 plastic flower pots (diameter 15 cm, height 11 cm) with 1.0 kg of fresh grassland soil and 20 pots with 1.0 kg of wheat field soil. Soil moisture was adjusted to 60% of the soil water holding capacity (WHC) and kept at this level for the duration of the experiment. In addition, six extra microcosms (three with grassland soil and three with wheat field soil) were constructed as explained above to evaluate the establishment of soil microfauna in the microcosms.

Faunal communities were established to the microcosms by first reinoculating all 40 microcosms with microbes + microfauna (MiF). Then the functional complexity of the soil food web was manipulated: five grassland microcosms and five wheat soil microcosms received mesofauna (unidentified enchytraeids, MeF), five grassland microcosms and five wheat soil microcosms received soil macrofauna (Lumbricidae *Aporrectodea caliginosa*, MaF), and five grassland microcosms and five wheat soil microcosms were inoculated with all of the aforementioned fauna (All). Five grassland microcosms and five wheat soil microcosms did not receive additional fauna (treatment MiF). Reinoculation of microbes + microfauna was achieved by adding a 10 ml soil–water suspension to the microcosms, which was filtered through 45 µm mesh. The suspension contained, on average, 16 nematodes (corresponding to 906 individuals m⁻²) and an unquantified number and diversity of soil microbes. The soil used in the suspension was a mixture of grassland soil and wheat field soil used in the experiment. Enchytraeids were added to the microcosms 23–26 days, and *A. caliginosa* 30 days after the initial inoculations with microfauna. Each microcosm with enchytraeid worms received 21 enchytraeids (corresponding to 1188 individuals m⁻²) and the treatment with *A. caliginosa* received two individuals (corresponding to 113 individuals m⁻², average fresh mass of the two individuals combined being 1.4 g).

Four wheat seeds (variety Belvoir) were planted in each microcosm 30 days after inoculation with the soil microfauna (considered as the beginning of the experiment). When more than one of the seeds germinated, extra seedlings were removed from the microcosms, resulting in one wheat plant per microcosm. The microcosms were incubated in a greenhouse (temperature adjusted to 23 °C, daily light/dark cycle 16/8 h) and watered daily to compensate evaporated water.

Table 2Abundances of the soil fauna at the end of the experiment in microcosms with grassland and wheat field soils at different functional complexities of the soil fauna (mean \pm SE).

SOIL	FAUNA	Total nematodes (ind. g ⁻¹ d.m. soil)	Bacterivorous nematodes (ind. g ⁻¹ d.m. soil)	Herbivorous + fungivorous nematodes (ind. g ⁻¹ d.m. soil)	Omnivorous + predatory nematodes (ind. g ⁻¹ d.m. soil)	Enchytraeids (ind. g ⁻¹ d.m. soil)	Earthworms (g fm microcosm ⁻¹)
Grassland soil	MiF	43.5 (4.9)	21.0 (3.0)	7.8 (0.4)	14.7 (3.0)	–	–
	MeF	34.2 (8.0)	15.4 (4.7)	8.6 (2.7)	10.2 (1.8)	0.24 (0.07)	–
	MaF	37.2 (7.4)	21.8 (6.1)	11.3 (1.8)	4.1 (1.0)	–	1.9 (0.4)
	All	27.9 (3.7)	12.1 (3.0)	13.3 (1.2)	2.5 (0.6)	0.43 (0.13)	1.8 (0.1)
Wheat field soil	MiF	23.7 (2.8)	11.8 (1.9)	9.1 (1.0)	2.8 (1.0)	–	–
	MeF	27.1 (2.9)	14.0 (1.7)	8.0 (1.5)	5.1 (1.4)	0.26 (0.06)	–
	MaF	22.9 (3.8)	11.6 (1.4)	9.4 (1.9)	1.9 (0.6)	–	1.6 (0.2)
	All	22.4 (4.0)	12.3 (2.5)	8.8 (1.5)	1.3 (0.3)	0.12 (0.03)	1.9 (0.1)

MiF, microfauna only; MeF, microfauna + mesofauna; MaF, microfauna + macrofauna; All, all groups together.

The six extra microcosms (three grassland and three wheat soil; identical to the All-fauna microcosms described above) were sampled for soil nematodes at the start of the experiment. The total number of nematodes was 30.7 and 22.0, herbivores + fungivores 20.2 and 14.8, bacterivores 9.0 and 6.8 and omnivores + predators 1.4 and 0.4 g⁻¹ d.m. soil in grassland and wheat field soils, respectively.

At week 13, the microcosms were treated with the herbicide metribuzin (Senkor[®], content of active ingredient 70%). Metribuzin (4-amino-6-tert-butyl-4,5-dihydro-3-methylthio-1,2,4-triazin-5-one) is a triazine herbicide, which is commonly used in the cultivation of potatoes. Metribuzin, especially its degradation product, is a water soluble compound with a relatively high risk for leaching (Harper, 1988; Henriksen et al., 2004; Kjær et al., 2005). The herbicide was added to the microcosms in water solution so that each herbicide-treated microcosm received 50 ml water containing 1.26 mg metribuzin (corresponding to 500 g of 100% metribuzin ha⁻¹). This herbicide was used because the soils had not been treated with metribuzin before and hence neither of the soils posed a legacy for metribuzin.

2.2. Sampling and analyses

The microcosms were destructively sampled 15 weeks after the start of the experiment. The wheat plants were cut just above soil surface and dried in at 105 °C for 24 h. Wheat dry mass (shoot and spikes), number of seeds and N and C content of the leaves and seeds (Leco CNS-2000 analyser) were determined. Ability of the soils to retain carbon, nutrients and the herbicide were analysed by watering the microcosms with 550 ml of water and collecting that which leached through the soil. The leachates were analysed for dissolved organic carbon (DOC), total organic carbon (TOC) (standard for DOC and TOC analyses: SFS-EN 1484:1997), total nitrogen (SFS-EN ISO 11905-1:1998), NO₂⁻ + NO₃⁻ – N (SFS-EN ISO 13395:1996), NH₄⁺ – N (SFS3032:1976) and metribuzin. Metribuzin in the leachates were analysed using gas chromatography–mass spectrometry (selected ion monitor-technique).

