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The role of hedgerows in soil functioning within agricultural landscapes

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ABSTRACT

Intensification of agriculture has led to major losses of hedgerows and field margins worldwide. Soil sample extraction, in situ time series of soil moisture, temperature and soil water quality analyses, annual earthworm sampling and arbuscular mycorrhizal (AM) fungi sampling enabled comparison of soil functions between typical hedgerows, grass field margins, pasture and arable (mainly winter wheat) fields in a temperate, lowland setting. Mean bulk density (upper 50 cm), surface compaction and soil moisture content were significantly lower while organic matter content and porewater dissolved organic carbon concentrations were significantly greater in hedgerow soils, than margins or fields. Mean nitrate and phosphate concentrations were three and ten times larger, respectively, in soil solutions under hedgerows than arable fields while ammonium concentrations were least in arable fields. Saturated hydraulic conductivity was significantly greater under hedgerows (median = 102 mm hr⁻¹) where it took an average of one hour longer for soils to reach maximum moisture content following rainfall, than adjacent arable (median = 3 mm hr⁻¹) or pasture fields and margins (median = 27 mm hr⁻¹). Hedgerow soils had a greater proportion of flow through micropores and less macropore flow than other soils. The pasture and margin soils had the largest proportion of macropore flow (> 85%) and more (and larger) anecic earthworm species, such as *Lunbricus terrestris* which produce vertical burrows. Earthworm density, biomass and diversity were greater in pasture and margin soils, followed by hedgerow soils, and tended to be lowest in arable soils. For both total and AM fungi, hedgerow soils hosted a distinct and heterogeneous soil community, margin and pasture communities were diverse but clustered together, and arable communities formed a distinct cluster, with low inter-sample variation and significantly lowest AM fungal richness. The findings demonstrate that soils under hedgerows, which should be conserved, can provide important functions on farmland including storing organic carbon, promoting infiltration and storing runoff, increasing earthworm diversity and hosting distinct AM communities.

1. Introduction

Soil degradation affects between a quarter to a half of the world's agricultural land (Bai et al., 2008; UNCCD, 2017). Soils under both pasture and crop production have been degraded, though the exact extent and severity of degradation is uncertain (Gibbs and Salmon, 2015). Declines in soil quality as a result of continuous cultivation, machinery and livestock overgrazing and trampling, have been associated with loss of soil organic carbon (SOC) and reduction in

infiltration and soil water holding capacity (Soane and van Ouwerkerk, 1995; Chyba et al., 2014) that together constrain crop and pasture yields (Lal, 2015; Smith et al., 2016). Nutrient and pesticide loss to waterways or groundwater are exacerbated when soils become depleted in organic C or become structurally degraded (Soane and van Ouwerkerk, 1995; Chen and Chen, 2008; Banwart et al., 2014; Holden et al., 2017). Structural damage often follows from intensive cultivation directly, enhanced through loss of important ecosystem engineers such as earthworms and mycorrhizal fungi (Edwards and Lofty, 1977;

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Helgason et al., 1998; Birkas et al., 2010) that normally generate and stabilize soil pore spaces. Declines in activities of these organisms can impair hydrological and biogeochemical functioning of soil systems (Antoninka et al., 2009; Blouin et al., 2013; Spurgeon et al., 2013).

There is increasing emphasis on securing wider ecosystem service benefits from agricultural land, beyond provisioning services of food and fibre (Bennett et al., 2009). For example, reducing flood risk by working with natural processes, enhancing water quality and increasing C sequestration are all important functions that are sought through multifunctional agricultural land management (Martin-Ortega et al., 2015; Holden et al., 2017). As such, features of the landscape that permit agricultural production but which help enhance soil function and associated ecosystem services, are highly sought after (Rey Benayas and Bullock, 2012).

Hedgerows and grassy field margins are common linear features in many farmed landscapes, both on gently rolling terrain, and on steeper slopes where there is a high erosion risk (Baudry et al., 2000; Van Vooren et al., 2017). In some locations tall stiff grass strips (e.g. *Panicum virgatum* L.) – also referred to as ‘hedgerows’ in the literature – have been created (e.g. Rachman et al., 2008), and in others woody hedgerows are used as part of alley cropping systems (e.g. Isaac et al., 2003). However, here, hedgerows are classed as human-created systems of closely spaced shrubs and trees that form the boundary to fields. These linear features may be 1–5 m wide and are generally managed by cutting and occasionally by bending into shape to improve their windbreak and livestock holding function.

In many regions with a history of hedgerows providing property and field boundary functions (sometimes going back thousands of years; Rackham, 1986), the advance of mechanised agriculture in the mid 20th Century meant widespread hedgerow destruction (e.g. Baltensperger, 1987). In the UK, there are around 500,000 km of hedgerows and a further 200,000 km in very poor or fragmented state (Carey et al., 2008), accounting for 1.7% of the UK’s arable land area. However, in England and Wales alone there was ~1.4 million km of hedgerow in 1945 (O’Connell et al., 2004). Now, however, there are locations of the world where, after decades of decline, there is legislation to protect and enhance hedgerows (e.g. California, UK, France, Belgium) but there are still other locations where hedgerows are being lost (e.g. Spain) (Baudry et al., 2000; Deckers et al., 2005; Sánchez et al., 2010; Rey Benayas and Bullock, 2012; Arnaiz-Schmitz et al., 2018). Under either situation it is important to understand the role that hedgerows have in altering soil function in agricultural landscapes or in providing wider ecosystem service benefits.

Hedgerows provide significant above-ground biodiversity benefits within farmed landscapes, enhancing small mammal populations (Silva and Prince, 2008; Boughey et al., 2011), and bird and insect (pollinator) diversity and abundance (Holland and Fahrig, 2000; Roy et al., 2003; Morandin and Kremen, 2013; Morandin et al., 2016; Heath et al., 2017). A two-year survey of plants, animals and macro fungi associated with a single hedge in southwest England found over 2000 species (Wolton, 2015). Hedgerows have also been shown to reduce sediment loss during storm events (Smolikowski et al., 2001; Van Vooren et al., 2017). Narrow grassy margins often occur adjacent to hedges and are intermediate graminoid-dominated zones at the side of fields. They have also been shown to reduce sediment loss (Yuan et al., 2009) and enhance plant and insect abundance and diversity in arable landscapes (Marshall et al., 2006). The margins are typically not intentionally tilled, sprayed or fertilised. They are, however, sometimes used by machinery traffic.

In contrast to understanding of above-ground hedgerow function, little is known about how hedgerows and associated grassy margins affect the below-ground soil system. The grey literature and farm advice on hedgerows suggests that enhanced infiltration and flood runoff benefits should occur (grey literature examples: O’Connell et al., 2004; Burgess-Gamble et al., 2018) but primary studies providing such evidence could not be found. Few published soil hydrological or physical

properties datasets (e.g. permeability, macropore flow, bulk density, compaction) on woody field boundary hedgerows exist, though Ghazavi et al., (2008) showed that a hedgerow system in Brittany, France, increased rainwater interception and was associated with lower soil moisture content during summer months than the surrounding fields. Lateral subsurface flow from upslope was probably reduced under the hedgerow, thereby slowing soil-water nutrient losses downslope. While the effects of hedgerows on soil pore water chemistry are poorly understood, the Brittany study also revealed that soil water nitrate (NO₃) concentrations were depleted under the hedge during summer months due to hedge uptake, whereas in winter saturated soil conditions encouraged denitrification, which were also associated with high dissolved organic carbon (DOC) concentrations (Grimaldi et al., 2012). Thomas and Abbott (2018) found a 25–63% reduction in NO₃ leaching downslope of arable fields in western France as a result of oak hedges, with strong seasonal effects on near-surface NO₃ dynamics. Monokrousos et al., (2006) studied a hedgerow site in Greece where extractable phosphorus (P) was lower and electrical conductivity higher than in adjacent arable fields. Van Vooren et al., (2017) derived a statistical model, based on an analysis of 60 published studies in temperate regions, suggesting that the SOC stock below hedgerows compared to adjacent fields was 22% greater, and 6% greater in the field margins next to hedgerows compared to arable fields.

