

# *Simple measures of climate, soil properties and plant traits predict national scale grassland soil carbon stocks*

Article

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1 **Simple measures of climate, soil properties and plant traits predict national**  
2 **scale grassland soil carbon stocks**

3

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45 **Summary:**

- 46 1. Soil carbon (C) storage is a key ecosystem service. Soil C stocks play a vital role in  
47 soil fertility and climate regulation, but the factors that control these stocks at regional  
48 and national scales are unknown, particularly when their composition and stability are  
49 considered. As a result, their mapping relies on either unreliable proxy measures or  
50 laborious direct measurements.
- 51 2. Using data from an extensive national survey of English grasslands we show that  
52 surface soil (0-7cm) C stocks in size fractions of varying stability can be predicted at  
53 both regional and national scales from plant traits and simple measures of soil and  
54 climatic conditions.
- 55 3. Soil C stocks in the largest pool, of intermediate particle size (50-250  $\mu\text{m}$ ), were best  
56 explained by mean annual temperature (MAT), soil pH and soil moisture content. The  
57 second largest C pool, highly stable physically and biochemically protected particles  
58 (0.45-50  $\mu\text{m}$ ), was explained by soil pH and the community abundance weighted mean  
59 (CWM) leaf nitrogen (N) content, with the highest soil C stocks under N rich  
60 vegetation. The C stock in the small active fraction (250-4000  $\mu\text{m}$ ) was explained by a  
61 wide range of variables: MAT, mean annual precipitation, mean growing season  
62 length, soil pH and CWM specific leaf area; stocks were higher under vegetation with  
63 thick and/or dense leaves.
- 64 4. Testing the models describing these fractions against data from an independent  
65 English region indicated moderately strong correlation between predicted and actual  
66 values and no systematic bias, with the exception of the active fraction, for which  
67 predictions were inaccurate.
- 68 5. *Synthesis and Applications:* Validation indicates that readily available climate, soils  
69 and plant survey data can be effective in making local- to landscape-scale (1-100,000

70 [km<sup>2</sup>](#)) soil C stock predictions. Such predictions are a crucial component of effective  
71 management strategies to protect C stocks and enhance soil C sequestration.

72

73 **Keywords:** carbon storage, carbon sequestration, community weighted mean, pH, particle  
74 size fractions, soil carbon, soil organic matter.

75

## 76 **Introduction**

77

78 Soil carbon (C) stocks exceed those in both vegetation and the atmosphere by 2-3 times, and  
79 play a vital role in climate regulation and the maintenance of soil fertility (Trumper *et al.*  
80 2009), but these stocks vary by orders of magnitude over regional and national scales, even  
81 within a single ecosystem type (Bellamy *et al.* 2005; Carey *et al.* 2008). Presently, their  
82 mapping either relies upon proxy measures that are often poor estimates of actual soil C  
83 stocks, particularly at local scales (Jones *et al.* 2005; Eigenbrod *et al.* 2010; Stevens *et al.*  
84 2013), or direct measurements, which are expensive and laborious (Bellamy *et al.* 2005; Carey  
85 *et al.* 2008). Models are also used to predict soil C, but these are typically used to make large-  
86 scale or scenario based projections and not fine-scale, extensive soil C stock mapping  
87 (Schimel *et al.* 1994; Smith *et al.* 2005).

88 Improved predictions of soil C stocks should be possible if the factors determining  
89 national, regional and local distributions of soil C are better understood. It has long been  
90 known that soil C is controlled by a wide range of factors (Jenny 1941; Schimel *et al.* 1994),  
91 [that can be viewed](#) as forming a ‘hierarchy of controls’ (Diaz *et al.* 2007, De Vries *et al.*  
92 2012), which impact the basic processes of plant growth and organic matter decomposition  
93 and stabilisation. [At the apex of the hierarchy is climate, which controls the metabolism of](#)

94 plants, fauna and microbes (Burke *et al.* 1989. Schimel *et al.* 1994; Conant *et al.* 2011) and  
95 determines rates of rock weathering (White 1997), thus influencing soil properties. The next  
96 level in the hierarchy are soil abiotic properties, such as texture and pH, which are largely  
97 controlled by underlying geology and processes of weathering (Jenny 1941; White 1997), and  
98 which in turn influence soil C storage by affecting plant growth and microbial activity (Pietri  
99 and Brookes 2008; Schmidt *et al.* 2011). At a local level, soil C storage is also strongly  
100 affected by land use type and intensity, which has an array of impacts on soil C cycling  
101 (Conant, Paustain & Elliot 2001; Smith 2014). Moreover, climate, soil properties and  
102 management all influence the composition and growth of the vegetation, which in turn affects  
103 the amount and chemistry of plant inputs, and the turnover of soil organic matter (SOM)  
104 (Cornwell *et al.* 2008; De Deyn, Cornelissen & Bardgett. 2008; De Vries *et al.* 2012).

