1 **OPTIMISING CARBON STORAGE WITHIN A SPATIALLY**

2 **HETEROGENEOUS UPLAND GRASSLAND THROUGH SHEEP**

3 **GRAZING MANAGEMENT**

4

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ABSTRACT

Livestock grazing is known to influence carbon (C) storage in vegetation and soil. Yet, for grazing management to be used to optimise C storage, large scale investigations that take into account the typically heterogeneous distribution of grazers and C across the landscape are required. In a landscape-scale grazing experiment in the Scottish uplands, we quantified C stored in swards dominated by the widespread tussock-forming grass species *Molinia caerulea*. The impact of three sheep stocking treatments ('commercial' 2.7 ewes ha^{-1} yr^{-1}, 'low' 0.9 ewes ha^{-1} yr^{-1} and no livestock) on plant C stocks was determined at three spatial scales; tussock, sward and landscape, and these data were used to predict long-term changes in soil organic carbon (SOC). We found that tussocks were particularly dense C stores (i.e. high C mass per unit area) and that grazing reduced their abundance and thus influenced C stocks held in *M. caerulea* swards across the landscape; C stocks were 3.83, 5.01 and 6.85 Mg C ha^{-1} under commercial sheep grazing, low sheep grazing and no grazing, respectively. Measured vegetation C in the three grazing treatments provided annual C inputs to RothC, an organic matter turnover model, to predict changes in SOC over 100 years. RothC predicted SOC to decline under commercial sheep stocking and increase under low sheep grazing and no grazing. Our findings suggest that no sheep and low-intensity sheep grazing are better upland management practices for enhancing plant and soil C sequestration than commercial sheep grazing. This is evaluated in the context of other upland management objectives.

INTRODUCTION

Appropriate management of vegetation and soil is important for the sequestration and retention of terrestrial carbon (C) (Guo and Gifford 2002; Dawson and Smith 2007; Ostle and others 2009). Livestock grazing has been identified as a potential management tool to influence ecosystem C storage (Conant and others 2001; Soussana and others 2004; Tanentzap and Coomes 2012), yet the mechanisms involved remain uncertain particularly in wet upland areas (Milchunas and Lauenroth 1993; Piñeiro and others 2010). One of the factors that currently hinders our understanding of livestock impacts on C sequestration is the reliance on studies that compare presence with absence of large herbivores using small-scale exclosures. For example, heavy sheep grazing of an alpine meadow was found to increase soil C storage relative to ungrazed controls by reducing net ecosystem CO_2 losses (Welker and others 2004). By contrast, light sheep grazing of a steppe plateau (Reeder and others 2004) and a peatland (Ward and others 2007) were found to have little impact on soil C stocks, despite significant changes in plant species composition and reductions in vegetation biomass. Although such studies are valuable, our understanding would be improved by using gradients of grazing pressure in single landscapes to inform optimal carbon management (Martinsen and others 2011; Van der Wal and others 2011). A lack of data on the effects of varying grazing intensities on C dynamics in upland plant communities, together with little consideration of spatial heterogeneity, impairs predictive C modelling used to guide future land management decisions (Worrall and others 2009). Equally, the impact of such grazing pressures should be studied at the landscape-scale. Thus, a 'realistic' approach would be to conduct investigations within an extensively grazed landscape, where the grazing pressure is influenced by foraging behaviour (Grant and Maxwell 1988). From a herbivore perspective, foraging is dependent on a range of factors, including plant quantity and quality (McNaughton and others 1983; Frank and others 1998), resulting in spatially heterogeneous grazing pressure. From a plant perspective, species composition and biomass allocation are themselves spatially heterogeneous, thus influencing the distribution of C in a landscape (Marriot and others 1997;

82   Garnett and others 2001; Frogbrook and others 2009). Therefore, to calibrate grazing as a C

83   management tool, we must consider the relationship between grazing and spatially

84   heterogeneous C stores.