Although it is broadly known that earthworm abundance is greater in pasture than arable soils (e.g. Spurgeon et al., 2013), knowledge of earthworm distribution across farmland landscapes is generally poor. Hof and Bright (2010) showed that fields with grassy margins in the UK had significantly greater earthworm abundance than fields without margins and that earthworm numbers were greater at field edges than within fields. It is unclear whether these authors sampled directly under the hedgerows, but they showed that earthworm abundance was greater at field edges where hedgerows had grassy margins rather than hedgerow sites without margins. Only one study (Denmark, barley, sandy loam) could be found examining both earthworm abundance and species for hedgerows and crop fields (290 earthworms m⁻² and 6 species compared with 9 earthworms m⁻² and 4 species) (Hansen et al., 1989). In one study in Greece, total fungal biomass was significantly higher under hedgerows than surrounding conventional or organically farmed fields (Monokrousos et al., 2006). However, while the loss of arbuscular mycorrhizal (AM) fungal diversity from conventional arable farming has been established (Barto et al., 2010; Manoharan et al., 2017) and can be compared to AM diversity in deciduous woodlands (Helgason et al., 2002) and grasslands (Dumbrell et al., 2011; Manoharan et al., 2017), to date the AM communities under hedgerows have not been studied.

This paper seeks to compare key soil properties and functions between soils under hedgerows and adjacent arable and pasture fields. Based on the limited available literature it was hypothesised that soils under hedgerows would have lower soil moisture content, have less surface compaction and lower bulk density than arable fields, with field margins and pasture being intermediate. It was hypothesised that near-surface hydraulic conductivity would be greatest under hedgerows but that the contribution of macropore flow would be greatest in field margins where earthworm abundance would be greatest (low disturbance, but wetter soil than under hedges). It was expected that SOC and total nitrogen contents would be greatest under the hedgerows, since C and N generally co-accumulate in soils in direct proportion to each other (e.g. see Meena et al., 2018). Finally, it was hypothesised that total fungal and AM fungal communities under hedges would be different to those in soils for the adjacent landscape components studied.

2. Materials and methods

2.1. Study site

The University of Leeds farm is a commercial mixed arable and pasture farm, near Tadcaster, northern England. Mean annual precipitation is 674 mm (max. = 925 mm in 2012, min. = 431 mm in 1975) with a mean annual temperature of 9.2 °C (max. = 10.6 °C, 2014; min. = 7.7 °C, 1963) (on-site Met Office weather station since 1961). The soil is a well drained, loamy, calcareous brown earth from the Aberford series of Calcaric Endoleptic Cambisols (Cranfield University, 2018), underlain by dolomitic limestone of the Cadeby formation (British Geological Survey, 2018). This soil type occurs extensively across the UK on gently sloping Permian and Jurassic Limestone and is mainly used for arable farming. Soil depths were typically around 50–90 cm.

Six fields were studied each bordered by hedgerows. All fields had grassy margins next to the hedgerow of 1.0–2.5 m width. Three fields were arable and three were under permanent grassland (for 6 to > 50 years), hereafter referred to as pasture. The arable fields were in a four year rotation of i) winter wheat, ii) winter wheat, iii) spring or winter barley and iv) oilseed rape, with cultivation and cropping every year since 1994 using conventional ploughing and power-harrowing to establish the seed beds. Pasture fields were used for periodic sheep grazing, with two cut for silage up to twice per year. Nutrient additions are described in the Supplementary Information. Hedgerows ranged from 1.8 m to 4.8 m height and 0.28 m to 1.31 m width. Hedgerows were continuous along the field boundary and consisted of 12 species, dominated by *Crataegus monogyna* (mean 60%; range 0–100%), *Sambucus nigra* (10%, 0–20%) and *Ilex aquifolium* (10%, 0–20%) with < 10% of each of *Corylus avellana*, *Cornus sanguinea* and *Rosa canina* (0–20% range for each). Other species present were *Prunus spinosa*, *Acer campestre*, *Fraxinus excelsior*, *Euonymus europaeus*, and *Rhamnus cathartica*.

2.2. Measurements

2.2.1. Soil physical properties

Soil samples were randomly extracted from under hedgerows, margins and arable and pasture fields using a 5-cm diameter bulk-density corer, (Eijkelkamp, Holland). Samples were analysed at 10-cm depth intervals (0–10, 10–20, 20–30, 30–40 and 40–50 cm) for bulk density by weighing after oven drying at 105 °C. Particle density was calculated by water and air displacement. Surface soil compaction was measured using an Eijkelkamp cone penetrometer, with measurements made at the surface under the hedge and in the field margin and at 1 m intervals from the field margin to 64 m into the field.

2.2.2. Soil hydrological properties

Intact core samples from 2.5 to 7.5 and 12.5–17.5 cm depths were analysed in the laboratory for saturated hydraulic conductivity (K_s) using an Eijkelkamp 25 place laboratory permeameter.

Soil moisture was surveyed at monthly intervals (February 2016 – January 2018) along transects, including the hedge and margin, and then at 1 m intervals from the field margin to 32 m into the field and then 2 m intervals to 64 m, using a Delta-T ML3 ThetaProbe at 0–6 cm depth. Automated soil temperature and moisture measurements were conducted using Decagon 5 T M sensors, positioned at 5, 20 and 50 cm depths under the hedgerows and at the same depths 5, 25 and 50 m into the field, logging at 15-min intervals between August 2015 and January 2018. Rainfall was recorded during this same period using an Adcon RG1 tipping bucket gauge. The response to 220 rainfall events was analysed for each soil moisture sensor by determining moisture at the event start, peak moisture content for each event, the time lag from rainfall start to peak soil moisture, and the lag from peak rainfall to peak soil moisture.

A tension infiltrometer was used to measure infiltration rates, near-surface K_s and unsaturated K . Experiments were conducted at tensions of –3 cm, –6 cm and –12 cm. From capillary theory these tensions exclude water flow through pore spaces of < 1 mm, < 0.5 mm and < 0.25 mm. Experiments were also conducted at 0-cm tension enabling flow through all pore spaces. Further details are in the Supporting Information.

2.2.3. Soil carbon and nitrogen

SOC and total N content were measured on 100 cm³ bulk density cores at 2–7 cm depth. Soil was passed through a 1 mm sieve to remove large stones and roots and the remaining soil was dried (105 °C for 24 h), weighed and then milled to a fine powder using a Fritsch Pulverisette agate ball mill. Inorganic C was removed from soil samples by reaction with acid. Approximately 90 mg of milled soil was placed into Eppendorf tubes and 500 µl of 6 M HCl was slowly added to each tube and stirred. The samples were left to react and settle for 24 h in a fume cupboard. The acid supernatant was pipetted off before the soil was dried at 105 °C. Losses of N in the acid discarded in the supernatant were assessed for a subset of 50 samples and found to be < 5% of total soil N. This small loss did not vary significantly between samples from different treatments. Duplicates of 25–30 mg of the acid-treated soil samples were analysed using an Elementar vario MICRO cube.

2.2.4. Soil solution chemistry

Eijkelkamp MacroRhizon soil moisture samplers (0.25 cm diameter, 9 cm length) extracted soil solution from under hedgerows and at 16 m into the arable and pasture fields at 5–10 cm and 35–40 cm depths ($n = 12$ per depth). Samplers were made from PTFE membrane that pre-filtered soil water to < 0.1 µm on extraction into a 10 mL leur-lock syringe. The syringe plunger was drawn out to the 10 mL mark to apply a 100 kPa suction, and was held open with a small board. Samples were collected on 23 occasions ~ every two weeks (October 2016–December 2017), with a gap between 2 May 2017 and 11 September 2017 when the soil was too dry. Soil solutions were analysed using a Mettler Toledo S20 pH meter, Horiba LAQUAtwin conductivity meter, and a Skalar San ++ continuous flow analyser for NO₃, NH₄ and PO₄ concentrations. Dissolved organic and inorganic carbon (DOC and DIC, respectively) concentrations were determined using an Analytik Jena Multi N/C 2100C combustion analyser.