Soil nematodes were extracted from ca. 20 g fresh mass soil samples using the wet funnel method (Sohlenius, 1979), and were identified into feeding groups after Yeates (1971). Enchytraeid worms were extracted from ca. 80 g fresh mass soil samples using wet funnels (O'Connor, 1962). Enchytraeid worm biomass was estimated according to Makulec (1983). Soil microarthropods were extracted using a modified high-gradient extractor (Macfadyen, 1961) from ca. 50 g fresh mass soil to check for possible contamination of the microcosms with fauna that were not intentionally introduced to the microcosms. *A. caliginosa* individuals were hand sorted from the soil and weighed for fresh mass. In addition to the faunal analyses, soil pH (in water), organic matter content (LOI%)

and percentual change in LOI% during the experiment were measured.

Soil microbial activity was estimated by measuring CO₂ production (UniQuant Carbon Analyzer) of the microcosm soils: 100 g (dry mass) of soil was placed into glass jars that were sealed with metal lids with ventilation holes. Soil moisture content was adjusted to 30% of soil dry mass and soils were incubated at room temperature (20 °C) for a period of 2 weeks, after which CO₂-measurements started. Air samples were taken with 1-ml syringes. After taking the first samples, the jars were sealed for 1 h after which a second air sample was taken. This procedure was repeated six times at 3–4 day intervals. CO₂ production was calculated as the difference between the second and first measurements, and cumulative CO₂-production during the measurement period was calculated.

The relative impact of complexity of the fauna on soil ecosystem services (retention of N, C and metribuzin, production of wheat biomass and acquisition nitrogen by the wheat plants) in the grassland and wheat field soils was estimated by comparing the percentual difference of a given ecosystem service between the MiF treatment and the other treatments (MeF, MaF and All). A difference between the soils was considered to denote a different impact of increasing complexity of fauna on the level of soil ecosystem services in the two soils.

2.3. Statistics

The impacts of land-use intensity (grassland vs. wheat field soil) and functional complexity of the soil fauna on measured variables were tested using two-way ANOVA, followed by Tukey HSD Post Hoc test. If the parametric assumptions of ANOVA were not met, data were transformed to log₁₀ (x+1) or a reciprocal transformation was used (DOC). The non-parametric Kruskal–Wallis test was applied when the assumption of normality could not be satisfied after transformations. Correlations between the measured variables were analysed using the Pearson's correlation test. Statistical analyses were performed using PASW Statistics 18 (SPSS Inc.).

3. Results

3.1. Soil biota

The total number of nematodes was higher in the grassland than in the wheat field soil, and the trophic structure of the nematode community differed between the two soils at the end of the experiment. Densities of herbivores + fungivores and bacterivores were significantly higher in the grassland than in the wheat field soil. Furthermore, omnivores + predators were more numerous in the grassland soil, although the difference between the soils was less evident when earthworms were present. Functional complexity

Table 3
Results of two-way ANOVA for the effects of soil (grassland and wheat field soil) and fauna (MiF, MeF, MaF and All) on the soil biota, wheat performance, leaching measurements and soil LOI.

Variable	Soil		Fauna		Soil × Fauna	
	F	P	F	P	F	P
<i>Soil biota</i>						
Total nematodes ^a	11.51	<0.01	1.06	0.38	0.94	0.44
Bacterivorous nematodes ^a	4.81	0.04	0.81	0.50	1.30	0.29
Herbivorous + fungivorous nematodes ^a	1.67	0.02	1.50	0.24	1.29	0.30
Omnivorous + predatory nematodes ^a	32.47	<0.01	13.18	<0.01	3.23	0.04
Earthworms (fm ^b g microcosm ⁻¹)	0.12	0.74	0.18	0.67	0.85	0.37
Cumulative CO ₂ -production	14.66	<0.01	0.34	0.80	4.29	0.01
<i>Wheat performance</i>						
Wheat aboveground biomass (g d.m.)	31.17	<0.01	6.96	<0.01	1.22	0.32
No. of seeds	68.47	<0.01	12.43	<0.01	1.34	0.28
Seed weight (g d.m.)	5.49	0.03	0.81	0.50	1.72	0.18
C% leaves	105.81	<0.01	4.29	0.01	3.13	0.04
N in seeds (mg)	24.77	<0.01	18.88	<0.01	0.31	0.82
C:N ratio of wheat leaves	2.97	(0.10)	1.08	0.37	0.15	0.93
C:N ratio of wheat seeds	6.45	0.02	1.18	0.33	1.75	0.18
<i>Leaching and LOI</i>						
Total N leached (mg microcosm ⁻¹)	10.30	<0.01	1.98	0.14	0.24	0.87
Inorganic N leached (mg microcosm ⁻¹)	13.61	<0.01	1.30	0.29	0.48	0.70
Organic N leached (mg microcosm ⁻¹)	4.82	0.04	3.67	0.02	1.12	0.36
DOC leached (mg microcosm ⁻¹)	9.02	0.01	5.25	0.04	2.28	(0.10)
Metribuzin leached (μg microcosm ⁻¹)	29.12	<0.01	3.87	0.02	1.88	0.15
% change in soil LOI (%)	0.59	0.45	0.35	0.79	4.37	0.02

^a ind. g⁻¹ d.m. soil.

^b Fresh mass.

of the soil fauna had no impact on total nematode numbers and the only trophic group of nematodes that was affected by the faunal community structure was omnivores + predators with lowest numbers in the presence of earthworms (Tables 2 and 3).

The number of enchytraeids (soil: $\chi^2 = 1.9$, $P = 0.17$; fauna: $\chi^2 = 0.1$, $P = 0.74$) and the biomass of *A. caliginosa* were neither affected by soil nor faunal community structure (Tables 2 and 3).

3.2. Leaching of C, N and metribuzin

Most (86%) of the organic carbon that leached through the soils was in the form of dissolved organic carbon (DOC). DOC leaching was higher in the grassland than wheat field soil and was stimulated by the presence of all the fauna (All vs. MiF $P = 0.01$, All vs. MeF $P = 0.02$ and All vs. MaF $P = 0.08$) (Fig. 1c and Table 3). NO₃⁻ - N accounted for 91% of the total N leaching. Also, leaching of total N (data not shown) and inorganic N (NO₂⁻ + NO₃⁻ + NH₄⁺) were higher from the grassland than wheat field soil (Fig. 1a and Table 3), but leaching of organic N showed an opposite trend (Fig. 1b and Table 3). Community structure of the soil fauna did not affect nitrogen leaching, although leaching of organic nitrogen tended to increase in the presence of the complex faunal community (All vs. MiF $P = 0.08$ and All vs. MeF $P = 0.02$).