105         Although it has long been acknowledged that the above factors are the primary  
106 regulators of soil C storage, their interdependence makes estimating their *relative* importance  
107 challenging. While some studies emphasise the importance of soil physical and chemical  
108 properties (Christensen 2001; Schmidt *et al.* 2011), there is also evidence that plant  
109 community composition plays a significant role (De Deyn, Cornelissen, & Bardgett 2008).  
110 While the importance of vegetation properties has long been recognised, and is represented in  
111 C models (Parton *et al.* 1993, Smith *et al.* 2005), they have typically been viewed only from a  
112 tissue chemistry perspective, and the importance of other plant traits have rarely been  
113 considered. This may be an oversight as plant species vary along a ‘fast-slow’ traits axis,  
114 which distinguishes between fast growing species with rapidly decomposing litters and fast  
115 tissue turnover times and their opposite (Reich 2014). Accordingly, if species effects on  
116 ecosystem function are proportional to their biomass (Grime 1998), then community  
117 abundance weighted means (CWM) of species-level traits may explain variation in soil C  
118 storage and sequestration (Garnier *et al.* 2004). In line with this prediction, recent work shows

119 that CWM trait measures can explain ecosystem-level variation in plant production,  
120 decomposition, photosynthesis, respiration and soil C concentration, and microbial  
121 community composition (Garnier *et al.* 2004; Diaz *et al.* 2007, De Vries *et al.* 2012; Grigulis  
122 *et al.* 2013; Everwand *et al.* 2014). While such studies point to the tractability of scaling up  
123 from traits of individual plants to ecosystem properties, the capacity of this approach to  
124 predict soil C at spatial scales large enough to matter to C stock management is unknown.

125 Another drawback of existing methods of soil C stock prediction is that they typically  
126 predict only the total amount of soil C and not its composition (Jones *et al.* 2005; Stevens *et*  
127 *al.* 2013). Soil C is diverse in its chemistry and interactions with soil particles, and as a result  
128 soil C particles vary greatly in their turnover rates (Trumbore 2000, Schmidt *et al.* 2011).  
129 Accordingly, soil C storage and sequestration is determined not just by the total soil C pool,  
130 but also by the half-lives of soil C components, which can be categorised into pools of  
131 varying stability (Schimel *et al.* 1994; Trumbore 2000). Such pools are arbitrarily defined but  
132 are represented in modern soil C models. Measuring them is inherently difficult, so we lack  
133 reliable baseline data on the amount of C in these pools for most of the Earth's land surface.  
134 While isotopic techniques ( $^{13}\text{C}$  and  $^{14}\text{C}$ ) can be employed (e.g. Trumbore 2000; Marschner *et*  
135 *al.* 2008), their use is impractical in large-scale surveys given their high cost and requirement  
136 for specialist equipment and personnel. An alternative approach is to use more readily  
137 measurable size and density fractions, which broadly correspond to C turnover times  
138 (Christensen 2001; Marschner *et al.* 2008). Fresh C inputs are predominantly found in large  
139 particles that constitute the active fraction, which turns over within months to a few years,  
140 making it the source of most soil C fluxes. In contrast, C found in particles of intermediate  
141 size is typically humified organic matter (OM) that turns over on decadal timescales; while  
142 small and dense soil particles of physically and chemically protected soil comprise the stable  
143 C fraction. This typically turns over on the scale of centuries to millennia and is crucial to soil



144 C sequestration (Schimel *et al.* 1994; Trumbore 2000; Christensen 2001). While relationships  
145 between many of the aforementioned drivers and *total* soil carbon over large scales have been  
146 quantified previously (e.g. Burke *et al.* 1989), their relationship with different C size fractions  
147 has received very little attention (Evans, Burke & Lauenroth *et al.* 2011). The relative  
148 importance of the aforementioned drivers in determining stable soil C may differ from those  
149 controlling rapid turnover fractions, and this could explain discrepancies between studies of  
150 soil C drivers, which typically focus upon total soil C.

151 In this study we set out to identify which factors best explain national scale patterns of  
152 different C fractions in the surface soil (0-7cm) of grassland. This was done for two reasons:  
153 a) to identify the potential abiotic and biotic (i.e. plant traits) determinants of these fractions at  
154 large spatial scales; and b) to assess the potential for using a combination of simple plant trait  
155 and abiotic measures that are readily available to surveyors to predict these soil C stocks, i.e.  
156 to identify potential variables to be used in pedotransfer functions and/or ecological  
157 production functions for these fractions. To do this we generated linear mixed-effects  
158 statistical models describing national scale patterns of surface soil C in different size fractions  
159 across a wide spectrum of the soil and climatic conditions found across England, and a broad  
160 range of grassland types (including calcareous, mesotrophic, wet and acid, Rodwell 1992).  
161 These quantified the relative importance and predictive capacity of several abiotic factors and  
162 various CWM plant traits with strong hypothetical or known links soil C cycling (De Deyn,  
163 Cornelissen, & Bardgett 2008). We hypothesised that stocks of the active soil C fraction are  
164 best predicted by the drivers of plant inputs to soil and the decomposability of these inputs  
165 (e.g. climate and plant traits), while the stable fraction is better explained by soil physical and  
166 chemical properties (e.g. soil texture and pH). We focussed on grasslands because they cover  
167 ~30% of the Earth's land surface and store ~23% of the global terrestrial ecosystem C stock  
168 (Trumper *et al.* 2009). Moreover, in the United Kingdom (UK), where our study was

169 performed, they cover 36% of the land surface and contain an estimated ~32% of national soil  
170 C stocks (Ostle *et al.* 2009).