2.2.5. Earthworms

Earthworm sampling took place in 2015 (7–14 April; 1 May), 2016 (12–22 April) and 2017 (3–13 April). At each sample point, soil blocks were removed (18 × 18 × 15 cm) and all living earthworms were collected by hand-sorting. Dilute allyl isothiocyanate (1.5 L; 0.1 g L⁻¹) was poured into each pit and left to drain into the soil to facilitate collection of deeper burrowing anecic species. Earthworm appearance was monitored over a 30-min period. All earthworms were stored in 80% ethanol for later identification and biomass (2016 and 2017 only). Adult individuals (with a clitellum) were identified following Sims and Gerard (1999). Juvenile individuals were grouped into functional group (endogeic, epigeic or anecic species). Individual earthworm biomass was also determined.

2.2.6. Fungi

DNA was extracted from the pooled roots of plants growing in the fields, margins and hedges. Roots were washed with water, frozen, freeze dried and ground using a TissueLyser and stainless steel grinding jars (Qiagen). Total DNA was extracted using MoBio PowerPlant DNA extraction (now Qiagen) kit according to the manufacturer's protocol. Primer sets for different regions of the rRNA operon were used to identify either total fungal species or to specifically target AM fungal species. Total fungal community was assayed with nested polymerase chain reaction (PCR) using ITS1f/ITS4 followed by gITS7/ITS4 (Ihrmark et al., 2012). AM fungal species were targeted by using a

nested PCR using AML1/AML2 followed by Wanda/AML2 (see Supplementary Information for sequences/methods). Amplicons were cleaned using AMPure beads (Agincourt) following the manufacturer's instructions. gITS7/ITS4 amplicons and Wanda/AML2 amplicons for each sample were pooled in a ratio of 1:3 before Nextera (Illumina) barcoding and sequence library preparation. 300 bp paired end read libraries were run on the Illumina MiSeq platform. gITS7/ITS4 and Wanda/AML2 sequence data were separated using QIIME 1.8. Sequence data were trimmed, quality filtered and clustered into unique OTUs using USEARCH8. Chimeras were removed using QIIME plus the dynamic Unite database (for gITS/ITS4) and Silva database (for WANDA/AML2). General fungal taxonomy was assigned to gITS7/ITS4 OTUs using QIIME plus the dynamic Unite database. To identify AM fungal species, WANDA/AML2 OTUs were compared to the AM fungal specific MaarjAM database (<https://maarjam.botany.ut.ee>) and assigned to virtual taxon using a 95% query coverage and 95% identity cut off. OTUs assigned to the same taxon were aggregated by summing read counts by sample. Singleton OTUs were excluded from each database. The AM dataset was rarefied by resampling to 500 reads per sample and ITS to 6000 reads per sample.

2.3. Statistical analysis

ANOVA (Minitab 17.1.0) was used to test for differences ($p < 0.05$) in soil properties for hedge, margin, pasture and arable fields with post-hoc Tukey tests determining differences between pairs. For parameters where the variance was quite different between categories, data were transformed to ensure near-equal variances. For variables which were repeatedly measured from the same points over time (e.g. pore water chemistry), repeated measures ANOVA was used. Where variables were measured in transects into the fields we found no significant within-field distance effects. Therefore these data were pooled and considered as either 'arable' or 'pasture' samples. For each variable, differences between hedge soils bordering pasture fields and hedge soils bordering arable fields were checked. In almost all cases, there was no significant difference and so hedge data were pooled. Where differences between hedge categories were found, these were treated as separate land-cover categories. Data transformations for earthworms failed to result in near-equal variances between categories and so non-parametric analyses were performed for earthworm density (number of individuals m^{-2}) and biomass ($g\ m^{-2}$) using Sigma Plot (v13.0). Diversity indices were calculated using Primer-E (Clarke and Gorley, 2006) and further details of these indices are provided in the Supporting Information. Non-metric multidimensional scaling (NMDS) plots for fungal community data were generated using Bray-Curtis similarity matrices using the metaMDS function Vegan R package. PERMANOVA were run on the Bray-Curtis matrices using the adonis function in Vegan (Oksanen et al., 2018).

3. Results

3.1. Soil physical properties

Both bulk density (mean over 0–50 cm depths for hedge = $1.259\ g\ cm^{-3}$; margin = $1.489\ g\ cm^{-3}$; pasture = $1.422\ g\ cm^{-3}$, arable = $1.540\ g\ cm^{-3}$) and surface compaction (mean hedge = $40\ N\ cm^{-2}$; margin = $61\ N\ cm^{-2}$; pasture = $61\ N\ cm^{-2}$, arable = $67\ N\ cm^{-2}$) were significantly smaller ($p < 0.001$) in the hedgerow soils than for other soils. Bulk density was significantly lower for all sampled depths for the hedgerow soils (Fig. 1). Particle density was significantly lower in the hedgerow soils when bulked across 0–50 cm depth ($p < 0.001$) compared to other soils. However, when data from each depth range were compared, these differences were only significant for the top and bottom 10 cm of the soil profile (Fig. 1).

Mean soil temperature at 5 cm depth from May 2016 to December 2017 (when all thermistors were fully operational), was $9.0\ ^\circ C$ for

hedgerow soils, $10.7\ ^\circ C$ for pasture and $8.8\ ^\circ C$ for the arable soils. Mean temperature for hedgerow, pasture and arable soils at a depth of 20 cm was 9.3, 10.6 and $8.9\ ^\circ C$ respectively and 9.5, 10.7 and $9.3\ ^\circ C$ respectively at 50 cm depth.

3.2. Soil hydrological properties

Mean soil moisture from the automated sensors at 5, 20 and 50 cm depths consistently showed that hedgerow soils were driest while pasture soils were wetter than arable soils ($p < 0.001$) (means at 5 cm depth for hedge, arable, pasture = 12.4, 14.4, 22.0%; 20 cm depth = 11.9, 15.5, 18.2%; 50 cm depth = 10.8, 14.3, 17.0%). For the upper 6 cm of soil using manual Theta probe sampling the moisture content was significantly lower ($p < 0.001$) under the hedgerow land cover in both the winter (October–March) and summer (April–September) half year periods, than for other land cover categories (Fig. 2). In the summer, the moisture content of the pasture fields and the margins were not significantly different whereas in winter the pasture fields were wetter than the margins ($p < 0.001$). The arable fields were significantly drier than the pasture fields ($p < 0.001$). The mean time from peak rainfall to peak volumetric water content was significantly greater ($p = 0.02$) for the hedge soils (3.5 h) compared to arable (2.7 h) and pasture (2.2 h) soils (no difference), as was the mean time from rainfall start to peak volumetric water content ($p < 0.001$, hedge mean = 5.0 h, pasture mean = 3.8 h, arable mean = 3.0 h). Two typical storm responses are shown in Fig. 3 indicating both the longer time and the larger increase from pre-storm levels in volumetric water content that occurred before the soil became saturated in hedge soils compared to arable and pasture soils.

K_s was affected by land cover (Fig. 4) and soil depth, with arable soils being associated with significantly lower K_s than the hedge soils ($p < 0.001$), meaning that infiltration-excess overland flow was much more likely to occur on the arable soils during heavy rainstorms than on hedge soils. The hedgerow soils were also associated with a greater proportion of flow moving both through pores smaller than 0.25 mm in diameter and through pores between 0.25 and 0.5 mm in diameter than for other land cover types (Fig. 5). The pasture and margin soils were associated with the largest proportion of flow moving through macropores ($> 1\ mm$ in diameter).

3.3. Soil carbon and nitrogen

Land cover was a significant control on near-surface (2–7 cm depth) SOC concentrations ($p < 0.001$; Fig. 6a). SOC concentrations were highest under hedgerows and pasture soils and lowest in arable fields (Tukey test, $p < 0.05$). SOC in arable soils was only ~40% that found under hedgerows. Total soil N was closely linearly correlated with the SOC across all samples ($R^2 = 0.95$), and there was no difference in C:N ratio between land-cover types (mean = $10.23 \pm 0.10\ SE$, $n = 49$). Consequently, total N in near-surface soil paralleled observations for SOC across the land-cover types (Fig. 6b), the hedge and pasture soils holding significantly higher concentrations of N (Tukey test, $p < 0.05$) than the field margins and cultivated areas.