85

86   Livestock grazing is a well-known driver of heterogeneity; altering plant species composition,

87   canopy structure and biomass distribution (Bakker and others 1984; Berg and others 1997;

88   Derner and others 1997; Adler and others 2001). Despite the fundamental role of plant C input

89   in soil C accumulation, little attention has been paid to the spatial heterogeneity of vegetation

90   C stores found in many grazed systems. In grasslands, tufts or tussocks formed by many grass

91   species are potentially dense C stores, containing a high C content per unit ground area. The

92   number per unit area and size of these tussocks may be influenced by grazing. For example,

93   on a steppe plateau, grazing has been shown to reduce litter accumulation and subsequently

94   soil particulate C under tussocks (Milchunas and others 1989; Burke and others 1999). In the

95   steppe plateau in the previous study, the low organic content of the soil facilitates the

96   detection of grazing influencing soil C accumulation, whereas in temperate organic soils such

97   effects may be more subtle and difficult to detect (Marriot and others 1997; Ward and others

98   2007; Medina- Roldán and others 2012). However, the effect of grazing on tussocks and plant

99   C storage can often be detected and quantified, with findings from such studies suggesting that

100   grazing could be used to manage above-ground C stocks. In a study of temperate upland

101   grasslands, high sheep grazing intensities reduced C stocks of the tussock foliage and roots;

102   however, this was offset by increased C stocks in the inter-tussock foliage and roots (Stewart

103   and Metherell 1999). The latter study highlights the importance of accounting for the scale of

104   observation when determining the influence of grazing on spatial heterogeneity (Augustine

105   and Frank 2001; Gillson 2004; Bråthen and others 2007).

106

107   The UK uplands (areas generally > 200 m a.s.l. where farming becomes less profitable due to

108   the limited productivity of the land; Orr and others 2008; Reed and others 2009) are

109   extensively grazed by livestock or deer. These systems typically have spatially heterogeneous

110   vegetation and organic and peaty soils, which are estimated to hold almost 30 % of the UK

111   national stock of soil C in the top 15 cm of the profile (Carey and others 2008). Therefore it is

112   vital that these extensively grazed uplands are managed appropriately to avoid the loss of

113   stored C from the soil and vegetation.

114

115   Approximately 10 % of the UK uplands are covered by *Molinia caerulea* (L.) Moench. (purple

116   moor grass) dominated vegetation (Bunce and Barr 1988). Given the large national extent of

117   *M. caerulea*-dominated vegetation (c. 6000 km^2), it should be represented in C budget

118   modelling for the uplands, particularly in relation to land-use change. *M. caerulea,* a

119   deciduous grass, forms dense tussocks consisting of compact aggregations of shoot-bases. In

120   between these tall growing, dense tussocks the 'inter-tussock' plant communities are short and

121   usually species poor (Rodwell 1991). The above-ground and below-ground productivity of *M.*

122   *caerulea* exceeds that of most other common upland plant species, including the widespread

123   *Calluna vulgaris* (Aerts 1989; Aerts and others 1992); thus *M. caerulea* is an ideal

124   management target for C sequestration (Gogo and others 2010) and can be managed using

125   livestock grazing. Light artificial defoliation has been shown to reduce shoot-base and root

126   biomass of *M. caerulea* (Latusek 1983; Thornton 1991) and *M. caerulea* cover has been

127   shown to reduce under extensive cattle grazing (Grant and others 1996). Sheep only consume

128   *M. caerulea* in spring before the new leaves become tough and unpalatable (Hunter 1962;

129   Taylor and others 2001) and cover was unaffected by sheep grazing from mid-late summer

130   onward (Fraser and others 2011). There has been little research undertaken with regards to

131   how year-round sheep grazing affects the abundance of *M. caerulea* and the structure of its

132   sward, despite the prevalence of both sheep and *M. caerulea* in extensively-grazed landscapes

133   (SAC 2008). Addressing this question is integral for gaining a predictive understanding of

134   whether grazing management can be used to optimise C storage in upland grasslands

135   dominated by *M. caerulea*.

