Legacy effects of grassland management on soil carbon to depth 1

Running header: Management and deep soil carbon 2

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Abstract

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The importance of managing land to optimise carbon sequestration for climate change mitigation is widely recognised, with grasslands being identified as having the potential to sequester additional carbon. However, most soil carbon inventories only consider surface soils, and most large scale surveys group ecosystems into broad habitats without considering management intensity. Consequently, little is known about the quantity of deep soil carbon and its sensitivity to management. From a nationwide survey of grassland soils to 1 m depth, we show that carbon in grasslands soils is vulnerable to management and that these management effects can be detected to considerable depth down the soil profile, albeit at decreasing significance with depth. Carbon concentrations in soil decreased as management intensity increased, but greatest soil carbon stocks (accounting for bulk density differences), were at intermediate levels of management. Our study also highlights the considerable amounts of carbon in sub-surface soil below 30cm, which is missed by standard carbon inventories. We estimate grassland soil carbon in Great Britain to be 2097 Tg C to a depth of 1 m, with ~60% of this carbon being below 30cm. Total stocks of soil carbon (t ha⁻¹) to 1 m depth were 10.7% greater at intermediate relative to intensive management, which equates to 10.1 t ha⁻¹ in surface soils (0-30 cm), and 13.7 t ha⁻¹ in soils from 30-100 cm depth. Our findings highlight the existence of substantial carbon stocks at depth in grassland soils that are sensitive to management. This is of high relevance globally, given the extent of land cover and large stocks of carbon held in temperate managed grasslands. Our findings have implications for the future management of grasslands for carbon storage and climate mitigation, and for global carbon models which do not currently account for changes in soil carbon to depth with management.

Introduction

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Permanent grasslands are found extensively across the temperate zone where they form the backbone of agricultural systems. Global land cover estimates for grasslands range between 20-40% of the Earth (FAO 2015), and for the UK, constitute the largest category of land use at 36% of land cover (Carey et al. 2008). The multiple values of grassland ecosystems to mankind has long been recognised, ranging from direct benefits of agricultural production, to indirect ecosystem services such as the regulation of climate and water quality, and pollination services (Heidenreich 2009). As such, grasslands are arguably one of the most valuable biomes for ecosystem service provision, but also are among the most threatened by anthropogenic activities (Gibson 2008). Threats include increasing pressures to meet the food demands of more affluent and larger global populations, and to deliver concomitant multiple ecosystem services demanded by the sustainable intensification agenda (Garnett et al. 2013). Of the multiple ecosystem services provided by grasslands, climate regulation via soil carbon storage and sequestration, is highly valued (Heidenreich 2009). In terms of terrestrial carbon storage, soils contain the largest global pool of terrestrial carbon, storing more carbon than is present in plant biomass and the atmosphere combined (Batjes 1996, Jobbagy and Jackson 2000). Temperate grasslands are the third largest global store of carbon in soils and vegetation (after wetlands and boreal forests), storing an estimated 304 Pg C, or 12.3% of global carbon (Royal Society 2001), most of which is in soil. Such carbon stocks are known to be vulnerable to changes in land use and intensification of agricultural management, with the conversion of croplands to permanent grassland generally increasing soil carbon, and the reverse change from grassland to croplands reducing soil carbon stocks (Guo and Gifford 2002, Smith et al. 2008). Moreover, such changes in land use can have a long lasting legacy effect on soil carbon, on a scale of

decades to several hundreds of years, which is often slow to reverse (Dupouey et al. 2002,

McLauchlan 2006, Smith 2014).

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Grassland soil carbon has been shown to respond to changes in management intensity, with agricultural practices such as fertiliser application, irrigation, and livestock grazing affecting soil carbon stocks (Soussana et al. 2004, Smith et al. 2008, van Wesemael et al. 2010). In many parts of Europe, the intensity of grassland management has substantially increased since the 1950's. This has been driven largely by agri-environmental policy and farm subsidies, combined with technological innovations, leading to widespread legacy effects of long-term management on soils and vegetation. In addition to the documented effects of management on soil carbon (Guo and Gifford 2002, Smith et al. 2008), intensification of farming practices has led to widespread reductions in botanical diversity and loss of speciesrich, traditionally managed grasslands, which now cover less than 3% of the area they did in the 1950's (Gamble et al. 2012). Furthermore, management intensification has caused major changes in plant functional composition, with intensively managed grasslands typically being dominated by fast-growing exploitative species, characterized by high specific leaf area (SLA) and leaf nitrogen concentration (LNC). This compares with less fertile, extensively managed grasslands that are dominated by slower-growing, conservative species of high leaf dry matter content (LDMC) and low leaf N content (Lavorel and Garnier 2002, de Vries et al. 2012). Such shifts in plant functional composition are known to have important effects on soil nutrient cycling and carbon dynamics (de Vries et al. 2012, Grigulis et al. 2013, Manning et al. 2015), and LDMC has been correlated with soil fertility (Hodgson et al. 2011, Duru et al. 2012). However, there is a lack of knowledge on the relationship between soil carbon and management intensity with depth linked to the legacy of vegetation change.