3.4. Soil solution chemistry

Land cover had a significant impact on soil solution chemistry (Fig. 7). For the arable fields and their hedgerow soils, pH was around neutral and increased with depth ($p = 0.009$ arable, $p = 0.002$ hedge). In contrast, pH displayed a much wider range in the pasture and associated hedgerow soils (Fig. 7), did not vary with depth but was significantly ($p = 0.008$) higher than in the arable fields and their hedges. Conductivity of the soil solution displayed a wide range under all land covers and was significantly ($p < 0.001$) lower in the pasture than the hedgerow and arable soils at both 5 and 35 cm depth. At 5 cm depth, NO_3 ($p < 0.001$), PO_4 ($p = 0.007$) and DOC ($p < 0.001$) varied

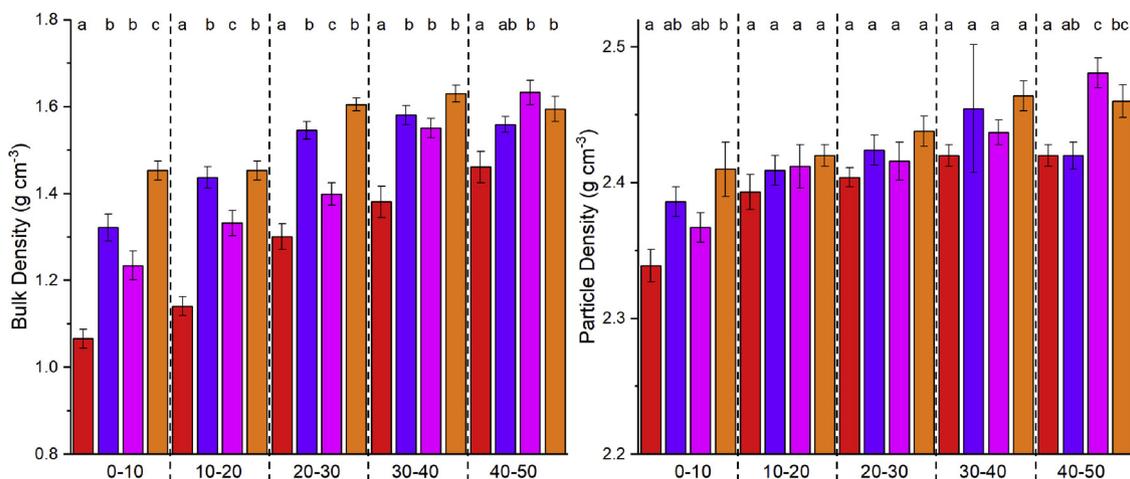


Fig. 1. Mean (and standard error) of bulk density and particle density with depth for each land cover category. Different letters denote significant difference for a particular depth category at $p < 0.05$.

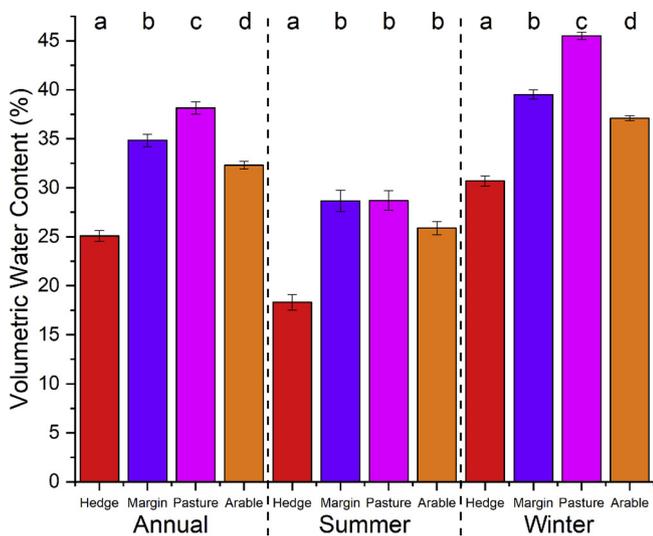


Fig. 2. Mean and standard error of monthly sampling of volumetric water content at 0–6 cm depth by land cover category, between February 2016 and January 2018. Summer half year data for months April – September; winter for October – November inclusive). Different letters denote significant difference at $p < 0.05$.

significantly between all land covers, with largest concentrations observed under the hedgerows and smallest concentrations in the arable fields. Mean NO_3 concentration at 5 cm depth was over four times larger in the pasture (120.4 mg L^{-1}) and five times larger under the

hedgerows (167.2 mg L^{-1}) than for the arable soil solutions (30.8 mg L^{-1}). At 35 cm depth, the mean NO_3 concentration was still almost double in the pasture (63.5 mg L^{-1}) and three times higher under the hedgerows (108.8 mg L^{-1}) than for the arable fields (36.5 mg L^{-1}). While NO_3 concentrations decreased significantly ($p = 0.006$) with depth in hedgerow soils, there was no significant difference with depth in the pasture and arable fields. Mean PO_4 concentration at 5 cm depth was over ten times greater in the hedgerow soil solutions (1.99 mg L^{-1}) and three times higher in the pasture (0.62 mg L^{-1}) than the arable (0.17 mg L^{-1}) fields. PO_4 concentrations declined with depth in all land covers, but at 35 cm soil solution concentrations were only significantly ($p = 0.006$) different between the hedgerows and arable fields. At 5 cm depth, mean DOC concentration under the hedgerows (51.4 mg L^{-1}) was over double that from the pasture (21.7 mg L^{-1}) and arable fields (18.1 mg L^{-1}). At 35 cm depth, DOC from under the hedgerows was significantly ($p < 0.001$) lower (mean = 33.6 mg L^{-1}) than at 5 cm depth, whereas mean DOC concentrations for pasture (20.8 mg L^{-1}) and arable (14.9 mg L^{-1}) soil water were similar to those at 5 cm depth. In contrast to DOC, DIC concentrations were significantly ($p < 0.001$) larger in the arable and pasture soils than the hedgerow soils at both depths. As would be expected in these well drained soils, NH_4 concentrations were generally low (mean concentrations $< 1 \text{ mg L}^{-1}$) for all land covers; and significantly ($p < 0.001$) lower in the arable soils at 5 cm depth than elsewhere.

3.5. Earthworms

Earthworm density varied between the three sampling occasions

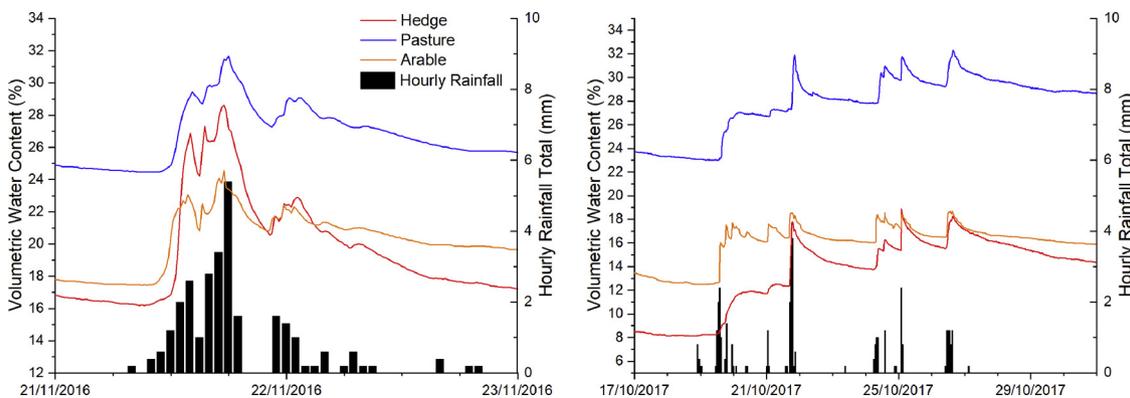


Fig. 3. Two example soil water content responses to storm events.