136

137   Most grazing experiments are too short to provide a definitive understanding of the soil C

138   storage potential (Tanentzap and Coomes 2012). This problem of limited experimental

139   duration can be addressed by the use of soil organic matter (SOM) turnover models. One such

140   model, RothC, divides SOM into a number of conceptual pools of C, each of which is defined

141   by its lability. Soil C input comes from plant material, which is divided into decomposable

142   (DPM) and resistant (RPM) plant material, with their ratio depending on the origin of the plant

143   material. Plant material as DPM and RPM becomes incorporated into SOC and decomposes at

144   different rates into microbial biomass (BIO) and humus (HUM), thereby releasing CO_2

145   (Coleman and Jenkinson 1999). BIO and HUM then decompose at different rates producing

146   more CO_2, BIO and HUM. The partitioning of the products of decomposition depends on the

147   soil clay content, whereas decomposition rates are modified by temperature and soil moisture

148   and whether vegetation cover is present or absent. The model also includes a pool of inert soil

149   organic matter (IOM). The RothC model has been applied to numerous sites worldwide under

150   various types of agricultural management (e.g. Smith and others 1997; Zimmermann and

151   others 2007). Following its thorough validation in upland grasslands and pastures, it has been

152   effectively used as a predictive tool for these systems (Guo and others 2007; Liu and others

153   2011).

154

155   We used a long-term, fully-replicated grazing experiment, established at a landscape-scale

156   (each plot is 3.3 ha) in central Scotland, to address the following three aims: (1) to determine

157   the effect of different sheep stocking densities on C stocks in *M. caerulea* swards; (2) to

158   describe the C stored in this grazed vegetation at three spatial scales (tussock, sward and

159   landscape), thereby accounting for spatial heterogeneity at each scale; and (3) to use resulting

160   data as vegetation C inputs to the RothC model to predict the long-term impact of different

161   sheep stocking densities on soil organic C (SOC) accumulation. Using this unique approach of

162   accounting for heterogeneous vegetation C coupled with model simulations of soil C, we aim

163   to identify an optimal grazing density for long-term C storage in an upland landscape that has

164   spatially heterogeneous vegetation, soil and grazing pressure.

165

166   **MATERIALS AND METHODS**

167   STUDY AREA AND EXPERIMENTAL SETUP

168   The study was carried out on the Glen Finglas estate (4039 ha) in central Scotland (56°16´N

169   4°24´W), an upland area (200 - 500 m a.s.l.) receiving a mean 1344 mm of annual rainfall and

170   with mean January and July temperatures of 2.6 ºC and 14.3 °C, respectively (1982-2000

171   average from Loch Venachar at ca. 5 km distance; UK Meteorological Office 2012). Glen

172   Finglas has organic soils, including blanket peats, peaty gleys and humus iron podzols with 60

173   % of the area having soil with a C concentration greater than 40% to a depth of 15 cm (Soil

174   Survey of Scotland 1984; SIFSS, 2013). The vegetation is a fine-grained mosaic of the

175   following dominant types, as classified by the British National Vegetation Classification

176   (NVC) communities (Rodwell 1991, 1992): M23 (*Juncus effusus-acutiflorus–Galium palustre*

177   rush-pasture), M25 (*Molinia caerulea–Potentilla erecta* mire), U4 (*Festuca ovina–Agrostis*

178   *capillaris–Galium saxatile* grassland) and U5 (*Nardus stricta–G. saxatile* grassland). The

179   defining characteristic of the vegetation at the study site is the presence of tussocks, which

180   primarily consist of *M. caerulea.* Swards are grazed by black-faced sheep and Luing cattle

181   with no burning management of the grassland vegetation, typical of many upland areas of

182   Scotland. Before the study was initiated, there was a low grazing pressure by black-faced

183   sheep (0.7 ewes ha^{-1}) across the estate.