171

## 172 **Materials and Methods**

173

### 174 GRASSLAND SURVEY

175

176 This work was conducted as part of a broader investigation aimed at quantifying relationships  
177 between agricultural intensification, botanical composition and soil properties, including  
178 microbial community composition, in temperate grasslands (De Vries *et al.* 2012). We  
179 sampled from twelve English regions during June and July 2005 (see Fig.1). Within each  
180 region there were five sites, each containing three fields, but subject to three broad  
181 management regimes: unimproved (U) and often designated as SSSI (Site of Special  
182 Scientific Interest), semi-improved (SI) or improved (I) grassland, resulting in a total of 180  
183 fields (Fig. S1 in Supporting Information). The survey represented the broad habitat  
184 classifications of acid (33 fields), calcicolous (42 fields), mesotrophic (81 fields) and wet  
185 grasslands (24 fields), the main grassland types in the UK (Rodwell 1992), and fields were  
186 allocated to land management intensity categories based on consultation with farmers and  
187 land managers, and expert opinion. This process also ensured that adjacent fields were of  
188 similar soil type and topography. Typically, unimproved grasslands receive  $<25 \text{ kg N ha}^{-1} \text{ y}^{-1}$   
189 and are lightly grazed by livestock and cut annually for hay, whereas semi-improved and  
190 improved grasslands receive  $25\text{-}50 \text{ kg N ha}^{-1} \text{ y}^{-1}$  and  $>100 \text{ kg N ha}^{-1} \text{ y}^{-1}$ , respectively, and are  
191 subject to higher grazing pressures and more frequent cutting for silage (Critchley, Fowbert &  
192 Wright 2007). This broad classification of grasslands has been used widely (e.g. De Vries et

193 al. 2012; Grigulis et al. 2013), and reflects the typical grassland farming systems that are  
194 found across the United Kingdom and other parts of Europe (Rodwell 1992).

195 There were many different plant community types present in the more botanically  
196 diverse unimproved grasslands, but the improved categories were mainly the *Lolium perenne*  
197 (L.) dominated MG6 and MG7 communities of the UK's National Vegetation Classification  
198 (Rodwell 1992). Within each field, percentage cover of each plant species was visually  
199 estimated from three random 1m<sup>2</sup> quadrats within a 25 × 25 m plot of homogeneous  
200 vegetation. These three cover values were averaged to obtain field level abundance estimates.  
201 Within each quadrat, five random 2cm diameter 7cm deep soil cores were taken and pooled.  
202 The use of 7 cm deep cores follows the UK's Department of Environment, Food and Rural  
203 Affairs (DEFRA) recommended sampling depth for assessment of soil abiotic properties in  
204 permanent grassland (DEFRA 2010), and was selected to capture the zone of soil most  
205 influenced by plant traits, and of greatest C content relative to sub-surface soil. We recognise  
206 that significant soil C stocks are found at depth in grasslands (Jobbagy and Jackson 2000), but  
207 sampling the whole soil profile was beyond the scope of this study, especially given the  
208 comprehensive suite of vegetation and soil properties measured.

209

## 210 SOIL ANALYSIS

211

212 Soil samples were sieved (4 mm), homogenised and air-dried, and analysed for moisture  
213 content, total C and pH, using standard methods (see Allen 1989 and Appendix A in  
214 Supporting Information for methods). Standardized wet sieving (De Deyn *et al.* 2011) was  
215 then used to separate the soil particles and the C within them into the active (250-4000 µm),  
216 intermediate (50–250 µm) and stable fractions (0.45-50 µm) (see Appendix A. for details). To

217 calculate soil C stocks on a per-area basis bulk density (BD) was calculated from core volume  
218 and dry soil weight after removing all stones and roots >3mm diameter. It is possible that  
219 black C (charcoal) and inorganic C [was present in our samples](#), though the proportion of these  
220 fractions is likely to be small (see appendix A). Soil texture was classified by expert judgment  
221 and transformed into clay-silt-sand percentages using the central point of each category of the  
222 triangular classification developed by the Soil Survey of England and Wales (Hodgson 1997).

223

## 224 CLIMATE DATA

225

226 Both long-term climate data from Met Office UKCP09 databases (Jenkins, Perry & Prior  
227 2009) and the grassland survey data were assigned to 5 × 5 km grid cells. Mean annual  
228 temperature (MAT) and mean annual precipitation (MAP) were calculated from monthly data  
229 from 1981-2006. Mean growing season length (MGSL) values were taken from the UKCP09  
230 database containing monthly values from 1961-2003 and calculated as the number of days  
231 bounded by a daily temperature mean > 5 °C and < 5 °C after 1st July for more than five  
232 consecutive days. Mean growing degree days (MGDD) was the day-by-day sum of the mean  
233 number of degrees by which air temperature exceeded 5.5 °C. It was calculated using the  
234 mean of values from 1961-2006. [The differences in time periods between these measures](#)  
235 [reflect data availability in the UKCP09 database.](#)

236

## 237 PLANT TRAIT DATA

238

239 Plant species composition data were combined with database values of plant traits to give  
240 field level CWMs for plant traits [with](#) hypothetical links to soil processes (Garnier *et al.* 2004;  
241 Diaz *et al.* 2007; De Deyn, Cornelissen, & Bardgett. 2008, De Vries *et al.* 2012). To do this  
242 trait values were assigned to all plant species occurring in the 180 fields sampled and plant  
243 cover was [used as the CWM weighting measure](#). Values for leaf dry matter content (LDMC)  
244 were taken from a published account of plant species in northern England (Grime, Hodgson &  
245 Hunt 2007). Values for specific leaf area (SLA), relative growth rate (RGR), and leaf nitrogen  
246 content (leaf N) were obtained from the TRY database (Kattge *et al.* 2011), which contains  
247 trait data from a wide range of authors and environments. See Appendix A for details of trait  
248 measurement and justification of trait choice.