Another factor contributing to uncertainty over legacy effects of management and land use change is that most studies on soil carbon stocks are on more easily sampled surface soils. Even the IPCC recommend soil carbon accounting for the surface 30 cm of soil only (IPCC 2006), and although they advocate sampling beyond 30cm, this is rarely done. As a result, soil carbon stocks at depth are largely ignored (Fontaine et al. 2007, Chapman et al. 2013), and little is known about the quantity of soil carbon at depth and how it responds to land management and associated vegetation change in grasslands (Jobbagy and Jackson 2000, Soussana et al. 2004, Fontaine et al. 2007). Given the substantial quantities of carbon in grassland soils, and the fact that grasslands worldwide are subject to increasing intensification of management, this represents a major gap in knowledge.

The overarching aim of our study was to quantify the distribution of soil carbon across

English grasslands to depth (1 metre), and the relationship of surface and deep soil carbon to grassland management at a national scale. To do this, we carried out a nationwide survey of English grasslands. This included all the main grassland habitats found in Great Britain, namely acid, calcareous, mesotrophic and wet grassland, sampled across the broad range of soil and climatic conditions (de Vries et al. 2012, Manning et al. 2015), thereby encompassing a wide range of variation across a representative spatial domain (Smart et al. 2012). Cumulative soil carbon stocks and mean depths from the survey were then used in conjunction with land cover data for matching grassland broad habitats from the Countryside Survey (Carey et al. 2008) to estimate total grassland soil carbon stocks in Great Britain to a depth of 1m, and to make comparisons with existing estimates of grassland soil carbon storage. Using two abundance-weighted leaf traits known to be indicators of soil fertility and management intensity (i.e., SLA and LDMC) (Hodgson et al. 2011; Grigulis et al. 2013), we

also sought to test whether surface carbon stocks are more related to current plant functional composition than deeper carbon.

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Methods

Field sampling.

A survey of 180 permanent grasslands was conducted in summer 2010 from a range of acid, calcareous, mesotrophic and wet grasslands, using a network of sites located throughout England (Fig. 1) (de Vries et al. 2012, Manning et al. 2015). Sampling sites were in 60 different geographical locations, from 12 broad regions of England. At each of the 60 locations, three different fields were selected to give a gradient of management intensity of extensive, intermediate and intensive management. These triplicate sets of fields were sited on the same soil type, with similar topography and edaphic characteristics, and all three fields at the same location were sampled on the same day. The three management intensity classifications were based on expert judgement using information from consultations with farmers and land owners, and from vegetation surveys (de Vries et al. 2012, Manning et al. 2015), and follow broad classifications that reflect dominant grassland systems in the UK and Europe (Tallowin and Jefferson 1999, Tallowin et al. 2005, Manning et al. 2015) (Table 1). There are clearly many different factors involved in the intensification of grassland management, including increased use of fertilisers, increased disturbance through greater cutting and grazing intensities, and changes in the amount and diversity of plant-derived organic matter inputs to soil due to vegetation change. Given that it is not possible to disentangle the individual effects of these factors on soil carbon stocks at the national scale of sampling done here, we therefore compared grasslands subject to broadly defined levels of agricultural intensification; this approach has been used widely to identify broad-scale trends

144 in, and relationships between, vegetation and soil properties along gradients of management intensity (Bardgett and McAlister 1999, Grayston et al. 2004, Allan et al. 2015). 145 146 147 The extensively managed grasslands had relatively high plant diversity and high conservation status, typically received less than 25 kg N ha⁻¹ yr⁻¹ and, have been managed in a traditional, 148 low intensity manner for many decades, with light grazing and annual cutting for hay. The 149 intensively managed agriculturally improved grasslands had low plant diversity of mainly 150 MG6 (Lolium perenne – Cynosurus cristatus) and MG7 (Lolium perenne leys and related 151 152 grasslands) communities (Rodwell 1992). These intensively managed grasslands typically receive >100 kg N ha⁻¹ yr⁻¹, and have been subjected to standard intensive management 153 154 practices since the 1950's, with higher grazing pressures and more frequent cutting for silage 155 than the extensively managed grasslands (Tallowin and Jefferson 1999, Tallowin et al. 2005, 156 Critchley et al. 2007). The third category of grasslands is that of intermediate management intensity, which falls between the two other categories, having typical inputs of ~ 25-50 kg N 157 ha⁻¹ yr⁻¹, and intermediate levels of plant diversity, grazing and cutting (Table 1). 158 159 Soil cores (3.5 cm diameter) were taken from three random areas in each field, to 1 m depth 160 161 (where possible) using an Eldeman auger, and divided into five depth increments: 0–7.5 cm, 162 7.5-20 cm, 20-40 cm, 40-60 cm and 60-100 cm. A soil pit was dug at one location in each field and three bulk density cores (6 cm length x 6.3 cm diameter) were taken horizontally for 163 164 each depth increment, from three different faces of the pit. This methodology builds on 165 information from the previous sampling campaign at these locations, where soil was collected from the surface 7.5 cm only (de Vries et al. 2012, Manning et al. 2015). 166 167 Soil Analyses. 168