184

185   In 2003, a landscape-scale grazing experiment was established across three sites, spaced

186   approximately 4.1 km apart within Glen Finglas, each containing two replicate blocks. Each

187   block is composed of four 3.3 ha fenced plots containing different grazing treatments,

188   randomly assigned to: (a) 'Commercial' stocking, 9 sheep per plot reflecting a typical

189   commercial stocking rate of 2.7 ewes ha^{-1} for nutrient-poor rough upland grassland

190 (Thompson and others 1995); (b) 'Low' stocking, 3 sheep per plot or one-third the commercial

191 rate at 0.9 ewes ha^{-1}, similar to stocking rates prior to the experiment; and (c) no livestock.

192 Sheep remained in the plots throughout the year and were only removed for normal farm

193 operations and during periods of severe weather.

194

195 TUSSOCK-SCALE CARBON SAMPLING

196 In November 2009, *M. caerulea* tussocks and inter-tussocks were sampled in the two different

197 sheep grazing treatments and the ungrazed treatment, replicated across four of the six blocks;

198 one site (two blocks) was not sampled due to the near absence of *M. caerulea* in some plots.

199 Within plots, sampling locations were selected at random from long-term vegetation survey

200 points (Dennis and others 2004) that were defined under the British National Vegetation

201 Classification (NVC) as M25 *Molinia caerulea – Potentilla erecta* mire (Rodwell 1991).

202

203 The distribution of C in plant parts was determined for one tussock and one inter-tussock area

204 (< 2 m apart) per plot (24 samples, namely: 3 grazing treatments × 4 blocks × tussock/ inter-

205 tussock). A 20 cm × 20 cm turf to a soil depth of 5 cm was collected to quantify C within

206 standing dead litter, shoot-bases and shallow roots (0 – 5 cm). Deep roots (5 - 15 cm) were

207 collected directly below the turf using a 4.2 cm diameter bevel-ended corer. All turfs and root

208 cores were stored at 4 °C prior to sorting.

209

210 Standing dead grass litter (predominately *M. caerulea*), hereafter termed 'shoots', were sorted

211 from each turf. Shoot-bases and shallow roots were sub-sampled from a 5 cm × 5 cm area of

212 the turf. Roots were recovered using a 0.5 mm sieve through repeated cycles of washing,

213 sedimentation and decanting. All above- and below-ground biomass was oven-dried for 48 hrs

214 at 80 ºC and weighed (± 0.01 g). Plant component samples were homogenized by stainless

215 steel ball-milling (F.Kurt Retsch GMbH & Co. KG, MM200, Germany; Smith *et al*. 2013a),

216 to generate a standard 5 mg sub-sample for elemental C analysis (Carlo-Erba NA 1500 Series

217 2, USA).

218

219 SWARD-SCALE VEGETATION SAMPLING

220 To determine the effect of grazing on the structure of the *M. caerulea* sward, plots of all three

221 sheep grazing treatments (ungrazed, low and commercial) were subdivided into four equal

222 parts and a 2 m × 10 m quadrat was randomly laid out within each part, at least 3 m away from

223 any fence, following random cardinal directions. Stream trenches, rocky terrain and areas

224 dominated by *J. acutiflorus/effusus* and *Pteridium aquilinum* were avoided. Sampling was

225 undertaken in April 2007, before new young shoots broke through the *M. caerulea* leaf litter.