249

## 250 STATISTICAL MODELLING

251

252 The grassland survey, climate and trait data were combined to form a single dataset ([see Table](#)  
253 [S1 to see the range of conditions covered](#)) that was used to parameterise and test the  
254 likelihood of competing mixed-effects statistical models according to a model selection  
255 procedure (Pinheiro and Bates 2000). A separate model was created to describe each soil C  
256 fraction as well as total C. Our model selection approach involved adding explanatory  
257 variables in fixed sequential order according to our hypothesised ‘hierarchy of controls’  
258 (Appendix A, Diaz *et al.* 2007). The process started with variables describing climatic  
259 conditions (MAP, MAT, MGSL, MGDD), then added physical and chemical soil properties  
260 that are driven mainly by underlying geology and local hydrology (soil pH, sand silt and clay  
261 content and soil moisture). The third set of terms was linked to management. Here, contrasts  
262 were made between three competing management terms, which either had three levels U, SI

263 and I or two, with either SI and U or SI and I merged. Finally we added trait CWMs to  
264 estimate plant functional trait effects. CWM's for RGR, SLA, LDMC and leaf N were placed  
265 in the model in all combinations of one and two traits. [Although microbial data were available](#)  
266 [\(De Vries \*et al.\* 2012\) they were not used to predict C stocks as they are not readily](#)  
267 [measurable by most surveyors](#). All models were linear mixed-effects models with a random  
268 effect for site to account for the spatial clustering of triplicate fields. Mixed models were  
269 fitted using maximum likelihood and the lme function of the statistical software R version  
270 2.11.1 (Pinheiro and Bates 2000). Throughout the modelling process quadratic terms were  
271 used when the [optimum of biological activity occurs at intermediate levels](#) (i.e. for  
272 temperature, pH, and moisture). See appendix A [and Table S2 for details](#).

273 The explained variance of the final model was calculated as the  $r^2$  when fitting a linear  
274 regression to the actual data, with the predicted values of the model as the explanatory  
275 variable. To estimate the variance explained by the fixed effects, we used the method of  
276 Nakagawa and Schielzeth (2013), which partitions explained variance by comparing the fit of  
277 model predictions to the data when these terms are absent from the model to calculate a  
278 'marginal  $R^2$ ' ( $R^2M$ ). We also used this technique to estimate the proportion of unique (total)  
279 variance explained by each class of variable in the model (soil, climate, plant traits). The  
280 importance of each variable in the model was also estimated by observing AIC change ( $\Delta i$ ) on  
281 deletion.

282

## 283 MODEL VALIDATION

284

285 To validate the fitted models [we collected new data](#) for all the variables retained in the models  
286 (Tables 1 and 2) in 20 fields in the county of Northumberland, England in summer 2012. [This](#)

287 is a separate region to the north east of the original 12 (Fig. 1). Methodology was identical to  
288 before with the exception of site selection. In this case we intentionally chose sites covering a  
289 wide range of the predictor variables found in the original dataset, but excluded sites from  
290 outside these ranges to avoid extrapolation (Table S1), because our models were not  
291 mechanistic. To validate the fitted models, predictor variable values for the Northumberland  
292 sites were fed into the fitted models to produce estimated values. These were then compared  
293 to actual values using Pearson's correlation and paired t-tests.

294

## 295 **Results**

296

297 Total soil C stock to 7cm depth was best described (Table 1, S3; explained variance (EV) =  
298 74.2%,  $R^2M = 26.9\%$ ) by a quadratic relationship for mean annual temperature (MAT) (Fig.  
299 2a), with C stocks being lowest at intermediate temperatures of  $\sim 8.5^\circ\text{C}$ . This temperature  
300 effect accounted for 13.7% of unique variance. Variation in total soil C stock was also related  
301 to soil pH, with stocks being lowest at intermediate pH values of  $\sim 6$  (Fig. 2a) (quadratic  
302 relationship). Finally, soil C stocks were related to soil moisture and maximal at moisture  
303 levels of  $\sim 100\%$ , on a dry soil weight basis. Together these soil terms accounted for 15.2% of  
304 unique variance.

305 Models explaining the three component fractions differed greatly in the variables they  
306 contained, indicating that each is controlled by different factors. The active fraction (4000-  
307 250  $\mu\text{m}$ ) (Fig. 3, Table 1, S4) accounted for 11.1% of total C stocks across grasslands, and the  
308 model describing it accounted for 41.0% of its variation ( $R^2M = 37.6\%$ ) and contained five  
309 variables, each strongly linked to plant productivity and litter decomposition. The most  
310 important of these were quadratic relationships with MAT (Fig. 2b) and MAP; stocks of this

311 C fraction were highest in cold, wet conditions. This pool was also positively associated with  
312 mean growing season length (MGSL), presumably via higher net primary productivity, and  
313 resulting inputs of C to soil (Table 1). Together, these climate factors accounted for 22.0% of  
314 unique variance. Soil pH accounted for 8.7% of unique variance and also displayed a  
315 quadratic relationship with the active C fraction, being greatest in acidic soils. Finally, we  
316 found that the active C fraction was predicted by the CWM of SLA; stocks were higher under  
317 vegetation with thick and/or dense leaves. This trait measure accounted for 4.3% of unique  
318 variance.