Soils were sieved (4 mm), oven dried at 60°C, ground using a ball mill, and analysed for total carbon by combustion and gas chromatography (Elementar Vario EL CN analyser). Total soil carbon (organic and inorganic) stocks per unit area (g C cm³) were calculated from carbon concentrations (%C) and bulk density measures (g cm⁻³) for all depth increments. A further sample of the three surface soils (0-7.5 cm) collected from each field were pooled in equal proportions for separation into soil organic matter (SOM) fractions (n=180). SOM fractionation was by the flotation and sedimentation method using a sodium iodide (NaI) solution (Sohi et al. 2001, Sohi et al. 2005). This fractionation method distinguishes between: (a) a free SOM fraction (FR-SOM) at density < 1.80 g cm⁻³ which represents discrete free organic particles located between stable soil aggregates; (b) an intra-aggregate SOM fraction (IA-SOM) at density < 1.80 g cm⁻³ which represents discrete organic particles located within stable soil aggregates; and (c) a residual heavy organo-mineral fraction at densities > 1.80 g cm⁻³. Briefly, 7.5 g (dry wt) soil was added to 90 ml NaI at a density of 1.80 g cm⁻³, centrifuged for 30 minutes and the first floating FR-SOM fraction removed by suction. The remaining centrifuge pellet was then re-mixed with the NaI, sonicated for 195 seconds, re-centrifuged for 30 minutes, and the second floating IA-SOM fraction removed by suction. The remaining pellet, thoroughly rinsed in water, forms the organo-mineral fraction. All soil fractions were dried, then ground in a ball mill and analysed for total C and N as above.

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Data analysis.

Effects of depth and management on soil carbon concentration, bulk density and soil carbon stocks were tested by ANOVA using generalised linear models (SAS Enterprise Guide 4.3), with grassland type and region as factors. Cumulative soil carbon stocks to depth were estimated by a Bayesian mixed modelling approach (supporting information S1), with

random effects of region and location included plus a fixed effect of soil depth. Estimates of cumulative soil carbon stocks were summarised by the posterior distribution of values estimated for each soil depth and each level of management intensity, with the clustering of samples within locations accounted for in the mixed effects model. Abundance-weighted means for plant traits SLA and LDMC were calculated for sample plots using plant species data, derived from field surveys carried out in 2005 to help classify management intensity classifications, and paired with soil carbon measurements at each soil depth. Plant trait information was derived from the LEDA database based on UK values reported for each species (Kleyer et al. 2008). We modelled the between-location variation in total soil carbon at each depth increment in terms of the abundance weighted plant traits, testing linear and quadratic models at each depth; region and location were introduced as random effects.

Upscaling

Cumulative soil carbon stocks and soil depths from our survey were combined with the UK Countryside Survey land cover data (Carey et al. 2008) to estimate total grassland soil carbon in Great Britain to a depth of 1m. Grassland types and management categories from our survey were matched with the UK Countryside Survey (CS) broad habitat classifications of improved, neutral, calcareous and acid grasslands (Emmett et al. 2010). Our 'intensively managed' grassland category mapped to the CS category 'improved grasslands'; our 'intermediate' grasslands mapped to CS 'neutral' grasslands; and, our 'extensive' grassland category mapped with the CS 'acid' and 'calcareous' grassland categories. These assumptions were successfully validated by comparing the total grassland soil carbon storage estimate from CS to a depth of 15cm with our modelled cumulative carbon stocks (see Fig. 3). Cumulative soil carbon stocks for each management category were multiplied by the land cover area, and adjusted to account for the fact that not all grasslands surveyed had soil to the

full 1m depth, to give an estimate of total grassland soil carbon stocks (supporting information S2).