Both soil and community structure of the soil fauna affected leaching of metribuzin from the microcosms: more metribuzin was leached from the wheat field than from the grassland soil, and the presence of all fauna tended to increase the leaching of metribuzin compared to the MeF ($P = 0.05$) and MaF ($P = 0.09$) treatments (Fig. 1d and Table 3). The retention of metribuzin in the soil was positively correlated with soil organic matter content (leaching of metribuzin vs. LOI (%): $r = -0.68$, $P < 0.01$). Moreover, leaching of metribuzin correlated positively with the leaching of DOC ($r = 0.46$, $P < 0.01$).

3.3. Soil OM and CO₂-production

Soil organic matter content decreased in all treatments during incubation. However, impacts of the soil fauna on SOM differed

between the two soils: in the grassland soil enchytraeids and earthworms decreased the loss of SOM whereas in the wheat field these fauna had an opposite effect (Fig. 1e and Table 3). The loss of SOM correlated negatively with the retention of DOC (loss of SOM vs. leaching of DOC: $r = 0.52$, $P = 0.01$); this correlation was, however, only significant for the wheat field soil ($r = 0.77$, $P < 0.01$).

Cumulative CO₂-production was higher in the grassland than wheat field soils (Tables 3 and 4). However, the impact of soil was dependent on the community structure of the fauna so that no statistically significant effect was observed in the microcosms with MeF or MaF. Faunal community structure had no clear impact on CO₂-production.

3.4. Wheat growth, seed production and nutrient acquisition

The total aboveground biomass and number of seeds produced by the wheat plants were higher in the wheat field than in the grassland soil. However, the mean weights of seeds were lower in the wheat field than in the grassland soil (Tables 3 and 4). Soil faunal community structure affected wheat performance in both soils: wheat biomass generally increased with the presence of earthworms, although wheat growth differed significantly only between the microcosms with enchytraeids only (MeF) and the microcosms with earthworms (MaF, All) (MaF vs. MeF $P < 0.01$, All vs. MeF $P < 0.01$). The presence of earthworms tended to enhance wheat seed production (MaF vs. MiF $P = 0.06$, MaF vs. MeF $P < 0.01$, All vs. MiF $P = 0.05$, All vs. MeF $P < 0.01$), while enchytraeids appeared to have the opposite effect (MeF vs. MiF $P = 0.07$). The average weights of seeds were not affected by the faunal treatments (Tables 3 and 4).

The C content (%C) of wheat leaves was higher in plants growing in the wheat field than the grassland soil, while the %C of wheat seeds did not differ ($\chi^2 = 0.9$, $P = 0.33$) between the soils (Tables 3 and 4). Soil did not have an effect on the %N of wheat leaves ($\chi^2 = 2.7$, $P = 0.10$). %N of the seeds was lower in the wheat field than in the grassland soil ($\chi^2 = 5.5$, $P = 0.02$), while the amount of N (mg) showed an opposite trend. C:N ratio of the leaves and seeds were higher ($P = 0.10$) in the wheat field than in the grassland soil, indicating a lower quality of seeds in the wheat field soils. The soil fauna