319 The intermediate fraction (50–250  $\mu\text{m}$ ) represented 54.7% of total soil C stocks to  
320 7cm depth across grasslands (Fig. 3) and was described by a model that was very similar to  
321 that describing total C stocks (EV = 78.4%,  $R^2M$  = 19.9%, Table 1, S5); the retained terms  
322 described quadratic relationships with MAT (Fig. 2c), soil moisture and pH (Fig. 2c). Stocks  
323 of this C fraction were lowest in soils of neutral grassland and at intermediate climates (MAT  
324  $\sim 9$  °C, pH  $\sim 6$ ). Of the retained variables climate terms were marginally more important  
325 (11.8% unique variance) than soil terms (9.6% unique variance).

326 The stable soil C fraction (0.45-50  $\mu\text{m}$ ), which comprised 32.4% of the total C stocks  
327 across grasslands (Fig. 3), was not explained by climate or management variables. The model  
328 (EV = 74.2%,  $R^2M$  = 17.53%, Table 1, S6) indicated a strong and quadratic relationship with  
329 soil pH, with the highest stocks being found in neutral and alkaline grassland soils (Fig 2d). C  
330 stocks in this fraction also increased subtly with increasing CWM leaf N content. This trait  
331 effect accounted for far less variance (1.9% unique variance) than pH (14.16% unique  
332 variance).

333 Comparison of predicted and observed values of soil C stocks demonstrated that the  
334 fitted models made reasonably reliable predictions of observed stocks of total C and the



335 intermediate and stable fractions but not the active fraction (Fig. S2). Correlations between  
336 predicted and observed values were  $r = 0.57-0.64$ , and there was no significant difference  
337 between them (paired t-tests  $P > 0.05$ ,  $t = < 2$ , d.f. = 19), with the exception of the active  
338 fraction ( $r = 0.03$ ,  $P < 0.05$ ) (Table S7, Fig. S1).

339

## 340 Discussion

341

342 Our results indicate that regional and national patterns of C fractions in the surface soils of  
343 grasslands can be predicted using fairly simple measures of the abiotic environment and  
344 community-level plant traits. Reasonably accurate prediction of soil C stocks across broad  
345 gradients of soil and ecosystem types has been achieved previously using dynamic models  
346 (e.g. Parton et al. 1993) and proxy measures (Paruelo et al 1998; Jones et al. 2005). However,  
347 it has not, to our knowledge, been achieved for different size fractions of soil C within a  
348 single land use type, as shown here. The relationships identified here may not always be  
349 mechanistically causative because climate, management and underlying geology all directly  
350 affect soil C stocks whilst also selecting for different plant trait syndromes (De Vries et al.  
351 2012), making trait measures an integrated measure of the environment. Nevertheless, all  
352 terms in the models accounted for unique variation, meaning that these relationships strongly  
353 indicate the primary regulators of these soil C fractions. Importantly, we found that several  
354 factors that influence soil C stocks at small scales, such as agricultural management (Conant,  
355 Paustain & Elliot 2001) and soil texture (Christensen 2001), do not explain national patterns  
356 in C stocks at these shallow depths. In contrast, plant traits did explain the C stocks of certain  
357 fractions. The surprising lack of soil texture effects on soil C pools may be because soil C is  
358 controlled by soil physical properties that were not captured by our field assessment, e.g.

359 mineral surface charges (Schmidt *et al.* 2011) and secondary and tertiary aspects of soil  
360 structure that determine the availability of C to decomposers, e.g. compaction,  
361 microaggregates and macropores (Christensen 2001). Alternatively, the lack of soil texture  
362 effects may be due to low data resolution or the rarity of clay rich soils sampled (Table S1).  
363 We also highlight that although plant traits explained a small proportion of variance their  
364 importance may be greater than it appears in our models, given their correlation with many of  
365 the other descriptor variables and their place at the base of our hierarchy of controls and  
366 modelling procedure.

367 Looking at each model in turn provides insight into the factors driving each pool and  
368 emphasises the need to view soil C as a heterogeneous material when attempting to  
369 understand its dynamics and meaningfully quantify C stocks. The active fraction model  
370 demonstrates that stocks in this fraction are highest where plant growth is high (high MAT  
371 and MGSL), but decomposition is possibly slow (low pH and high MAP) (Cornwell *et al.*  
372 2008; Pietri and Brookes 2008). Despite a low overall model fit, there was, as hypothesised, a  
373 strong relationship with the CWM of SLA. Where vegetation possessed leaves that were thin  
374 and/or low density and lacked more slowly decomposing structural materials (Reich 2014),  
375 stocks of this fraction were lower (Fig. 2b), a finding that is consistent with previous studies  
376 linking SLA to litter decomposition rates (e.g. Garnier *et al.* 2004). The poor predictive  
377 capacity of our active fraction model may be due to the dynamic nature of this pool, which is  
378 highly variable seasonally (Christensen 2001). It may be better predicted by models in which  
379 plant production and decomposition are more explicitly defined.