Results

224 Field survey

Across all sites, the greatest concentrations of total carbon (% total C) were in surface soils to 7.5 cm depth ($F_{4,2096}$ = 288, P < 0.0001) (Table 2). Soil carbon concentration decreased with increasing management intensity ($F_{2,2096}$ = 10.9, P < 0.0001), with significantly lower carbon in the most intensive relative to intermediate and extensively managed grasslands, based on all soils at all depths sampled (Table 2). Management effects were strongest in the surface 7.5 cm soil (supporting information S3), where total carbon concentration decreased with intensification, being 19% and 25% lower in intensively managed than intermediate and extensively managed grasslands respectively (Table 2). The effects of management intensity on total % carbon decreased with depth, but were still significant to 40cm depth (P < 0.05) and weakly significant (P < 0.10) at 60 cm depth. 70% of fields contained soils to 60cm depth, and 55% of all fields had soils to the full 1 m depth; therefore, the number of samples analysed decreased down the profile (Table 2). Those with deeper soils tended to be from more carbon rich mesotrophic and wet grasslands, hence the observed trend for increased mean carbon concentration at the 60-100 cm depth (Table 2).

Soil bulk density increased with depth down the soil profile ($F_{4,2011} = 57.5$, P < 0.0001), and was also influenced by grassland management ($F_{4,2011} = 25.9$, P < 0.0001) (Table 3, Table S3.1). The strongest effects of management were in the top 20 cm of the profile, where bulk density was lowest in extensively managed and greatest in intensively managed grasslands,

and a trend for greater bulk density in intensively managed grasslands continued to 1 m depth. Total soil carbon stocks per unit area (g C cm⁻³), calculated from both the soil carbon concentration and bulk density, were also strongly influenced by depth, with greatest mean carbon stocks per unit area in the top 7.5 cm of the profile ($F_{4.1965} = 228$, P < 0.0001), and by management intensity ($F_{2,2096} = 3.1$, P = 0.05) (Fig. 2). Specifically, for all soils analysed, total soil C stocks (g C cm⁻³), were significantly greater in grasslands of intermediate management intensity relative to both the extensive and intensive managed grasslands (Fig. 2.). When analysed by depth increments, soils from grasslands at intermediate levels of management had greater soil carbon stocks relative to extensive grasslands at 7.5 cm, and relative to intensive grasslands at 7.5 to 20cm depth (P < 0.05), with a trend for greatest C stocks at intermediate levels of management detected to 60 cm depth (P = 0.1) (supporting information S3). We estimated cumulative soil carbon storage per m², at 5 depth increments to 1 m depth (Table 4) using a Bayesian mixed effects model (supporting information S1). Uncertainties in carbon stock estimates increased with depth (Table 4), reflecting greater incremental size categories and smaller sample numbers because fewer profiles reached the full 1 m depth. This is a pattern commonly encountered with soil carbon measurements at depth (Syswerda et al. 2011), and in our sites, soils with samples present at 1m depth also tended to be those with greater carbon concentrations. Cumulative stocks of carbon to 1 m depth in grasslands with intermediate levels of management were 10.7 and 7.8% greater than for grasslands with intensive and extensive management respectively (Table 4). This unimodal relationship between soil carbon stocks and management is less apparent in other studies where bulk density has not been taken into account.

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Although we measured total carbon in bulk soils, fractionation of surface soils (7.5 cm depth) showed that it was only the relatively labile soil organic matter (SOM) fractions that

responded to management (Table 2). More specifically, the amount of carbon (g C kg⁻¹ soil) in the free SOM, which represents ~15% of soil mass (mean of all samples), reduced with increasing management intensity. The amount of carbon in the intra-aggregate SOM fractions (~2% of soil mass) was also lower in the intensive compared with the other two levels of management intensity. In contrast, the amount of carbon present in the recalcitrant organo-mineral fraction, which accounted for the largest remaining proportion of soil mass, did not respond to management intensity.

Plant traits and soil carbon at varying depth

Of 20 model tests (linear and quadratic fits attempted for two traits at five depths) only two significant relationships were found. These were for a unimodal and linear model between abundance-weighted SLA and soil carbon at 40 and 60cm depth, respectively. Consequently there was little evidence for consistent relationships with the plant traits SLA and LDMC and their systematic change down the soil profile.

Discussion

The aim of this study was to investigate the amount of soil carbon in grasslands to 1 m depth, and the sensitivity of soil carbon to management intensity at depth increments to 1 m. Our study was carried out at a national scale across a broad range of grasslands and soil conditions, thus extending knowledge from past studies into land management and deep carbon at the field scale. We reveal two key findings. First, we show that long-term changes in grassland management intensity have strongly influenced soil carbon, and that this effect is seen to considerable depths down the soil profile, albeit at decreasing significance with depth. Second, we show that considerable stocks of carbon are contained in sub-surface grassland soils, below the standard carbon inventory default depth of 30cm under tier 1 of the IPCC

(2006), suggesting that large stocks of unaccounted for carbon are sensitive to management change.