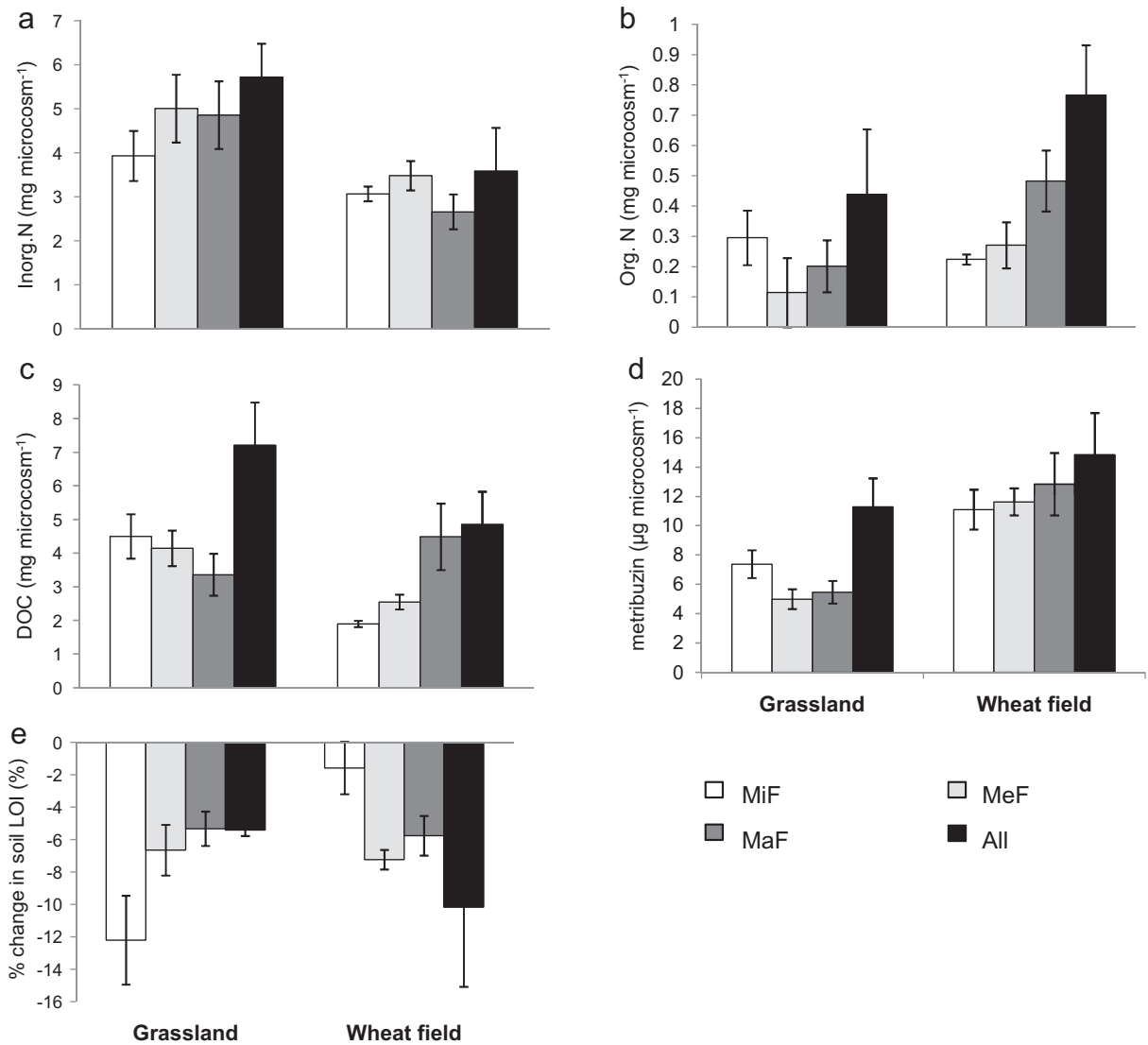


Fig. 1. Leaching of (a) inorganic nitrogen (mg microcosm⁻¹), (b) organic nitrogen (mg microcosm⁻¹), (c) dissolved organic carbon (mg microcosm⁻¹), (d) herbicide metribuzin (µg microcosm⁻¹) from the microcosms and (e) percentual change in soil matter content (LOI) during the experiment. Abbreviations: MiF, microfauna only; MeF, microfauna + mesofauna (enchytraeids); MaF, microfauna + macrofauna (*A. caliginosa*); All, all groups together. Error bars represent ±SE.

Table 4

Soil cumulative CO₂-production and wheat growth, seed production and nutrient acquisition in microcosms with grassland and wheat field soils at different functional complexities of the soil fauna (mean ± SE).

	Grassland				Wheat field			
	MiF	MeF	MaF	All	MiF	MeF	MaF	All
Cumulative CO ₂ -production (µg g ⁻¹ d.w. soil)	189.1 (20.9)	163.0 (16.5)	146.3 (10.0)	185.2 (10.3)	112.8 (8.7)	149.3 (2.6)	144.2 (10.5)	129.7 (12.2)
Wheat aboveground biomass (g d.w.)	3.8 (0.4)	3.7 (0.2)	4.3 (0.3)	4.7 (0.4)	5.4 (0.2)	4.3 (0.2)	6.1 (0.4)	5.9 (0.4)
No. of spikes	1.4 (0.5)	1.6 (0.5)	1.6 (0.5)	1.6 (0.5)	2 (0)	1.4 (0.5)	2 (0)	2 (0)
Seed production per wheat (no.)	48.0 (5.6)	43.6 (3.9)	61.2 (6.7)	67.0 (5.3)	81.6 (1.6)	63.6 (3.9)	91.6 (2.2)	86.4 (3.6)
Weight of a seed (mg d.w.)	39.1 (0.8)	40.6 (2.0)	33.2 (3.7)	34.4 (2.4)	32.2 (2.4)	32.0 (2.5)	32.4 (2.7)	34.8 (1.7)
%C wheat leaves	33.2 (0.43)	32.7 (0.47)	35.3 (0.53)	35.4 (0.32)	38.1 (0.32)	37.8 (0.89)	37.8 (0.65)	38.3 (0.37)
%N wheat leaves	0.71 (0.24)	0.45 (0.02)	0.47 (0.01)	0.50 (0.03)	0.52 (0.02)	0.50 (0.01)	0.47 (0.02)	0.50 (0.02)
%C wheat seeds	42.5 (0.13)	42.5 (0.10)	42.7 (0.04)	42.6 (0.17)	42.4 (0.08)	42.7 (0.10)	42.5 (0.08)	42.5 (0.04)
%N wheat seeds	2.45 (0.15)	2.38 (0.17)	2.65 (0.15)	2.47 (0.31)	1.93 (0.12)	2.51 (0.14)	2.11 (0.12)	2.24 (0.13)
Amount of N in the seeds (mg)	44.4 (1.8)	41.0 (0.8)	50.9 (2.5)	54.2 (2.6)	49.8 (1.1)	48.4 (1.9)	59.5 (3.1)	63.4 (2.3)
C:N ratio of wheat leaves	70.7 (3.8)	72.6 (2.2)	74.9 (2.9)	72.0 (4.1)	73.9 (3.2)	74.8 (1.1)	81.7 (5.5)	76.8 (2.2)
C:N ratio of wheat seeds	17.7 (1.1)	18.1 (1.1)	16.3 (1.0)	18.3 (2.1)	22.4 (1.5)	17.2 (0.8)	21.1 (1.1)	20.2 (1.3)

MiF, microfauna only; MeF, microfauna + mesofauna; MaF, microfauna + macrofauna; All, all groups together.

had only minor impacts on C and N acquisition in the wheat; the presence of earthworms (treatments MaF and All) increased the %C of wheat leaves in the grassland soil, and the amount of N (mg) in the seeds from both soil treatments (Tables 3 and 4).

3.5. Relative impact of increasing functional complexity of the fauna on soil ecosystem services between the two soils

The complexity of the soil faunal community tended to have a greater effect on wheat biomass production in the grassland than in the wheat field soil ($F=3.5$, $P=0.07$), while the effect was opposite on the %N in wheat seeds ($F=3.9$, $P=0.06$) (Fig. 2a and b).

The leaching of DOC ($\chi^2=9.1$, $P<0.01$) and organic N ($\chi^2=7.4$, $P=0.01$) were relatively more stimulated by increased functional complexity of soil fauna in the wheat field than the grassland soil (Fig. 2c and e). Higher functional complexity of the soil fauna enhanced cumulative CO₂ production ($\chi^2=15.7$, $P<0.01$) in the wheat field soil but retarded it in the grassland soil, whereas the impact of faunal complexity on SOM content (LOI%) ($F=52.3$, $P<0.01$) was the opposite (Fig. 2g and h). The relative importance of increasing functional complexity of the soil fauna did not differ between the two soils with respect to the leaching of inorganic N ($F=2.5$, $P=0.13$) or metribuzin ($\chi^2=2.0$, $P=0.16$) (Fig. 2d and f).