226

227 Within all 48 quadrats (3 grazing treatments × 4 blocks × 4 replicate quadrats) records were

228 made of each individual tussock. These included a record of other plant species found in each

229 *M. caerulea* tussock and two measures of tussock diameter, one at the widest point and the

230 other perpendicular to it. The surface area of each tussock was calculated using the equation

231 for the area of an ellipse: πab (a = ½ largest diameter and b = ½ perpendicular diameter),

232 hereafter termed 'tussock size'. Total tussock area was the sum of all tussock areas within a

233 quadrat, and inter-tussock area was the remaining quadrat area. A mean tussock and inter-

234 tussock area was obtained for each plot. Carbon held in the *M. caerulea* sward was then

235 determined by multiplying the mean tussock and inter-tussock area by the quantities of C in

236 the tussock and inter-tussocks, respectively. These plot-specific measures of *M. caerulea*

237 sward C were then averaged for each sheep grazing treatment (ungrazed, low and

238 commercial).

239

240 LANDSCAPE-SCALE COVER OF M. CAERULEA-DOMINATED COMMUNITIES

241 The total plot-area dominated by *M. caerulea* was derived from long-term point survey data

242 (Dennis and others 2004). Within each plot 81 points, ca. 20 m apart, were described using the

243   National Vegetation Classification (NVC; Rodwell 1992) in September 2009. Points identified

244   as representing M25, *Molinia caerulea – Potentilla erecta* mire, were used to map the *M.*

245   *caerulea*-dominated area in a Geographic Information Systems (GIS) package (ESRI®

246   ArcGIS^TM 9.3). *M. caerulea*-dominated points were transformed into an estimated area for

247   each plot using inverse-distance interpolation. The quantity of C held in *M. caerulea* sward for

248   the relevant plot was then combined with the estimated *M. caerulea*-dominated area within

249   each plot to generate a landscape estimation of C stocks under the different grazing treatments.

250

251   STATISTICAL ANALYSIS

252   Measured parameters from 2092 tussocks dominated by *M. caerulea* were used in the

253   statistical analysis. All statistical analysis was conducted in R using the lme4 package (version

254   2.10.1, R Development Core Team 2009; Bates and Maechler 2010). Differences in total

255   tussock area, number of tussocks and average tussock size were explored for all stocking

256   treatments (ungrazed, low, and commercial) using a linear mixed-effect model with residual

257   maximum likelihood estimations (REML). The number of tussocks was analysed using a

258   Poisson error structure, and average tussock size was $\log_{10}$ transformed to achieve a normal

259   distribution. The random structure was defined as plot nested within block nested within site.

260   To justify the inclusion of grazing treatments in the model we used a likelihood ratio deletion

261   test (LRT), comparing a model with and without (null) grazing treatments (Pinheiro and Bates

262   2000). Statistical significance of the different grazing treatments was obtained through

263   formulating contrast statements between each grazing treatment within the same model

264   structure (see Hothorn and others 2008; Cichini and others 2011). Untransformed *M. caerulea*

265   sward cover as a percentage of each plot was analysed using a similar linear mixed-effect

266   model structure without plot in the random structure.

267

269   RothC (Coleman and Jenkinson 1999) was used to calculate soil organic C (SOC) dynamics.

270   To achieve this RothC was used in three stages; first, to establish the historic SOC for the

271   original, forested land (pre 1860s) before the site was transformed to grassland; second, to

272   estimate SOC at the time of tussock carbon measurements in 2009, after a century and a half

273   of light grazing; and third, to predict the long-term (100 years) impact of the different

274   experimental grazing treatments. To estimate SOC under the historic forest vegetation cover

275   at Glen Finglas, RothC was run to equilibrium for a mixed forest, with an annual C input

276   (from plant material) of 2.95 Mg C ha^{-1} and a DPM/RPM (Decomposable Plant

277   Material/Resistant Plant Material) ratio of 0.25. These values were taken from Coleman and

278   Jenkinson (1999) and are commonly used for the equilibration of models starting with

279   deciduous forest cover (Smith and others 1997). Glen Finglas has been grazed by livestock

280   since the 1860s (Sanderson 1998), so to establish SOC content in different soil pools at the

281   point of measurement (2009) the model was run for 149 years using plant inputs from the low

282   sheep stocking treatment, assuming traditional management in the uplands. The annual C