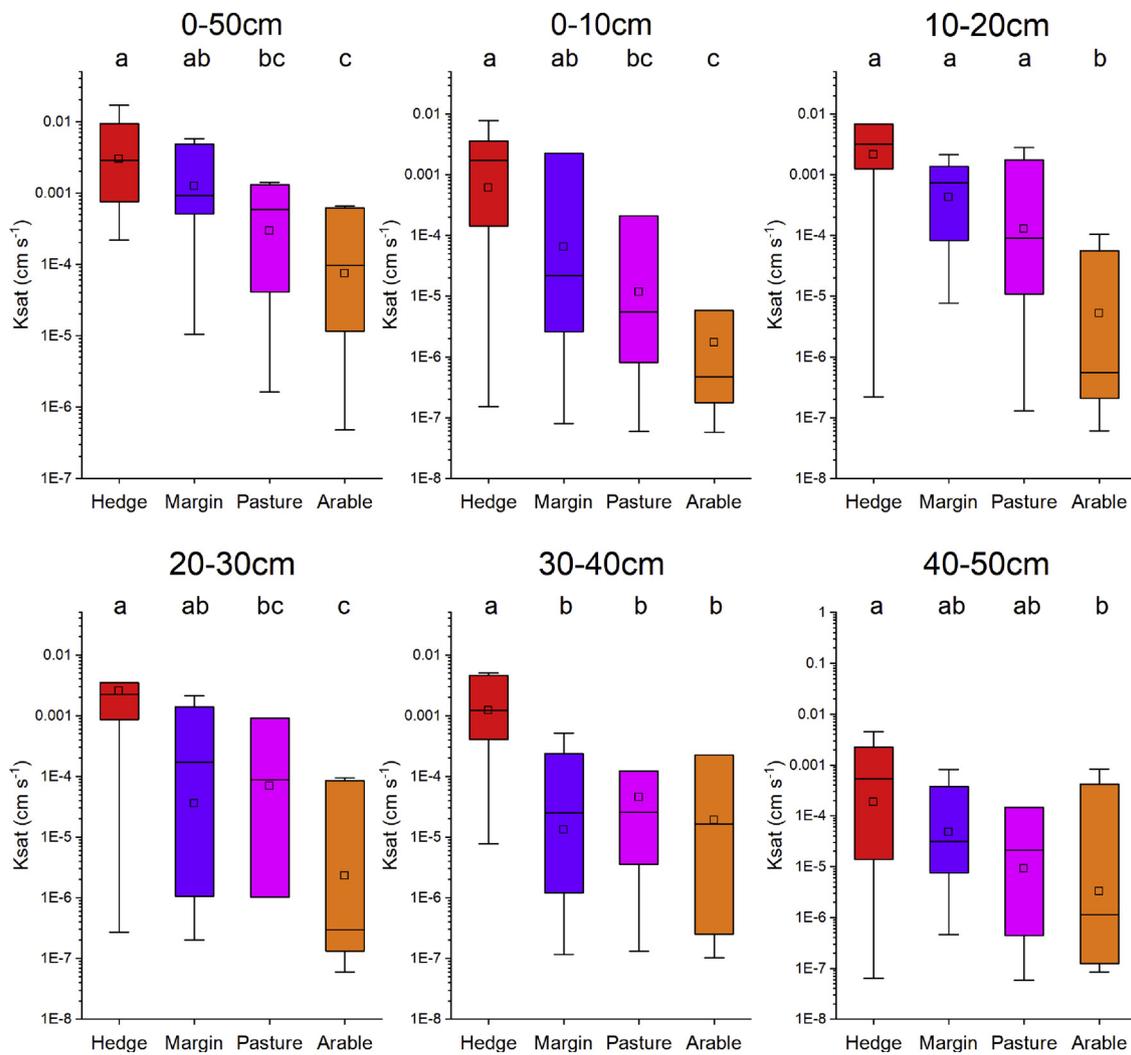


Fig. 4. Saturated hydraulic conductivity by land cover and soil depth measured on permeameter samples. Geometric mean indicated by open squares. Box plots show median, interquartile range, maximum and minimum. Different letters denote significant difference ($p < 0.05$) within the depth range shown for each plot.

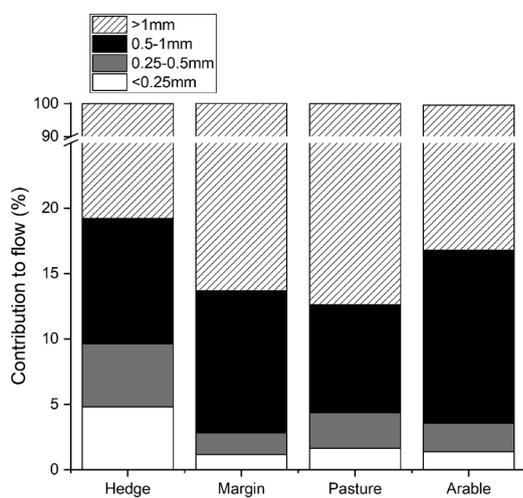


Fig. 5. Mean proportion of flow through each pore size class by land cover category.

($p = 0.004$), being highest in 2015 (688.4 ± 444.2 individuals m^{-2}) and lowest in 2017 (447.3 ± 262.1 individuals m^{-2}). Land cover had a significant effect on overall earthworm density ($p < 0.001$) (Fig. 8a). Earthworm density was highest in the pasture (757.5 ± 426.2

individuals m^{-2}) and margin (673.6 ± 326.9 individuals m^{-2}) soils, and lowest in the arable soil (325.5 ± 254.7 individuals m^{-2}). On each sampling occasion, earthworm density was affected by land cover ($p < 0.001$). In 2015, earthworm density in pasture soil was significantly higher compared to arable or hedge soil (Dunn's tests); earthworm density in margin soil was higher compared to hedge soil. In 2016 and 2017, earthworm density in arable soil was the lowest (compared to hedge, margin or pasture). There was no temporal effect on earthworm biomass but land cover was a significant factor ($p < 0.001$; Fig. 8b). Earthworm biomass was similar in margin (167.5 ± 125.5 g m^{-2}) and pasture (119.9 ± 62.2 g m^{-2}) soils. Earthworm biomass in the margins was greater compared to arable (50.9 ± 53.0 g m^{-2}) or hedge (80.9 ± 63.5 g m^{-2}) soils; and biomass in pasture soil was greater compared to arable soil. Biomass in the hedge soil was similar compared to pasture or arable soils.

Twelve earthworm species were identified, but three species occurring at $< 0.1\%$ of total abundance (< 5 individuals) were removed (*Dendrodrilus rubidus*, *Eisenia fetida*, *Lumbricus rubellus*) (Fig. 8c and d). Earthworm density was dominated by juveniles (Fig. 8c) comprising 58% of the total in hedgerow soil, 65% in margin and pasture soil, to 76% in arable soil. Within the juveniles, the functional groups were in the order endogeic (49%) $>$ epigeic (8.9%) and anecic (8.4%) across land cover types. Endogeic juveniles were relatively more abundant in arable soil (55%) compared to hedgerow (43%), margin (45%) and pasture (52%). The adult species were dominated by endogeics which

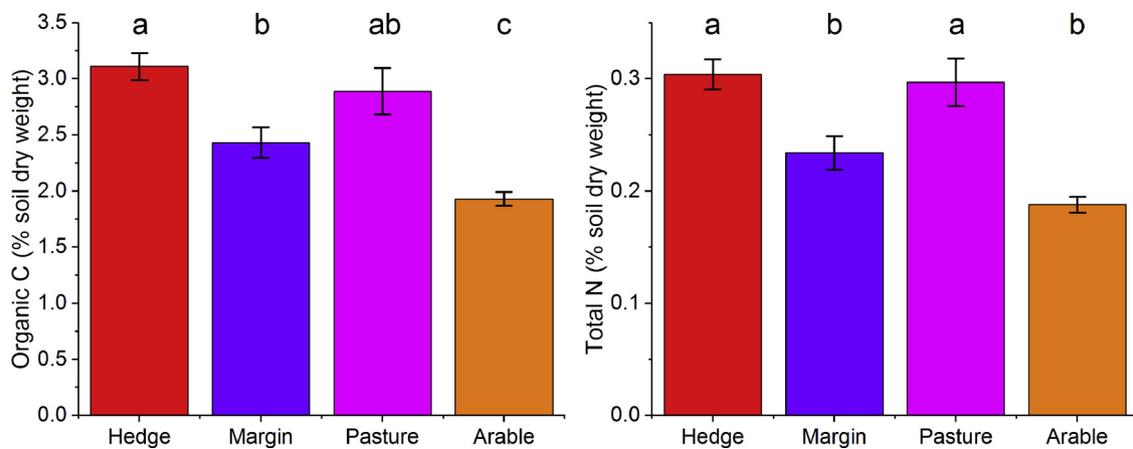


Fig. 6. Mean and standard error of soil organic carbon and total soil nitrogen content by land cover. Different letters denote significant difference by land cover category for each variable measured.