Management intensity

Our data show that intensive management has reduced the concentration of carbon in soil (% total C), and that soil carbon stocks per m² are greatest at intermediate levels of grassland management intensity. This sensitivity of soil carbon to management has been found in other grassland studies for surface soils in Europe (Soussana et al. 2004, Allard et al. 2007). However, by sampling to 1 m depth from a large number of sites across a broad range of grassland and soil types, our study extends the knowledge of grassland management effects on soil carbon by demonstrating that, although management effects on soil carbon were strongest in surface soils, they are still observed to considerable depth down the soil profile, indicating that extensive stocks of soil carbon at depth are sensitive to management change.

We suggest that both biological and physical mechanisms contributed to the greater cumulative carbon stocks observed at intermediate levels of grassland management. Soil carbon sequestration is dictated by processes controlling the balance of carbon inputs and carbon outputs. Carbon inputs are derived from primary productivity through photosynthetic uptake of carbon, input to soil in the form of root exudates and litter; plus additional inputs from animal manure. Carbon losses are through a range of biological and physical processes including respiration, decomposition, erosion, leaching and removal of biomass by harvesting or grazing animals. Because we measured total rather than organic soil carbon, it is possible that differences in total soil carbon are due, in part, to variations in inorganic carbon, from liming or the influence of parent bedrock, particularly in calcareous soils. It is also possible that black carbon (charcoal) made up a small proportion of the total carbon observed

(Manning et al. 2015). However, by sampling triplicate groups of fields from the same bedrock across a management intensity gradient, we suggest that these effects would be minimal.

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There are clearly many factors involved in the intensification of grassland management, such as fertiliser addition, the intensity of grazing and biomass removal, and compaction associated with livestock and machinery, and it is difficult to separate out the effects of each of these in terms of their influence on soil carbon. Such management factors also impact on plant community composition, which is known to influence soil carbon dynamics (De Deyn et al. 2008, Manning et al. 2015). We did not directly measure plant productivity, decomposition, or other processes involved in carbon cycling. However, it has been shown in other studies that extensive grassland management can reduce soil carbon accumulation over time as plant productivity declines in response to nutrient limitation (Allard et al. 2007), and that intensive management involving the application of large amounts of fertiliser can be detrimental to soil carbon (Mack et al. 2004, Soussana et al. 2004, Schipper et al. 2007). Conversely, the application of fertiliser in modest amounts in intermediate grasslands has been shown to enhance soil carbon (Conant et al. 2011, Leifeld et al. 2011, Smith 2014), which is likely related to an increase in primary productivity without over-stimulating decomposition, although, as pointed out, the effect of other concomitant management factors cannot be ruled out.

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In addition to changes in bulk soil carbon, we also found that different fractions of carbon in surface soils to 7.5 cm depth varied in their sensitivity to management. In particular, both the labile free SOM and intra-aggregate SOM fractions were reduced by management intensification. While these two SOM fractions make up less than a quarter of total soil mass,

they are of vital importance to soil carbon storage as they contain a greater concentration of carbon than the recalcitrant organo-mineral fraction and account for 31% of soil carbon in intensively managed soils, rising to 37% and 44% of soil carbon in intermediate and extensively managed grassland soils respectively. We found no evidence of a systematic relationship between total soil carbon at varying depth and community weighted values of two key leaf traits (i.e. SLA and LDMC) that are known to be responsive to grassland intensification and to mediate effects on carbon storage via differences in the decomposability of plant material (De Deyn et al. 2008). We expected that the relationship between leaf traits and soil carbon would be strongest at the soil surface and decline in strength with soil depth, reflecting historic plant traits prior to intensification in the last 60 years. Using the same network of grassland sites, Manning et al (2015) investigated relationships between plant traits and soil carbon fractions in surface soil (7.5 cm soil depth) and found that only the labile carbon fraction was partially explained by community weighted SLA, with soil carbon stocks being greatest under vegetation with thick and/or dense leaves. In contrast, the less active fractions, which make up the bulk of the carbon pool, were better explained by abiotic factors, including pH and climate (Manning et al. 2015). Our results indicate that the lack of correlation between leaf traits and soil carbon propagates down the soil profile, suggesting that the mediating effect of current plant trait variation on soil carbon is weaker than the long-term effect of other environmental controls on the production and storage of carbon at depth.

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Differences in carbon stocks between management levels were also strongly influenced by variations in soil bulk density, which increased as management intensified and with depth.