283   input was an average of the sward-scale (including tussock and inter-tussock) *M. caerulea* C

284   stock of 7.87 Mg C ha^{-1} with a measured DPM/RPM ratio of 1.5; this value is similar to that

285   for improved grasslands in Coleman and Jenkinson (1999). The amount of RPM, the lignin

286   and lignin-like plant material, used to calculate the previous DPM/RPM ratio, was determined

287   using a sulphuric-acid digestion method (Woodin and others 2009) and was averaged for both

288   roots and above-ground (shoot-base and leaf) tissue from the low intensity sheep grazing

289   treatment. The DPM was calculated as (Total Dry Material − RPM). Inert Organic Matter

290   (IOM), the biologically inert SOC pool, was set at zero due to a lack of radiocarbon data

291   essential to quantify this pool. Changes in IOM estimates are likely to result in only small

292   errors in predicting SOC (Fallon and others 2000). The SOC of experimental plots was

293   measured in 2009 (16 soil cores, 4.2 cm diameter, 15 cm deep; adjusting bulk density for stone

294   content > 1 mm and determining C via elemental analysis) to validate the model estimate. An

295   overall average SOC, across all grazing treatments, was used for validation as the treatments

296   had not been established long enough to have generated detectable differences in SOC

297   between them.

298

299   RothC was then run from 2009 for 100 years following three scenarios, commercial sheep

300   stocking, low sheep stocking, and no livestock, using the average tussock and inter-tussock C

301   stock measured in each grazing treatment as the annual inputs of plant residues, again with a

302   DPM/RPM ratio of 1.5. Predicted confidence intervals (CI) were generated using the upper

303   and lower 95% CI of plant C stocks as inputs for each grazing treatment. The meteorological

304   data used to drive RothC to equilibrium were precipitation data from Glen Finglas 1982 –

305   2000 (UK Meteorological Office 2012) and average temperature data from two Scottish

306   upland sites Glensaugh and Invercauld 2010 -2011 (Artz and others unpublished). This

307   alternative source of upland temperature data was used due to a lack of annual measurements

308   for Glen Finglas and was assumed not to influence predicted treatment effects from RothC. As

309   a multipool model, RothC is relatively insensitive to differences in temperature compared to

310   other single C pool models (Jones and others 2005).

311

312   **RESULTS**

313   TUSSOCK AND INTER-TUSSOCK SCALE PLANT C DISTRIBUTION

314   Total C stored in *M. caerulea* tussocks was reduced by commercial sheep stocking (Figure 1),

315   while values from low sheep stocking and ungrazed plots were similar. Treatment effects on

316   plant C pools were due to the influence of grazing on vegetation biomass: the C concentrations

317   in *M. caerulea* shoots, shoot-bases and roots were unaffected by grazing treatment. *M.*

318   *caerulea* shoot-bases comprised the largest tussock C pool, which was approximately 50 % or

319   11 Mg C ha^{-1}, smaller under commercial sheep grazing compared to low and ungrazed

320   treatments. There was no effect of grazing on the C pools of the shallow or deep roots under