4. Discussion

Increased land-use intensity is commonly believed to relate to the lowered ability of soils to retain nutrients due to lower SOM (Barrett and Burke, 2000) and the increased dominance of bacteria in the soil microbial community (Bardgett et al., 2003; de Vries et al., 2006; Vauramo and Setälä, 2010). These effects are often long lasting and changes in soil properties and the biota can be detected even hundreds of years after the abandonment of intense agricultural practises (Buckley and Schmidt, 2001; Dupouey et al., 2002; Foster et al., 2003; McLaughlan, 2006). In this study our main goal was to study if the legacy of intensive land-use on soil ecosystem services can be dispelled by restoring soil faunal communities with varying functional complexity in disturbed soils (i.e. wheat field soil), and whether the response of the soils to soil faunal complexity differs between soils of different disturbance status (wheat field vs. grassland soil). We expected that intensive wheat cultivation leaves a legacy in the soil and on soil-derived ecosystem services due to its adverse effects on soil physico-chemical and biological characteristics. Hence the ability of wheat field soils to retain N and metribuzin and availability of C would be lower, but plant biomass production and N acquisition higher than in the extensively used grassland soil – even after homogenising the soils with respect to soil macrostructure and the soil faunal community. As soil decomposition processes and plant growth can be stimulated by increasing functional complexity of the soil fauna (Setälä et al., 1996; Bardgett and Chan, 1999; Bradford et al., 2002), we further expected that the availability of N and C in the soil as well as plant growth would be higher in the microcosms with a more complex faunal community, but that this impact is more pronounced in the biotically impoverished wheat field soil than in the grassland soil.

The results of our experiment suggest that the history of land-use can affect the level of ecosystem services provided by soils. In contrast to our hypotheses, wheat field soil retained more N than grassland soil, but in line with our hypotheses, plant biomass, seed production and N acquisition was higher and the retention of metribuzin and loss of C lower in the wheat field than the grassland soil. In general, faunal effects were mostly similar in both soils: the retention of inorganic nitrogen was not affected by faunal community structure, but plant performance was improved by the presence of earthworms, while enchytraeids reduced plant growth.

In addition, the retention of metribuzin was impaired in the most diverse systems in both soils. Even though the retention of carbon, when measured as DOC leaching, was lower in the most diverse system in both soils, our results suggest that functionally complex faunal community has distinctively different effects on soil organic matter dynamics in the two soils of different management history: in the grassland soil meso- and macrofauna decreased the loss of SOM whereas in the wheat field soil these fauna accelerated SOM loss.

The legacy of land-use intensity may be the reason why plants grew larger and sequestered more nutrients in the wheat field soil, and that the amount of leachable N was lower than in the grassland soil at the end of the experiment. Tillage breaks up micro- and macroaggregates in the soil, rendering formerly physically protected soil organic carbon and nitrogen available for microbial consumption (Ladd et al., 1993; Beare et al., 1994). However, in regularly tilled soils (as is the case with the wheat field soil in this study), stimulation of decomposition and nutrient mineralisation seems to be negligible (Kristensen et al., 2000; Thomsen and Sørensen, 2006). Therefore, it is possible that in this study the relatively high amounts of N and C leaching from the grassland soil was due to sieving of the soil, which accelerated decomposition of soil organic matter and/or release of microbiologically bound nitrogen especially in these originally undisturbed soils with comparatively high soil N and C content (Kristensen et al., 2000). This inference is also supported by the higher CO₂-production from the grassland soil at the end of the experiment indicating higher microbial activity in these soils. The reason why wheat plants did not take up the excess N for biomass production in the grassland soil is probably also directly related to the legacies of land-use intensity. Due to long-term fertilisation of wheat field soils, initial levels of plant available nutrients were higher in the wheat field than in the grassland soil (de Vries et al., in press) and, most importantly, the concentration of phosphorus of the soil was double compared to the grassland soil. Therefore, plants growing in the grassland soil were probably P limited and could not use excess N liberated through decomposition for the production of biomass.

SOM plays a significant role in the retention of nutrients in soils as well as in the retention of pesticides (Sha'ato et al., 2000; Henriksen et al., 2004; Kah et al., 2007). We showed that retention of the herbicide metribuzin in the soils was strongly correlated with SOM content, and consequently the retention of metribuzin was impaired in the wheat field soil compared to the grassland soil. In general, the availability of metribuzin in soils and hence its vulnerability to leaching, is controlled by both abiotic (Henriksen et al., 2004) and biotic (Allen and Walker, 1987; Benoit et al., 2007) degradation, and by sorption to soil particles, especially to soil organic components (Sha'ato et al., 2000). However, separating the factors that influence the availability of metribuzin in the soil is difficult as these factors are often interrelated (Henriksen et al., 2004; Kah et al., 2007). This also seems to be the case in our study as the retention of metribuzin was affected by both SOM content (hence the origin of the soil) and the structure of the soil faunal community. We observed that the retention of metribuzin, together with soil carbon, was impaired in the microcosms with the most complex faunal community. Both enchytraeids (e.g. Cole et al., 2000) and earthworms (e.g. Postma-Blaauw et al., 2006) can increase C mineralisation in soils, but their impact on different soil carbon pools varies (Fox et al., 2006). Earthworms can stimulate mineralisation of stable soil C with large particle size, whereas enchytraeids utilise more labile C pool (Fox et al., 2006). Moreover, enchytraeids can consume smaller particles than earthworms. Therefore it is possible that the availability of C, and concomitantly metribuzin availability (Sha'ato et al., 2000) was enhanced in the microcosms with the most complex faunal community because of complementary resource use of the two oligochaetan groups. As enchytraeids

