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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)

* 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).

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 (Barrios, 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 enchy-traeids 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,

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

Soil	LOI (%)	$pH(H_2O)$	C (%)	N (%)	C:N	$\operatorname{Ca}\left(mgl^{-1}\right)$	$P(mgl^{-1})$	$K(mgl^{-1})$	$Mg(mgl^{-1})$	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 (McLauchlan, 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 *Arrhenatarium 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.

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