This increase in bulk density with more intensive management is likely largely explained by soil compaction from a greater use of machinery and trampling from grazing animals

(Gifford and Roderick 2003, Batey 2009), but also the greater proportion of higher density soil fractions in fertilised soils (Fornara et al. 2011). The combination of low carbon concentration with high bulk density in intensive grasslands, and high carbon concentration with low bulk density in extensive grasslands, contributed to the equivalence of carbon stocks observed at high and low levels of management intensity, and their lower levels relative to intermediate intensity. This highlights a dilemma in comparing soil carbon stocks both spatially and temporally, in that soil carbon stocks calculated per unit area could be increased by simple physical compaction without a change in soil carbon concentration, particularly if measured at shallow sampling depths. Gifford and Roderick (2003) propose an alternative way of calculating soil carbon based on soil mass rather than volume to avoid this problem of bulk density change associated with land use. For comparison, we estimated cumulative carbon stocks on a soil mass rather than volume basis, using approximated soil mass values (supporting information). On this approximated soil mass basis, differences in cumulative carbon stocks between intermediate and extensive grasslands were reduced, whereas the difference in cumulative carbon stocks for intensive relative to both intermediate and extensive grasslands increased, to an estimated 15% less carbon in intensively managed grasslands (supporting information). This differs from our findings on a bulk density basis, where soil carbon stocks were greatest under intermediate compared with both intensive and extensive intensity of management, but highlights the strong detrimental effect of intensive management on grassland soil carbon stocks. However, these results need to be treated with caution as calculations were made retrospectively on approximated soil mass values without following the recommended protocol (Gifford and Roderick 2003), and did not meet the requirement for samples to be taken from adjacent positions (Chapman et al. 2013).

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Carbon stocks at depth

Our study revealed that considerable stocks of soil carbon are contained in sub-surface grassland soils below the standard carbon inventory default depth of 30cm (IPCC 2006). Using Great Britain as a case study, we combined our model of cumulative soil carbon stocks across a range of grasslands and management intensities with land cover data (Carey et al. 2008) for comparable grassland categories, to estimate total grassland soil carbon storage to 1 m depth. Cumulative soil carbon stocks were adjusted for depth, based on our survey results of a decreasing proportion of grasslands having soil to the full sampling depth, with 55% of all fields having soil to the full 1 m depth (Table 4). From this, we estimate a total carbon stock in British grassland soils of 2097 Tg C to a depth of 1 m (Fig. 3). This is over three times the amount for soil organic carbon estimated by the latest Countryside Survey to 15 cm depth (660 Tg), and more than double the amount when extrapolated to the standard IPCC recommended carbon accounting depth of 30 cm (estimated at 880 Pg, Fig. 3). Of this figure of 2097 Tg C for grassland carbon storage to 1 m depth, the greatest proportion of grassland soil carbon stocks (1130 Tg C) were in improved grasslands, which account for the largest land cover of all grasslands in Great Britain (Carey et al. 2008) and are most likely to contain soil to 1 m depth. Total stocks of soil carbon to 1 m depth (Table S2.2) were 10.7% greater at intermediate relative to intensive management, which equates to 10.1 t ha⁻¹ in surface soils to 30 cm depth, and an additional 13.7 t ha⁻¹ in soils from 30-100 cm depth.

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At shallower soil depths, our soil carbon values of 76 and 97 t ha⁻¹ at 15 and 30 cm depths respectively, are in line with those reported elsewhere for the UK, of 48-90 t ha⁻¹ at 15 cm and 100 t ha⁻¹ at 30 cm depth (Bradley et al. 2005, Emmett et al. 2010, Chapman et al. 2013). However, our estimation of grassland soil carbon stocks of 2097 Tg C to 1 m depth is considerably greater than that of Bradley et al. (2005), estimated at 1345 Tg C for UK pasture, and of Chapman (2013), who reported 138 t ha⁻¹ for improved and 185 t ha⁻¹ for

semi-natural grasslands, compared with our value of at 229 t ha⁻¹ at 1 m depth. This suggests that grassland carbon stocks at depth may be greater than previously thought. However, extrapolation of data needs to be treated with caution, due to the high variability of carbon stocks at depth and regional differences between management and grassland types (Maskell et al. 2013), and our modelling results explicitly quantify the uncertainty associated with our estimates and how the uncertainty increases with depth (Table 4). Differences in soil carbon accounting at depth between studies are likely due to increased uncertainties caused by lower sample numbers and greater incremental size categories (Syswerda et al. 2011), and differences between land use classifications; for example, Bradley et al (2005) estimate a further 2015 Tg C to 1m depth in their semi natural category. Our data also show that around 60% of the total grassland soil carbon stocks to 1 m depth are found in sub-surface soils below 30 cm depth. Previous estimates, albeit for organic not total carbon, commonly quote a 50/50 split between surface and sub-surface (30-100 cm) soil carbon (Batjes 1996, Jobbagy and Jackson 2000, Schils et al. 2008), although 60% sub-surface organic carbon has been previously estimated for some grassland soils (Hiederer 2009).