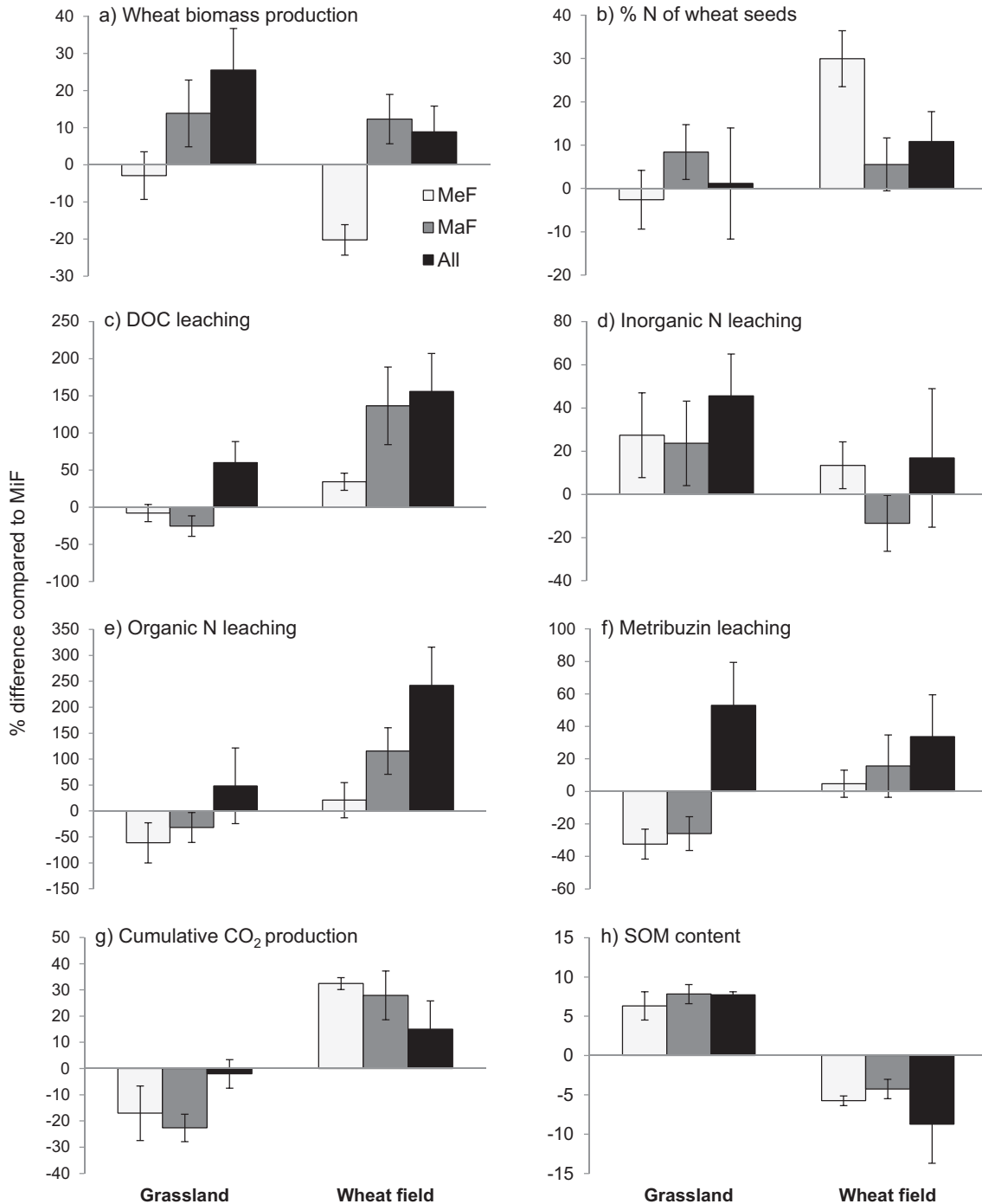


Fig. 2. Relative impact of increasing functional complexity of the soil fauna (% difference of treatments MeF, MaF and All to MiF) on (a) wheat biomass production, (b) %N of wheat seeds, (c) dissolved organic carbon leaching, (d) inorganic nitrogen leaching, (e) organic nitrogen leaching, (f) herbicide (metribuzin) leaching, (g) cumulative CO₂ production and (h) SOM content. For abbreviations see Fig. 1. Error bars represent \pm SE.

also feed on earthworm faeces (Dawod and Fitzpatrick, 1993; Topoliantz et al., 2000), it is possible that enchytraeids accelerated C release from these otherwise decomposition resistant (Martin and Marinissen, 1993) faecal structures.

Even though the retention of C, as depicted by DOC leaching, was impaired in the biotically most diverse systems in both soils, it is evident that enchytraeids and earthworms had a distinctly different impact on soil carbon dynamics in the two soils. This suggests that soil characteristics related to land-use history can affect the functioning of complex soil faunal communities. Even though it

is known that both enchytraeids and earthworms can stimulate C mineralisation (see above), these animals can also stabilise SOM (Koutika et al., 2001; Pulleman et al., 2005). It has been suggested that initial soil characteristics (Marhan and Scheu, 2005) and land-use intensity (Pulleman et al., 2005) can determine whether the soil fauna, especially earthworms, enhance or impair the stabilisation of SOM. The effects of earthworm may depend on the availability of C in soils: in soils with high C inputs and high C availability, earthworms can stabilise SOM while in soils with low C inputs and availability, earthworms have to consume older SOM leading to

losses of C from the soil (Pulleman et al., 2005; Fonte and Six, 2010; Fonte et al., 2010). It is therefore possible that the divergent effects of functionally complex soil faunal communities on soil C dynamic in the grassland and wheat field soil in our study were related to the availability of C in the soils, as the higher SOM content, DOC leaching and CO₂ production indicates better C availability in the grassland soil.

As differences in the levels of ecosystem services between the grassland and wheat field soils were detected even in structurally homogenised soils, we conclude that land-use history – at least in the short-term – is an important driver of soil processes and consequently ecosystem service provided by soils, and that restoring a functionally complex faunal community cannot dispel the legacies of land-use. However, to what extent our results apply to field conditions needs to be confirmed with large-scale and long-term field experiments.