made up 68.8% of total adult density (5 species), epigeics comprised 22.1% (2 species) and anecics 9.1% (2 species). The dominant species in all land cover types was the endogeic *Allolobophora chlorotica*, making up ~17% of earthworm density in each. The main epigeic species was *Lumbricus castaneus* (9% of earthworms per land cover type) and the main anecic species was *Aporrectodea longa* (~2% of earthworms per land cover type). Land cover had a significant effect on absolute earthworm species density ($p < 0.001$ for all), except for *A. longa* and the epigeic juveniles, where land cover effects were not significant. In general, earthworm species densities were similar in pasture and margin soils, but higher in these compared to the arable (and sometimes hedgerow) soil. For example, *Lumbricus terrestris* was more abundant in margin compared to hedgerow or arable soils. *A. chlorotica* was more abundant in pasture and margin soils compared to hedge soil, while abundance of *Aporrectodea rosea* and *L. castaneus* were both lowest in the arable soil. Juvenile anecic and endogeic earthworms were more abundant in margin and pasture soils compared to arable or hedge soils.

Anecic, endogeic and epigeic juveniles made up 28, 14 and 3% of average earthworm biomass across land cover types respectively (Fig. 8d). Juvenile biomass was relatively high in the arable soil (56%) and low in the hedge soil (35%). Anecic juveniles and adults tend to be large organisms compared to other earthworms, and therefore they dominated earthworm biomass in all soils. The biomass of the anecic adult earthworms, especially *L. terrestris* (which was not the dominant anecic earthworm in terms of abundance) was highest in the margin soil (32% biomass). Hedgerow soil had the highest biomass of the dominant endogeic (*A. chlorotica*, 20%) and epigeic (*L. castaneus*, 12%) species.

In terms of absolute biomass per individual, anecic earthworms in margin and pasture soils tended to be larger compared to anecic earthworms in hedge and arable soils: *A. longa* ($p = 0.007$, pasture > arable), *L. terrestris* ($p < 0.001$, margin > arable) and anecic juveniles ($p = 0.001$, margin > hedge, arable). The biomass (per individual) of endogeic species such as *A. chlorotica*, *A. rosea* and endogeic juveniles was significantly lower in the arable soil ($p < 0.001$, =

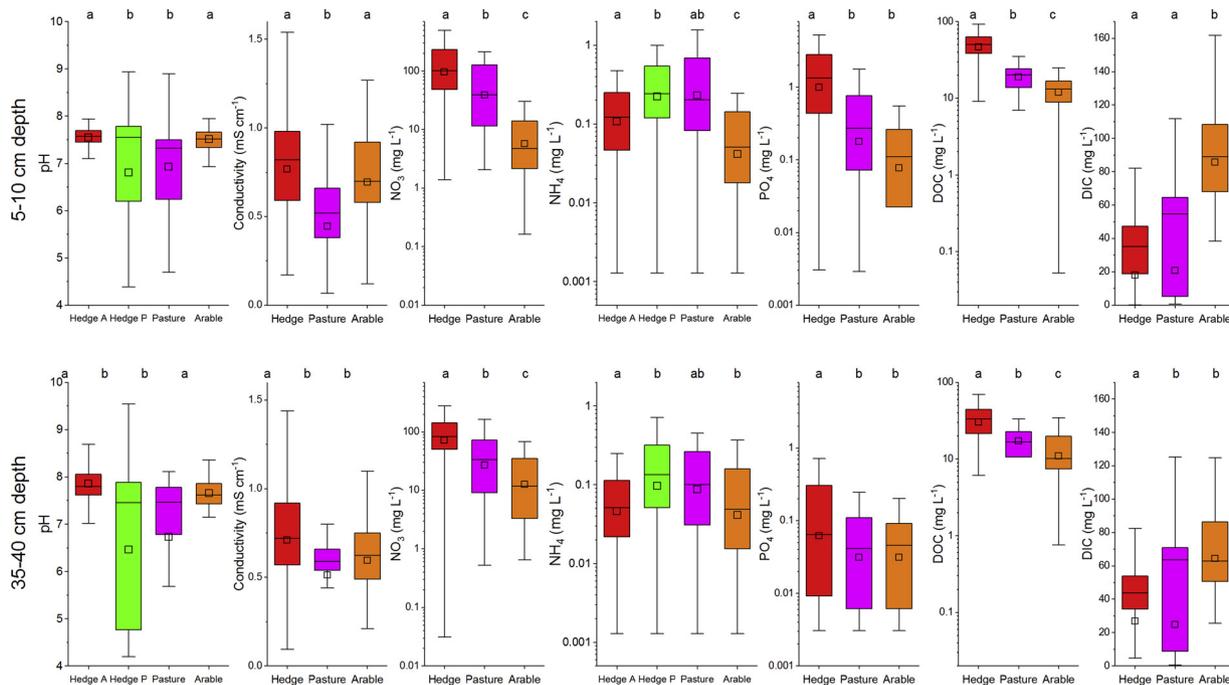


Fig. 7. Pore water pH, conductivity and solute concentrations for 5–10 cm depth (upper row) and 35–40 cm depth (lower row). Hedge A and Hedge P refer to cases where there was a significant difference in soil water solutes between hedge soils bordering arable (A) and pasture (P) fields. Geometric mean indicated by open squares. Box plots show median, interquartile range, maximum and minimum. Different letters denote significant difference by land cover category for each variable measured.

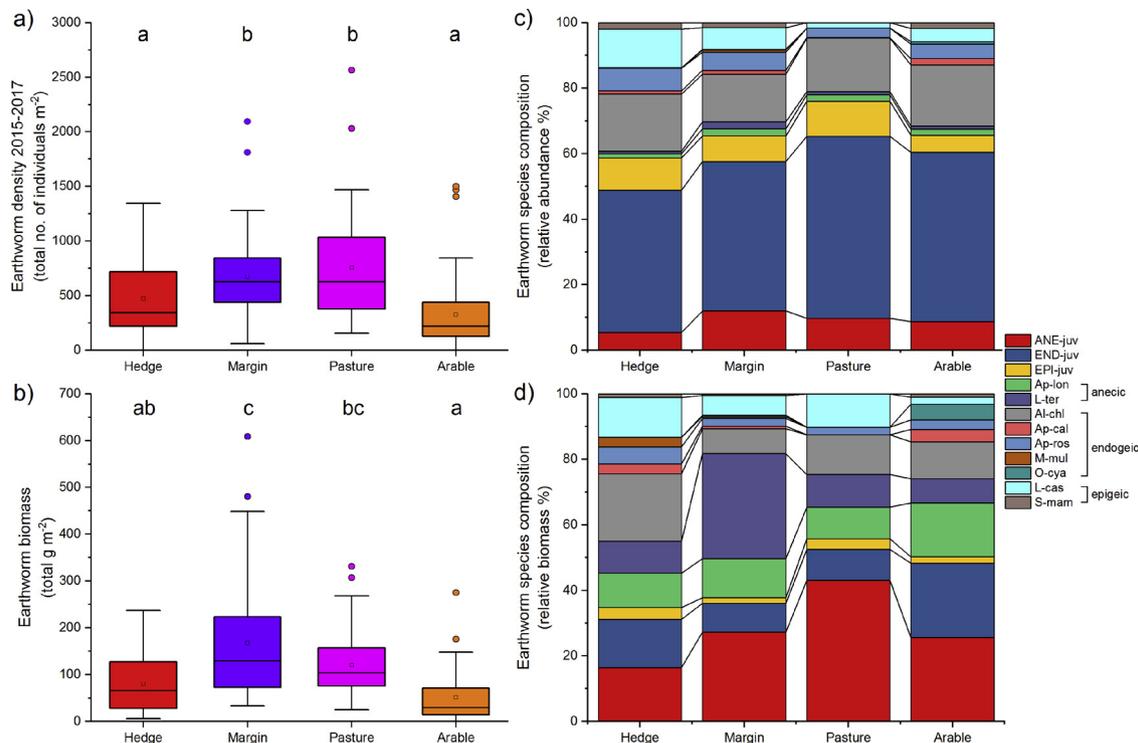


Fig. 8. Earthworm density (a), biomass (b) and species composition by abundance (c) and biomass (d) for each land cover category. Data are averaged over the three sampling years. Geometric mean indicated by open squares. Box plots show median, interquartile range, maximum and minimum and outliers. Outliers are defined as being $1.5 \times$ the interquartile range below or above the first and third interquartile range respectively. Different letters denote significant difference by land cover category (one way ANOVA on Ranks, Dunn's test, $p \leq 0.05$). Abbreviations: Anecic juveniles (ANE-juv), Endogeic juveniles (END-juv), Epigeic juveniles (EPI-juv). Anecic species: *Aporectodea longa* (Ap-ion), *Lumbricus terrestris* (L-ter); Endogeic species: *Allolobophora chlorotica* (Al-chl), *Aporrectodea caliginosa* (Ap-cal), *Aporrectodea rosea* (Ap-ros), *Murchieona muldali* (M-mul), *Octolasion cyaneum* (O-cya); Epigeic species: *Lumbricus castaneus* (L-cas), *Satchellius mammalis* (S-mam).