380 Unlike the other C fractions the stable pool was not explained by climate, possibly  
381 because much of this C would have entered this pool and become stabilised in different  
382 climatic conditions to those experienced today. This finding is consistent with some large-  
383 scale gradient studies, which show stable soil C stocks to be largely insensitive to temperature

384 (Conant *et al.* 2011), although in other regions (e.g. Inner Mongolia) mineral associated C is  
385 the largest C pool and shows a strong relationship with climate (Evans, Burke & Lauenroth  
386 2011). In contrast, but in line with our hypotheses, the stable C pool was strongly influenced  
387 by soil pH. Higher stocks in more neutral and alkaline soils may reflect greater microbial  
388 processing of SOM in higher pH soils, resulting in greater transfer of C to chemically  
389 protected pools (Fornara *et al.* 2011). There was also a relatively small and unexpected effect  
390 of CWM leaf N content, which might be explained by N rich plant material reducing the need  
391 for ‘microbial mining’, a process where soil microbes decompose SOM to acquire N (Craine,  
392 Morrow & Fierer 2007). Given that CWM leaf N is higher in improved, fertilised grasslands  
393 (De Vries *et al.* 2012), it might also reflect higher inorganic N availability in a more  
394 statistically parsimonious way than the deleted management term. Management was not  
395 retained in any of our models, and this may reflect the very broad categories used, which  
396 cover a range of fertilizer and mowing regimes, and grazing intensities. Gathering detailed  
397 and accurate data for such factors requires considerable effort and plant traits, which respond  
398 to all these factors, may act as a good proxy substitute for them.

399 Models describing the total C stocks and the intermediate fraction were extremely  
400 similar, which is unsurprising given that most soil C was in the intermediate fraction. The  
401 decline of soil C stocks at intermediate pH is likely caused by the balance of two contrasting  
402 processes: reduced decomposer activity and the accumulation of plant inputs in low pH  
403 conditions (Pietri and Brookes 2008), and greater transfer of C to the stable C fraction in more  
404 neutral and calcareous soils (Fornara *et al.* 2011). The moisture term in the total C model  
405 demonstrates that stocks peaked at soil moisture levels typical of waterlogged, or wet  
406 grasslands where soil microbial activity is low. The lack of plant trait terms in these models  
407 may reflect the fact that most older soil C has either undergone chemical and/or physical

408 transformation into more complex forms, or because current plant community composition  
409 does not reflect its origin.

410 Previous studies have shown that regression models can predict soil C variation using  
411 climate and soil texture data at very large scales and within several continents (>100,000 km<sup>2</sup>)  
412 (Burke *et al.* 1989, Paruleo *et al.* 1998, but see Evans, Burke and Lauenroth 2011). Our  
413 findings indicate that a combination of plant trait data and simple climate and soil measures,  
414 can also help to predict regional and national scale soil C stocks (1-100,000 km<sup>2</sup>) in the  
415 surface soil, in a range of C pools of varying stability. It is possible that this approach could  
416 greatly improve regional and national level predictions of surface soil C stocks compared to  
417 current land cover proxy methods (Eigenbrod *et al.* 2010). Climate data are available for  
418 many parts of the world, soil pH can be measured quickly and with little equipment, and  
419 many countries produce regular national surveys of plant community composition (e.g. Carey  
420 *et al.* 2008). Furthermore, large international trait databases now exist (Kattge *et al.* 2011) and  
421 some traits, such as leaf N, may also be predictable from remote sensing (Dahlin, Asner &  
422 Field 2013). Our approach may also prove complementary to current soil C mapping  
423 approaches, which use a combination of dynamic models such as CENTURY (Parton *et al.*  
424 1993) and RothC (Smith *et al.* 2005), direct measurements (Bellamy *et al.* 2005; Carey *et al.*  
425 2008) and proxy measures (Jones *et al.* 2005; Eigenbrod *et al.* 2010), in two ways. First, it  
426 could be used to parameterise the starting conditions for soil C pools in models; and, second it  
427 could provide more extensive and fine-scale coverage than might be possible from direct  
428 measurement, e.g. for cases in which landowners seek to map soil C.

429 The large amount of variation captured by the random effects in our models is likely  
430 to represent site differences in geology and legacies of landscape history (e.g. land use and  
431 glaciation), which may already be captured in coarse scale soil surveys. The measures here  
432 could help refine these coarse maps using local scale-information about soils, climate and

433 plant communities. Similarly, this approach could help refine existing models that use proxy  
434 measures with extensive geographic coverage (e.g. land cover and climate) (e.g. Jones *et al.*  
435 2005; Smith *et al.* 2005, [Paruolo et al. 1998](#)), by improving the characterisation of existing  
436 relationships and including trait based vegetation measures that are general, more detailed and  
437 mechanistically informative. Such an approach requires extension to a wider range of soil  
438 depths, environmental conditions and ecosystem types before it can be widely applied.  
439 Nevertheless, our results show that it has great potential, especially given the urgent need for  
440 large-scale, cost effective and accurate soil C stock characterisation. Such information is a  
441 precursor for the inclusion of soil C into C trading schemes and improved ecosystem service  
442 management.