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References

- Allen, R., Walker, A., 1987. The influence of soil properties on the rates of degradation of metatamitron, metazachlor and metribuzin. *Pestic. Sci.* 18, 95–111.
- Bardgett, R.D., Chan, K.F., 1999. Experimental evidence that soil fauna enhance nutrient mineralization and plant nutrient uptake in montane grassland ecosystems. *Soil Biol. Biochem.* 31, 1007–1014.
- Bardgett, R.D., McAlister, E., 1999. The measurement of soil fungal:bacterial biomass ratios as an indicator of ecosystem self-regulation in temperate meadow grasslands. *Biol. Fertil. Soils* 29, 282–290.
- Bardgett, R.D., Streeter, T.C., Bol, R., 2003. Soil microbes compete effectively with plants for organic nitrogen inputs to temperate grasslands. *Ecology* 84, 1277–1287.
- Barrett, J.E., Burke, I.C., 2000. Potential nitrogen immobilization in grassland soils across a soil organic matter gradient. *Soil Biol. Biochem.* 32, 1707–1716.
- Barrios, E., 2007. Soil biota, ecosystem services and land productivity. *Ecol. Econ.* 64, 269–285.
- Beare, M.H., Cabrera, M.L., Hendrix, P.F., Coleman, D.C., 1994. Aggregate-protected and unprotected organic matter pools in conventional and no-tillage soils. *Soil Sci. Soc. Am. J.* 58, 787–795.
- Benoit, P., Perceval, J., Stenrød, M., Moni, C., Eklo, O.M., Barriuso, E., Sveistrup, T., Kvarner, J., 2007. Availability and biodegradation of metribuzin in alluvial soils as affected by temperature and soil properties. *Weed Res.* 47, 517–526.
- Bot, A., Benites, J., 2005. The Importance of Soil Organic Matter – Key to Drought-resistant Soil and Sustained Food Production. *FAO Soils Bulletin* 80.
- Bradford, M.A., Tordoff, G.M., Eggers, T., Jones, T.H., Newington, J.E., 2002. Microbiota, fauna, and mesh size interactions in litter decomposition. *Oikos* 99, 317–323.
- Bradford, M.A., Tordoff, G.M., Black, H.I.J., Cook, R., Eggers, T., Garnett, M.H., Grayston, S.J., Hutcheson, K.A., Ineson, P., Newington, J.E., Ostle, N., Sleep, D., Stott, A., Jones, T.H., 2007. Carbon dynamics in a model grassland with functionally different soil communities. *Funct. Ecol.* 21, 290–697.
- Bruckner, A., Wright, J., Kampichler, C., Bauer, R., Kandeler, E., 1995. A method of preparing mesocosms for assessing complex biotic processes in soils. *Biol. Fertil. Soils* 19, 257–262.
- Buckley, D.H., Schmidt, T.M., 2001. The structure of microbial communities in soil and the lasting impact of cultivation. *Microbial Ecol.* 42, 11–21.
- Chen, J., Ferris, H., 2000. Growth and nitrogen mineralization of selected fungi and fungal-feeding nematodes on sand amended with organic matter. *Plant Soil* 218, 91–101.
- Cole, L., Bardgett, R.D., Ineson, P., 2000. Enchytraeid worms (Oligochaeta) enhance mineralization of carbon in organic upland soils. *Eur. J. Soil Sci.* 5, 185–192.
- Culman, S.W., Young-Mathews, A., Hollander, A.D., Ferris, H., Sánchez-Moreno, S., O'Geen, A.T., Jackson, L.E., 2010. Biodiversity is associated with indicators of soil ecosystem functions over a landscape gradient of agricultural intensification. *Landscape Ecol.* 25, 1333–1348.
- Dawod, V., Fitzpatrick, E.A., 1993. Some population sizes and effects of the enchytraeidae (Oligochaeta) on soil structure in a selection of Scottish soils. *Geoderma* 56, 173–178.
- de Vries, F.T., Hoffland, E., van Eekeren, N., Brussaard, L., Bloem, J., 2006. Fungal/bacterial ratios in grasslands with contrasting nitrogen management. *Soil Biol. Biochem.* 38, 2092–2103.
- de Vries, F.T., Liiri, M.E., Bjørnlund, L., Bowker, M.A., Christensen, S., Setälä, H.M., Bardgett, R.D. Land use alters the resistance and resilience of soil food webs to drought. *Nat. Clim. Change*, in press.
- DeFries, R.S., Foley, J.A., Asner, G.P., 2004. Land-use choices: balancing human needs and ecosystem function. *Front. Ecol. Environ.* 2, 249–257.
- Diden, W.A.M., 1990. Involvement of enchytraeidae (Oligochaeta) in soil structure evolution in agricultural fields. *Biol. Fertil. Soils* 9, 152–158.
- Diden, W.A.M., 1993. Ecology of terrestrial enchytraeidae. *Pedobiologia* 37, 2–29.
- Dupouey, J.L., Dambrine, E., Laffite, J.D., Moares, C., 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology* 83, 2978–2984.
- Edwards, C.A., 2004. *Earthworm Ecology*, 2nd ed. CRC Press, Boca Raton, USA.
- Eriksen-Hamel, N.S., Whalen, J.K., 2007. Impacts of earthworms on soil nutrients and plant growth in soybean and maize agroecosystems. *Agric. Ecosyst. Environ.* 120, 442–448.
- Fonte, S.J., Six, J., 2010. Earthworms and litter management contributions to ecosystem services in a tropical agroforestry system. *Ecol. Appl.* 20, 1061–1073.
- Fonte, S.J., Barrios, E., Six, J., 2010. Earthworm impacts on organic matter and fertilizer dynamics in tropical hillside agroecosystems of Honduras. *Pedobiologia* 53, 327–335.
- Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2003. The importance of land-use legacies to ecology and conservation. *Bioscience* 53, 77–88.
- Fox, O., Vetter, S., Ekschmitt, K., Wolters, V., 2006. Soil fauna modifies the recalcitrance-persistence relationship of soil carbon pools. *Soil Biol. Biochem.* 38, 1353–1363.
- Harper, S.S., 1988. Sorption of metribuzin in surface and subsurface soils of the Mississippi Delta region. *Weed Sci.* 36, 84–89.
- Henriksen, T., Svensmark, B., Juhler, R.K., 2004. Degradation and sorption of metribuzin and primary metabolites in a sandy soil. *J. Environ. Qual.* 33, 619–627.
- Jenks, B.M., Roeth, F.W., Martin, A.R., McCallister, D.L., 1998. Influence of surface and subsurface soil properties on atrazine sorption and degradation. *Weed Sci.* 46, 132–138.
- Kah, M., Beulke, S., Brown, C.D., 2007. Factors influencing degradation of pesticides in soil. *J. Agric. Food Chem.* 55, 4487–4492.
- Kjær, J., Olsen, P., Henriksen, T., Ullum, M., 2005. Leaching of metribuzin metabolites and the associated contamination of a sandy Danish aquifer. *Environ. Sci. Technol.* 39, 8374–8381.
- Koponen, H.T., Jaakkola, T., Keinänen-Toivola, M.M., Kaipainen, S., Tuomainen, J., Servomaa, K., Martikainen, P.J., 2006. Microbial communities, biomass, and activities in soils as affected by freeze thaw cycles. *Soil Biol. Biochem.* 38, 1861–1871.
- Koutika, L.-S., Didden, W.A.M., Marinissen, J.C.Y., 2001. Soil organic matter distribution as influenced by enchytraeid and earthworm activity. *Biol. Fertil. Soils* 33, 294–300.
- Kristensen, H.L., McCarty, G.W., Meisinger, J.J., 2000. Effects of soil structure disturbance on mineralization of organic soil nitrogen. *Soil Sci. Soc. Am. J.* 64, 371–378.
- Ladd, J.N., Foster, R.C., Skjemstad, J.O., 1993. Soil structure: carbon and nitrogen metabolism. *Geoderma* 56, 401–434.
- Lal, R., 2008. Soil carbon stocks under present and future climate with specific reference to European ecoregions. *Nutr. Cycl. Agroecosyst.* 81, 113–127.
- Levanon, D., 1993. Roles of fungi and bacteria in the mineralization of the pesticides atrazine, alachlor, malathion and carbofuran in soil. *Soil Biol. Biochem.* 25, 1097–1105.
- Liiri, M., Setälä, H., Haimi, J., Pennanen, T., Fritze, H., 2001. Influence of *Cognettia sphagnetorum* (Enchytraeidae) on birch growth and microbial activity, composition and biomass in soil with or without wood ash. *Biol. Fertil. Soils* 34, 185–195.
- Macfadyen, A., 1961. Improved funnel-type extractors for soil microarthropods. *J. Anim. Ecol.* 30, 171–184.
- Mäder, P., Fliessbach, A., Dubois, D., Gunst, L., Fried, P., Niggli, U., 2002. Soil fertility and biodiversity in organic farming. *Science* 296, 1694–1697.
- Makulec, G., 1983. Enchytraeidae (Oligochaeta) of forest ecosystems. I. Density, biomass and production. *Ecol. Pol.* 31, 9–56.
- Marhan, S., Scheu, S., 2005. Effects of sand and litter availability on organic matter decomposition in soil and in cast of *Lumbricus terrestris* L. *Geoderma* 128, 155–166.
- Martin, A., Marinissen, J.C.Y., 1993. Biological and physico-chemical processes in excrements of soil animals. *Geoderma* 56, 331–347.
- McLaughlan, K., 2006. The nature and longevity of agricultural impacts on soil carbon and nutrients: a review. *Ecosystems* 9, 1364–1382.
- Mishra, U., Ussiri, D.A.N., Lal, R., 2010. Tillage effects on soil organic carbon storage and dynamics in Corn Belt of Ohio, USA. *Soil Till. Res.* 107, 88–96.
- O'Connor, F.B., 1962. The extraction of enchytraeidae from soil. In: Murphy, P.W. (Ed.), *Progress in Soil Zoology*. Butterworth, London, pp. 279–285.
- Pan, G., Smith, P., Pan, W., 2009. The role of soil organic matter in maintaining the productivity and yield stability of cereals in China. *Agric. Ecosyst. Environ.* 129, 344–348.
- Peters, R.H., 1983. *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, UK.
- Postma-Blaauw, M., Bloem, J., Faber, J.H., van Groenigen, J.W., De Goede, R.G.M., Brussaard, L., 2006. Earthworm species composition affects the soil bacterial community and net nitrogen mineralization. *Pedobiologia* 50, 243–256.
- Postma-Blaauw, M.B., De Goede, R.G.M., Bloem, J., Faber, J.H., Brussaard, L., 2010. Soil biota community structure and abundance under agricultural intensification and extensification. *Ecology* 91, 460–473.
- Pulleman, M.M., Six, J., Uyl, A., Marinissen, J.C.Y., Jongmans, A.G., 2005. Earthworm and management affect organic matter incorporation and microaggregate formation in agricultural soils. *Appl. Soil Ecol.* 29, 1–15.