0.001, < 0.001 respectively, all hedgerow, pasture, margin > arable). For the epigeic species *L. castaneus*, individual earthworm biomass was greater in margin and hedgerow soils compared to pasture soils ($p < 0.001$). The biomass of the epigeic juveniles (per individual) was higher in the margin and hedgerow soil compared to the arable soil (Kruskal-Wallis, $p = 0.009$).

Adult earthworm species richness (Margalef) was not affected by sampling year or land cover (median = 1.21, IQR = 0.64). Shannon diversity index was not affected by year but was affected by land cover ($p = 0.002$). Diversity in arable soil (median = 0.69, IQR = 0.23) was significantly lower compared to margin (median = 1.04, IQR = 0.58) or pasture (median = 0.98, IQR = 0.54) soil. Diversity in the hedgerow soil (median = 0.95, IQR = 0.46) was similar to other soil types. Earthworm species evenness was not affected by year or land cover (median = 0.90, IQR = 0.17).

3.6. Fungi

The MiSeq run yielded 954,132 ITS reads and 441,647 18S reads. After quality control, 918,629 ITS reads yielded 1484 OTUs. Removal of singletons, curation to remove non-fungal reads, rarefaction and aggregation yielded 401 OTUs from 251,574 reads. For the 18S AM fungi, after quality control 320,157 reads yielded 250 OTUs. Removal of singletons, curation to remove non-AM reads, rarefaction and aggregation yielded 36 OTUs from 52,275 reads.

There was no significant difference in total fungal OTU richness among the four land cover types, (range per sample 75–137, ANOVA $F = 1.69$, $df = 3$, $p > 0.05$), but by contrast, AM fungal richness in the arable soils was significantly lower than under hedgerows, margins or pasture fields (range per sample 1–17, Kruskal-Wallis $\chi^2 = 12.16$, $df = 3$, $p < 0.01$). NMDS ordination of Bray-Curtis dissimilarity showed that, for both total fungi (Fig. 9a) and AM fungi (Fig. 9b),

margin and pasture samples were diverse but clustered together, hedge samples were variable and distinct from other groups, and that finally, arable samples form a distinct cluster, with low inter-sample variation.

4. Discussion

The functioning of soils below hedgerows was found to be significantly different from those in adjacent arable or pasture fields, for most measured parameters. The lack of farm traffic or sheep trampling and greater incorporation of organic matter meant that soils under hedgerows were less compacted at the surface and had much smaller bulk density at depth than nearby fields.

The hydrological functioning of hedgerow soils enhanced water storage during rainstorms. Hedges have been previously shown to store more canopy interception water with 2.6 mm (summer) and 1.2 mm (leafless winter) event storage capacity reported in UK hedgerows (Herbst et al., 2006). In addition, as hedgerow soils were generally drier, including during winter, on average these soils would take around an hour longer to reach maximum water content during storms compared to arable or pasture fields. K_s was significantly greater for hedgerow soils than below other land covers, facilitating enhanced infiltration and percolation even when fully wet. The median K_s could be crucial to controlling flood risk since for arable fields this value was only 3.4 mm hr^{-1} whereas for hedge soils it was 102.4 mm hr^{-1} , with pasture and margin soils around $20\text{--}30 \text{ mm hr}^{-1}$ (Fig. 4). Hourly rainfall data, available from 2001 at the study site, show that on only six occasions did rainfall intensity exceed 20 mm over a full hour, with a maximum of 39.8 mm. This is fairly typical for the UK where for any given location rainfall intensities $> 100 \text{ mm hr}^{-1}$ are rare. The low K_s of the arable soils is a major concern for flood risk, as infiltration-excess overland flow will be a regular occurrence on these soils, whereas the hedgerow soils show a capacity to buffer some of this risk by enabling

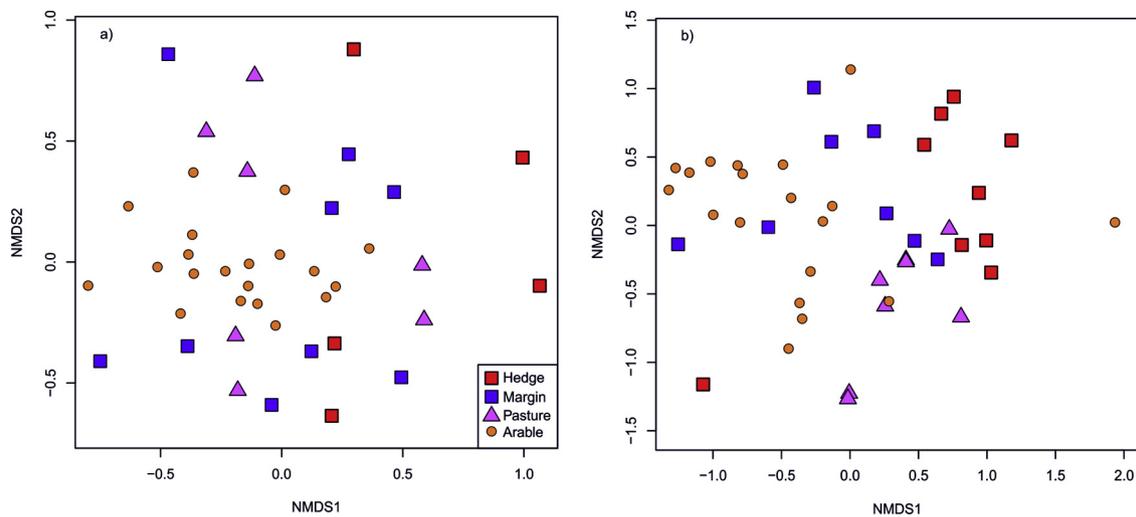


Fig. 9. NMDS ordination plot for a) total fungi and b) arbuscular mycorrhizal fungi for each land cover category.

infiltration and percolation of runoff water from the surrounding fields. Such hydrological functioning will also contribute to hedgerows trapping surface sediments and associated nutrients that runoff from surrounding fields. While additional research at other sites is required to confirm how widespread these differences in soil permeability are between hedgerows and adjacent arable fields, the results strongly suggest that hedgerow soils can absorb and hold water during storm events which may reduce downstream flood risk. These effects are likely to be greatest in some parts of catchments due to topographic sensitivities, soil type variability, and river flow synchronisation effects (Holden, 2005; Gao et al., 2016; Rogger et al., 2017) and so further work is required to understand how hedgerow soils and investment in hedgerow maintenance or creation may contribute to landscape-scale flood risk reduction.

The drier hedgerow soils may have also contributed to the margins being significantly drier than the pasture fields during winter as strong hydraulic gradients may have developed between the wet margins and the adjacent hedgerow soils, thereby drawing some moisture from the adjacent margins (Herbst et al., 2006; Ghazavi et al., 2008). It is not clear, however, why this effect was not evident in the summer half year. The margins had a surprisingly high bulk density, similar to that of the arable fields and the surface compaction was not significantly different to that of the pasture or arable fields. This may be because of trafficking on the margins, nevertheless, differences in the margin soil properties (perhaps related to earthworm activity, see below) allowed significantly higher infiltration and percolation rates than for the arable fields.