443

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445

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453

#### 454 **Data Accessibility**

455 [Data used in this article are available in Dryad \(details to be populated once accepted\)](#)

456

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570

571

572 **Supporting information:**

573 Appendix A1 contains the following:

574 Details of soil C measurement and statistical modelling procedures

575 Table S1. The mean and range of data used in model fitting and validation

576 Table S2. Parameter combinations fitted in the statistical modelling procedure

577 Table S3-S6. Model statistics for total soil carbon, and the active, intermediate and stable  
578 fractions

579 Table S7. Model validation comparison of predicted and actual values

580 [Fig. S1. Demonstration of sampling strategy](#)

581 [Fig. S2. Comparison of soil carbon stocks predicted by the statistical models and actual stocks](#)

582 Appendix S1. Additional references for trait data sources

Variable	Total soil carbon			Active fraction (4000-250 $\mu\text{m}$ )			Intermediate fraction (50-250 $\mu\text{m}$ )			Stable fraction (0.45-50 $\mu\text{m}$ )		
	Param. Est.	AIC change ( $\Delta i$ )*	<i>P</i> value*	Param. Est.	AIC change ( $\Delta i$ )*	<i>P</i> value*	Param. Est.	AIC change ( $\Delta i$ )*	<i>P</i> value*	Param. Est.	AIC change ( $\Delta i$ )*	<i>P</i> value*
Intercept	64.35		<0.0001	12.57		<0.0001	39.21		0.0001	4.22		0.12
MAP (mm)			0.0001	-6.4e-4	14.21	0.0001						
MAP (mm) <sup>2</sup>			0.0001	5e-6	18.71	0.0009						
MAT (°C)	-10.72	14.64	0.025	-2.28	17.99	<0.0001	-6.91	10.37	0.0008			
MAT (°C) <sup>2</sup>	0.62	13.23	0.0067	0.11	8.97	<0.0001	0.40	10.81	0.0003			
Soil moisture (% dry weight)	0.035	-3.36	0.0002				0.021	2.05	0.049			
Soil moisture (% dry weight) <sup>2</sup>	-1.8e-4	-5.36	<0.0001				-1.1e-4	4.02	0.014			
MGSL (days)				0.010	4.17	0.013						
Soil pH	-5.86	18.89		-0.99	5.51	0.0086	-2.95	9.38	0.0012	-1.59	17.57	<0.0001
Soil pH <sup>2</sup>	0.52	11.64		0.077	4.3	0.012	0.26	6.69	0.0032	0.16	2.35	0.037
CWM SLA (mm <sup>2</sup> mg <sup>-1</sup> )				-0.024	9.09	0.0009						
CWM leaf N content (mg N g <sup>-1</sup> )										0.039	4.13	0.01

583 **Table 1.** Selected models for total soil carbon to 7cm depth and soil carbon fractions of a range of size classes (kg C m<sup>-2</sup>)

584 <sup>a</sup>Assessed with a likelihood ratio deletion test. This was a single d.f. test for most terms but 2 for the main effects of variables with a quadratic  
585 function. In these cases both the main effect and the quadratic tern were removed.

586 **Figure legends**

608

609 **Fig. 1.** Sampling regions within England. In each region five farms were selected and in each  
610 of these three fields were sampled, one unimproved grassland, one semi-improved and one  
611 improved. Regions are: (a) Worcester, (b) Upper Thames, (c) Somerset, (d) Devon, (e)  
612 Cotswolds, (f) High Weald, (g) South Downs, (h) Breckland, (i) Dales Meadows, (j)  
613 Yorkshire Ings, (k) Yorkshire Dales/South Lake District, (l) Lake District. In the validation  
614 region (m), Northumberland, 20 fields were sampled.

615

616 **Fig. 2.** Fitted relationships between abiotic and plant community trait variables and grassland  
617 soil carbon stocks. In all figures the other variables in the models (Table 1) were held constant  
618 at their mean in the dataset (Table S1). Relationships are between: A) MAT and pH with total  
619 soil carbon stocks. B) MAT and mean annual precipitation with carbon in the active fraction.  
620 C) Soil pH and MAT with carbon in the intermediate fraction d) soil pH and the CWM of leaf  
621 nitrogen content and carbon in the stable fraction. Stocks are for the top 7 cm of the soil.

622

623 **Fig. 3.** Changes in grassland soil carbon stocks across (A) temperature and (B) soil pH  
624 gradients. MAT is mean annual temperature. The stocks shown are the three size fractions  
625 predicted by the fitted models when all other variables are held constant at their mean in the  
626 dataset (Table S1).