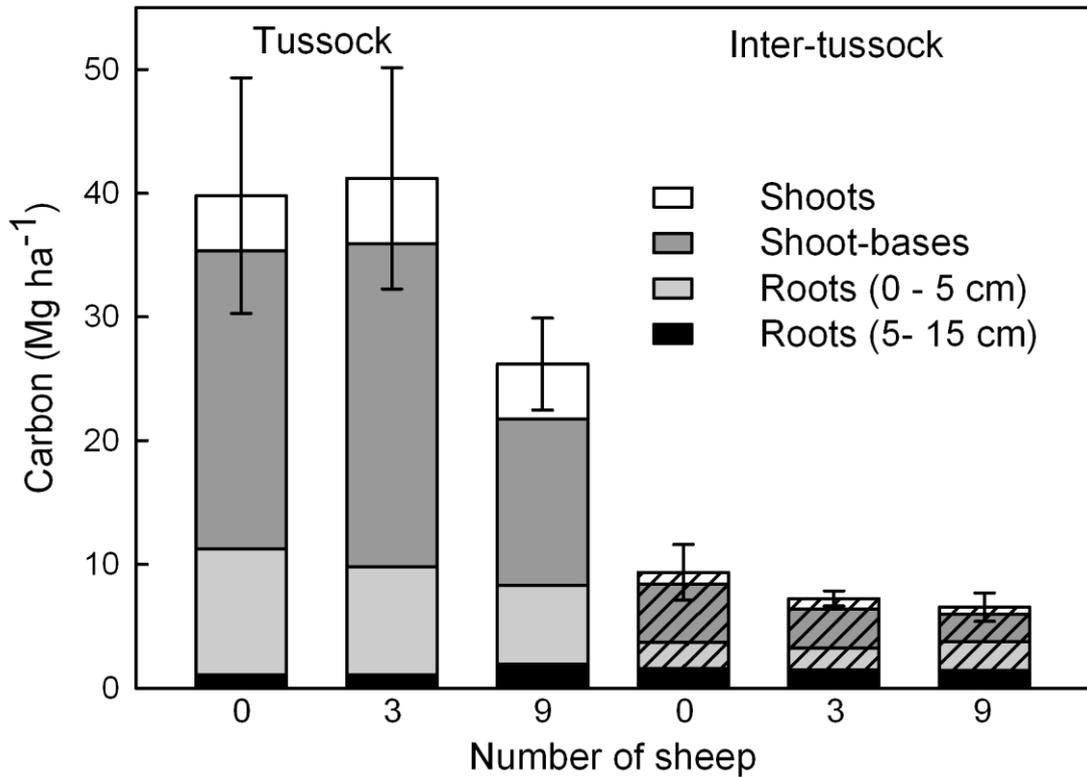321   tussocks. Quantities of C in inter-tussock vegetation were 81.0 ± 8.7 %

Figure 1 *Molinia caerulea* carbon pools within tussock (solid bars) and inter-tussock (hashed-bars) in three sheep grazing treatments (ewes plot^{-1}). Sheep grazing treatments of 0, 3 and 9 ewes plot^{-1} are the equivalent of 0, 0.9 and 2.7 ewes ha^{-1}, respectively. Error bars are only for the total, ± 1 SE, *n* = 4 per treatment.

322 (mean ± 1 SD) less than in tussock vegetation across all grazing treatments, but the influence

323 of grazing on plant C pools followed a similar pattern to tussocks (Figure 1).

324

325 SWARD SCALE TUSSOCK AND INTER-TUSSOCK AREA AND C STOCKS

326 Overall livestock grazing treatments significantly explained variation in total tussock area,

327 ($\chi 2(2)$=6.419, p=0.04), the number of tussocks ($\chi 2(2)$=12.205, p=0.002), but not average

328 tussock size ($\chi 2(2)$=0.2878, p=0.866) when compared to a null model without treatments.

329 Within the *M. caerulea* sward, the total area of tussocks under commercial sheep stocking

330 densities was significantly lower (z_{36} = 2.54, p = 0.030), covering 30 % less area than in

331 ungrazed plots (Figure 2). Low sheep stocking reduced total tussock area in comparison to the

332 ungrazed treatment, but not significantly so (z_{36} = 1.61, p = 0.242), due to large variability in

333 total tussock area within plots.