Our data clearly reveal an important stock of carbon in grassland soil at depth, which is unrecognised in current surface soil carbon accounting (IPCC 2006, Emmett et al. 2010). Despite the tier 1 default soil sampling depth being 30 cm, the IPCC advocate sampling beyond 30 cm depth, although in likelihood this is rarely done. Our findings provide clear support for the IPCC recommendation of the need for deeper C sampling, not only to improve soil C inventories, but also to take into account changes in soil carbon at depth due to management intensification.

In conclusion, the findings of our national-scale study, which encompassed a broad range of grasslands and environmental conditions, show that carbon in grasslands soils is vulnerable to management, and that the legacy of long-term grassland management impacts on soil carbon to considerable depth down the profile. Moreover, we highlight the presence of substantial stocks of carbon in sub-surface soil in grasslands, which are not accounted for by the majority of standard carbon inventories (IPCC 2006, Emmett et al. 2010, Sanderman et al. 2011), indicating that large stocks of unaccounted for soil carbon are sensitive to changes in land management intensity. Our finding suggest potential future benefits for soil carbon sequestration alongside biodiversity through extensification of the most highly managed and fertilised grasslands, given that soil carbon concentrations decrease with management intensity, and that cumulative stocks of soil carbon to depth when bulk density was accounted for were greatest in grasslands managed at intermediate levels of intensity and plant diversity. Given the global extent of managed grasslands, these findings not only have implications for their future management for soil carbon storage and climate mitigation, that would benefit future global carbon targets (United Nations FCCC 2015), but also for global carbon models which need to take account of deep soil carbon stocks, and changes in this soil carbon at depth due to management.

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Supporting Information

- S1. Methods for modelling cumulative soil carbon.
- 644 S2. Upscaling cumulative soil carbon to the whole of Great Britain.
- S3. Statistical effects for soil carbon and bulk density.
- 646 S4. Estimating soil C stocks on soil mass basis.
- S5. BUGS code for modelling cumulative soil carbon stocks.

Tables

Table 1. Typical values for grassland management practices, including fertiliser use, grazing management (LU -= livestock units), cutting regimes, and plant species diversity for the three levels of management intensity.

	Extensive	Intermediate	Intensive
Fertiliser application rate	< 25 kg N ha ⁻¹ yr ⁻¹	25 – 50 kg N ha ⁻¹ yr ⁻¹	> 100 kg N ha ⁻¹ yr ⁻¹
Grazing	Set stocking or continuous grazing at stocking rates generally below 1.0 LU ha ⁻¹	Set stocking or continuous grazing at stocking rates up to 1.5 LU ha ⁻¹	Rotational/paddock grazing commonly used with stocking rates of 2.0 – 3.5+ LU ha ⁻¹
Cutting	Generally one cut in mid – late summer for hay or haylage. Regrowth generally grazed in late summer/autumn	Generally one cut in mid- summer for silage or haylage. Regrowth generally grazed in late summer/autumn	Two – three silage cuts per year (May, July, September/October)
¹ Plant diversity	High diversity (Mean 21 sp. m ⁻²)	Intermediate Diversity (Mean 15 sp. m ⁻²)	Low Diversity (Mean 10 sp. m ⁻²)

¹Data on plant species diversity are derived from De Vries et al. (2012).

Table 2. Effects of management intensity on soil carbon, measured as (a) % C of bulk soil and (b) C content of soil fractions in surface soils.

Soil de	epth (cm)	(n)	Extensively managed	Intermediate management	Intensively managed	
(a) Bulk soil	carbon conce	entration	(%C)			
Depth (cm)	0 - 7.5	(515)	$11.53 (\pm 0.54)^{a}$	$10.60 (\pm 0.54)^{b}$	$8.59 (\pm 0.44)^{c}$	**
	7.5 - 20	(499)	$8.18 (\pm 0.59)^{a}$	$7.77 (\pm 0.53)^{a}$	$6.13 (\pm 0.47)^{b}$	**
	20 - 40	(446)	$6.48 (\pm 0.84)^{ab}$	$6.34 (\pm 0.74)^{a}$	$5.59 (\pm 0.72)^{b}$	**
	40 - 60	(359)	$6.85 (\pm 1.28)$	6.51 (± 1.12)	$5.35~(\pm~0.96)$	*
	60 – 100	(277)	9.76 (± 1.66)	$7.25 (\pm 1.43)$	$7.55 (\pm 1.37)$	
(b) Carbon content of soil fractions in surface soils (0-7.5 cm) (g C kg ⁻¹ soil)						
Free SON	Л		$43.9 (\pm 9.1)^a$	$34.3 (\pm 8.9)^{b}$	$23.6 (\pm 7.9)^{c}$	**
Intra-agg	regate SOM		$3.0 (\pm 0.5)^{a}$	$2.6 (\pm 0.3)^{a}$	$1.8 (\pm 0.2)^{b}$	**
Organo-n	nineral		59.9 (± 4.0)	62.3 (± 3.9)	56.7 (± 3.8)	