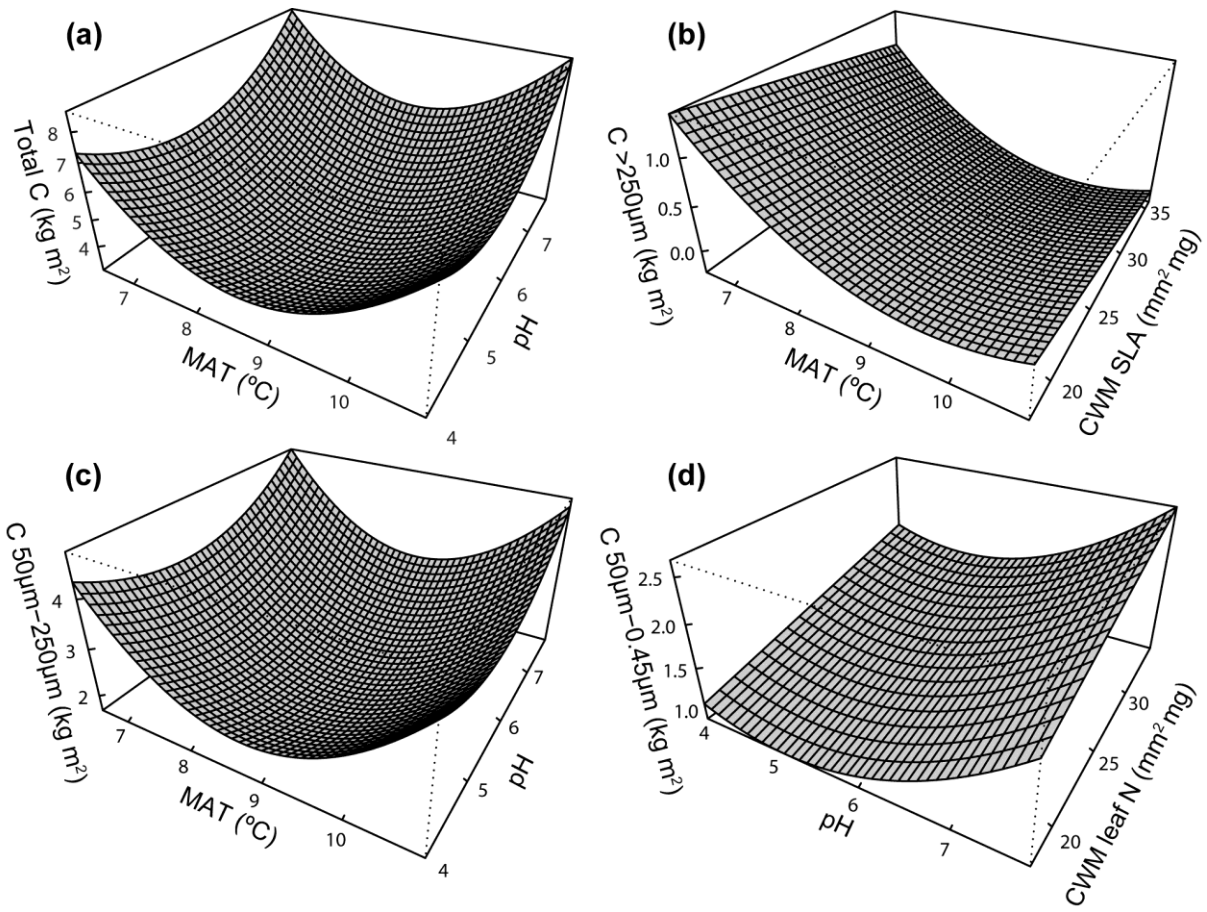
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631 Fig. 1



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633 Fig. 2.

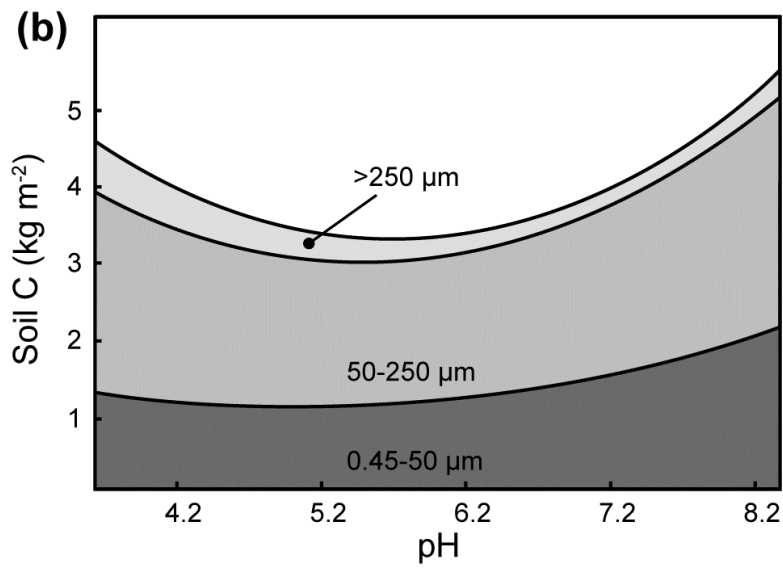
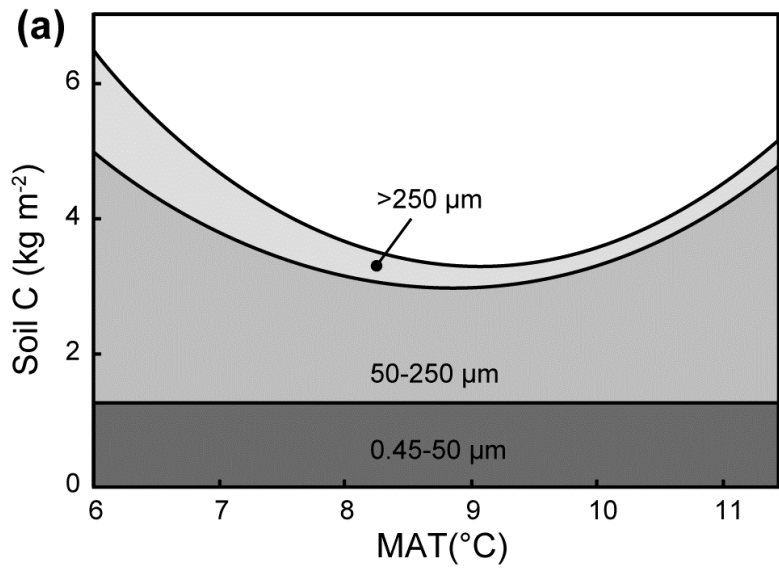
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640 **Fig. 3.**

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