- Rodríguez, J.P., Beard Jr., T.D., Bennett, E.M., Cumming, G.S., Cork, S.J., 2006. Trade-offs across space, time, and ecosystem services. *Ecol. Soc.* 11, 28. <http://www.ecologyandsociety.org/vol11/iss1/art28/>.
- Setälä, H., Marshall, V.G., Trofymow, J.A., 1996. Influence of body size of soil fauna on litter decomposition and ¹⁵N uptake by poplar in a pot trial. *Soil Biol. Biochem.* 28, 1661–1675.
- Sha'ato, R., Buncel, E., Gamble, D.G., Van Loon, G.W., 2000. Kinetics and equilibria of metribuzin sorption on model soil components. *Can. J. Soil Sci.* 80, 301–307.
- Six, J., Frey, S.D., Thiet, R.K., Batten, K.M., 2006. Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Sci. Soc. Am. J.* 70, 555–569.
- Smith, P., 2008. Land use change and soil organic carbon dynamics. *Nutr. Cycl. Agroecosyst.* 81, 169–178.
- Sohlenius, B., 1979. A carbon budget for nematodes, rotifers and tardigrades in a Swedish coniferous forest soil. *Holarctic Ecol.* 2, 30–40.
- Thomsen, I.K., Sørensen, P., 2006. Tillage-induced N mineralization and N uptake in winter wheat on a coarse sandy loam. *Soil Tillage Res.* 89, 58–69.
- Topoliantz, S., Ponge, J.-F., Viaux, P., 2000. Earthworm and enchytraeid activity under different arable farming systems, as exemplified by biogenic structures. *Plant Soil* 225, 39–51.
- Vauramo, S., Setälä, H., 2010. Urban belowground food-web responses to plant community manipulation—impacts on nutrient dynamics. *Landscape Urban Plan.* 97, 1–10.
- Villenave, C., Charpentier, F., Lavelle, P., Feller, C., Brossard, M., Brussaard, L., Pashanasi, B., Barois, I., Albrecht, A., 1999. Effects of earthworms on soil organic matter and nutrient dynamics following earthworm inoculation in field experimental situations. In: Lavelle, P., Brussaard, L., Hendrix, P. (Eds.), *Earthworm Management in Tropical Agroecosystems*. CAB International Press, Wallingford, UK, pp. 173–197.
- Wardle, D.A., 1995. Impacts of disturbance on detritus food webs in agro-ecosystems of contrasting tillage and weed management practices. *Adv. Ecol. Res.* 26, 105–185.
- Yeates, G.W., 1971. Feeding types and feeding groups in plant and soil nematodes. *Pedobiologia* 11, 173–179.