There were temporal differences in soil moisture and temperature over the sampling period which affected overall earthworm densities. For example, spring 2015 had slightly wetter than average rainfall and around average temperatures compared to the 1981–2010 average (National Climate Information Centre, 2015) while spring 2017 was very warm and dry in the study region (National Climate Information Centre, 2017). Despite these temporal variations, the overall land-cover control on earthworm populations remained dominant throughout. Earthworm density, biomass and diversity were generally greatest in pasture and margin soils, followed by hedgerow soils, and tended to be lowest in arable soils. Field margins closely resembled pasture fields in terms of earthworm density, diversity and biomass, probably because of similar soil conditions (moisture, temperature, plant type and biomass, lack of tillage disruption). Hedgerow soils tended to be drier and had cooler temperatures (in line with previous studies; e.g. Homininck and Briscoe, 1990), which affect earthworms. Earthworm communities had the lowest abundance, biomass and diversity in arable soils, presumably due to disturbance and poor quality resources (Hendrix et al., 1992;

Spurgeon et al., 2013). Here, juveniles made up a much larger proportion of the abundance and biomass than for other land cover types, while hedge soils had the greatest proportion of adult earthworms, clearly demonstrating that arable agriculture and hedgerows impact earthworm life histories in different ways.

Soil fauna can impact soil hydrological functioning and vice versa (Holden and Gell, 2009; Fischer et al., 2014). Earthworm density and diversity were different between land cover types at the study site. The pasture and margin soils had more (and larger) anecic species, such as *L. terrestris* which produce vertical burrows, often lacking branches (Shipitalo and Butt, 1999). These soils were also the ones with the greatest proportion of flow through macropores > 1 mm in diameter. While the hedgerow soils were the most permeable, they were also the soils with the greatest proportion of flow through micropores, suggesting that bypassing flow was reduced below hedgerows compared to the soils under other land cover types. This enhanced micropore flow may be related to a balanced community of vertically and horizontally burrowing earthworms in the hedgerow soils enabling good soil mixing, but importantly it also suggests that loss of nutrients and pesticides through macropores may be reduced under hedgerows, providing an additional ecosystem service benefit. Field edge stiff-stemmed switchgrass - *Panicum virgatum* L. - strips (sometimes also termed ‘hedges’) in the USA have previously been shown to enhance soil infiltration and the rates of flow through smaller pore size classes (Rachman et al., 2004) but such functioning has not been studied for woody hedge systems until now.

As expected, SOC below hedgerows was significantly higher than in the arable fields. Results from a study in Greece, observed that SOC from beneath a hedge (SOC = 2.8%) was almost double that from the adjacent arable field (SOC = 1.5%) growing asparagus (Monokrousos et al., 2006), which is similar to findings reported above (Fig. 6). Under natural conditions, the SOC content of soil is constant; the rate of decomposition is equal to the rate of supply from plants. However, agriculture disturbs the equilibrium by reducing the amount of C returned to the soil in litter by harvesting and removing the crop via grazing and by tillage practices that break up the soil. This disturbance increases decomposition rates of soil organic matter (SOM) that leads to an increase in the release of carbon dioxide, resulting in a decline in SOC. Average losses of SOC after conversion of forest to cropland is 48%, to grassland 28% and to mixed agricultural land use 35% (Buringh, 1984). If it is assumed that all soil in the study area originally had a SOC content similar to that under the hedgerows then arable practices have led to a decline in SOC of 40% which is similar to the data reported by Buringh (1984) on a global scale. However, no significant difference in SOC between hedgerow soils and those in permanent pasture were

found at the study site.

The higher solute concentrations of NO_3 and PO_4 under hedgerows compared to pasture and arable soils were surprising given applications of fertiliser, manure and slurry to pasture and arable fields which the hedgerows do not receive. There are, however, a number of possible explanations for enhanced hedgerow NO_3 and PO_4 . Firstly, mineralization rates could be higher under hedgerows due to larger amounts of SOM. However, Monokrousos et al. (2006) found no significant difference in C or N mineralization rates between a conventional arable field and its surrounding hedge despite the soil beneath the hedge containing almost double the SOC than the arable field. Secondly, hedgerow plants may take up fewer nutrients than cereal crops and grass. However, even if this was the case, it is unlikely to account for the large difference in soil solution nutrient content if mineralization rates are similar for all soils. Thirdly, the solutes are more concentrated in soil solution under the hedgerows due to lower soil moisture. The mean electrical conductivity of hedgerow soil solution was higher than that for the other treatments (Fig. 7). Monokrousos et al. (2006) observed higher soil solution electrical conductivity values from beneath hedges than conventional and organic arable fields in Greece. Greater evaporation from the hedge canopy than from cereal crops and grasses (Herbst et al., 2006) is likely to concentrate solutes more beneath the hedge. Lastly, canopy leaching of dry deposition from surfaces of leaves and bark, as observed in forested ecosystems (e.g. Lovett, 1994; Gallagher et al., 2002), is also likely to lead to enhanced DOC and nutrient concentrations in soil solutions below hedgerows compared to the pasture and arable fields. The study site is within 25 km of a large fossil fuel power station and there are also nearby pig units: dry deposition of NH_3 occurs especially close to its source (Pitcairn et al., 1998; Hellsten et al., 2008; Misselbrook et al., 2010). Compared to forested systems, no data on the chemical composition of throughfall and stemflow beneath hedges was found in the literature and only one study has investigated the impact of a hedge on soil and ground water NO_3 concentrations (Grimaldi et al., 2012). This is a significant shortcoming given that many agri-environmental schemes across Europe promote hedge planting to benefit ecosystem services including water purification.

Grimaldi et al. (2012) found that absorption by trees removed the NO_3 from the unsaturated soil during the growing season and denitrification occurred in the organic enriched soils downslope of the hedge during the dormant season. However, their study was in organic rich soils (10–40% SOC), which had not received fertiliser for > 10 years, with downslope waterlogging near a stream, and where the ‘hedge’ consisted of a row of mature oak trees. Thus the impact of hedges on water quality could vary with landscape, hydrological and climatic setting, soil type and hedge species. There is therefore a need for further studies of hedgerow impacts in different global environments and topographic settings.

The fungal diversity we found was consistent with previous studies showing reduced AM diversity in arable soils (Helgason et al., 1998; Verbruggen et al., 2010). Change in total fungal communities among different agricultural systems has been observed (e.g. Hartmann et al., 2014), though diversity effects are less clear. The reduction in AM fungal diversity has been attributed to disturbance, but the evidence for other significant differences in soil compaction, moisture content and solute chemistry suggests the drivers may be a more complex effect of overall change in niche properties for these fungi and the roots they inhabit. A number of studies have shown that the broad spectrum herbicide glyphosate, which is used routinely in the arable fields we sampled for weed control, has adverse impacts on AM fungi (Druille et al., 2013), so it is likely that some of the impacts of arable management relate to effects of agro-chemicals.

Fungal diversity patterns closely resembled the macrofauna, also showing that the margin and pasture sites had similar diversity although composition was variable. Here too, the hedgerows also have a distinct and variable community, suggesting that the soil hydrology and

structure is a significant driver of biodiversity across a wide range of taxonomic groups. This is the first study to show that hedgerows within agricultural landscapes are a reservoir of a distinct and heterogeneous soil community.

5. Conclusions

Both hedgerows and grassy field margins can provide a wide range of enhancements to soil function that may provide wider ecosystem service benefits to accrue from agricultural systems. Given that global food security is a pressing issue and more intensive farm production may be required in some regions, it will be important to develop simple land management strategies that can enable food and fibre production to occur in a sustainable way. Enhancing the area of both field margin woody hedgerows and grass strips globally could be an important technique for reducing flood risk as well as for enhancing total soil C storage and the diversity of soil ecosystems across agricultural landscapes. One trade off that requires further research is the potential of hedges to capture pollution from the atmosphere which may result in reduced water quality in runoff and groundwater flow emerging from soils below hedges.

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Appendix A. Supplementary further methods and other information

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2018.11.027>. Additional sequencing data associated with this paper are available upon request from Thorunn Helgason, University of York.

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