Values are means \pm s.e. Significant management effects shown by ** (P<0.05) and *

(P<0.10), with letters denoting differences between the 3 levels of management.

Table 3. Soil bulk density (g cm⁻³), for grassland soils at each of five depth increments sampled, by management intensity and depth.

Soil depth (cm)	(n)	Extensively managed	Intermediate management	Intensively managed	
0 - 7.5	(486)	0.64 (+0.02)	0.73 (+0.02)	0.83 (+0.03)	**
0 - 7.3 7.5 - 20	(464)	$0.64 (\pm 0.02)$ $0.85 (\pm 0.02)$	$0.73 (\pm 0.02)$ $0.91 (\pm 0.02)$	$0.83 (\pm 0.02)$ $0.98 (\pm 0.02)$	**
20 - 40	(399)	$1.06 (\pm 0.02)$	$1.00 (\pm 0.03)$	$1.06 (\pm 0.02)$	**
40 - 60	(362)	$1.05 (\pm 0.04)$	$1.06 (\pm 0.04)$	$1.13 (\pm 0.03)$	**
60 - 100	(300)	$1.02 (\pm 0.05)$	$1.05 (\pm 0.04)$	$1.09 (\pm 0.04)$	**

Values are means \pm s.e. Significant management effects shown by ** (P < 0.05).

Table 4. Mean cumulative soil carbon (kg C m⁻²).

	Extensively managed	Intermediate management	Intensively managed
Surface to 7.5cm depth	6.61 (± 5.26-8.32)	$7.14~(\pm5.68\text{-}8.96)$	$6.45~(\pm~5.12\text{-}8.11)$
Surface to 20 cm depth (97% of samples)	8.47 (± 6.75-10.65)	9.15 (± 7.29-11.47)	8.26 (± 6.56-10.37)
Surface to 40 cm depth (87% of samples)	12.59 (± 10.04-15.82)	13.60 (± 10.83-17.02)	12.28 (± 9.76-15.40)
Surface to 60 cm depth (70% of samples)	18.71 (± 14.90-23.54)	20.21 (± 16.07-25.36)	18.24 (± 14.53-22.92)
Surface to 100 cm depth (55% of samples)	41.38 (± 32.65-52.33)	44.62 (± 35.20-56.47)	40.30 (± 31.84-50.98)

Values are best estimates of the mean carbon stock where soil samples were present, with

lower and upper credible intervals (2.5 and 97.5% tiles of the posterior distribution from a

Bayesian mixed effects model).

663

667	Figure captions
668	
669	Figure 1. Sampling locations in England (DeVries et al. 2012). Five farms were selected in
670	each of the 12 regions, and three fields in each farm were sampled: one extensively managed,
671	one of intermediate management and one intensively managed. Regions are: (a) Worcester,
672	(b) Upper Thames, (c) Somerset, (d) Devon, (e) Cotswolds, (f) High Weald, (g) South
673	Downs, (h) Breckland, (i) Dales meadows, (j) Yorkshire Ings, (k) Yorkshire Dales/South
674	Lake District, (1) Lake District.
675	
676	Figure 2. Total carbon per unit area in grassland soils (g C cm ⁻³ soil). Shown for each of five
677	depth increments sampled, with management intensity indicated by coloured bars: white for
678	extensively managed, grey for intermediate management and black for intensively managed
679	soils. Values are means +/- s.e.
680	
681	Figure 3. Estimated cumulative total soil carbon stocks for grasslands in Great Britain (Tg
682	C), adjusted for the availability of soil at depth. Shown in depth increments to 1 m, with
683	management intensity indicated by colour: white for extensively managed, grey for
684	intermediate management and black for intensively managed soils. The solid black circle
685	shows the current GB estimate of soil carbon at 15 cm depth. Dashed lines indicate

recommended soil sampling depths (GB Countryside Survey 15cm, IPCC at 30cm).