334

335 The significantly lower tussock area in grassland subject to commercial grazing was due

336 mainly to the low number of tussocks rather than these being smaller in size. The number of

337 tussocks was significantly lower only under the commercial sheep grazing intensity compared

338 to other treatments; average densities were 2.0 ± 0.46   tussocks per m^2 (mean ± 1 SD) under

339 high grazing, compared to 2.5 ± 0.49 tussocks per m^2 under low (z_{36} = 3.22, p = 0.004) and

340 2.7 ± 0.42 tussocks per m^2 under ungrazed (z_{36} = 4.41, p = <0.001) treatments. The size of

341 established tussocks varied greatly, averaging 0.085 ± 0.069 m^2 (mean ± 1 SD) across all

342 treatments, and was not significantly influenced by any grazing treatment, even under

343 commercial sheep grazing compared to low (z_{36} = 0.06, p = 0.998) and ungrazed (z_{36} = 0.49, p
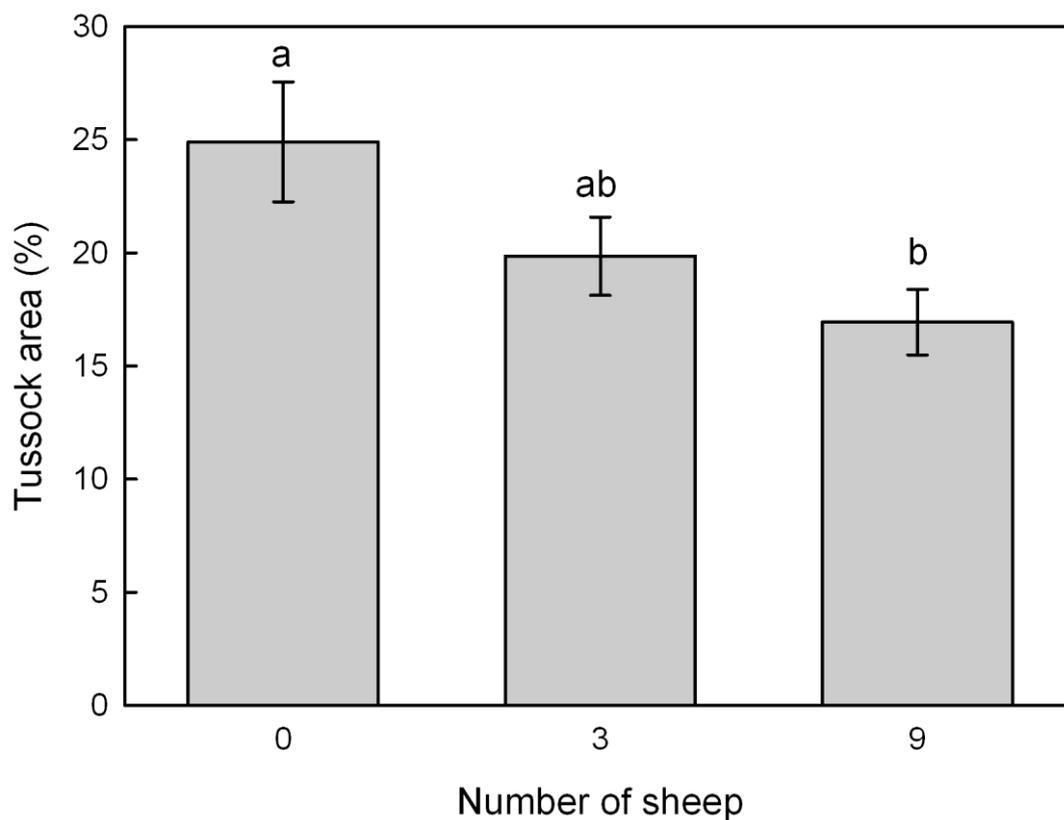
344 = 0.874) treatments.

Figure 2 Total tussock area within 2 m × 10 m transects in three sheep grazing treatments (ewes plot^{-1}). Sheep grazing treatments of 0, 3 and 9 ewes plot^{-1} are the equivalent of 0, 0.9 and 2.7 ewes ha^{-1}, respectively. Different letters above bars represent a significance difference (P<0.05), derived from contrasts between each grazing treatment within a linear mixed model. Bars are means ± 1 SE, n = 4 per treatment.

345   At the sward scale, the C stocks of *M. caerulea* tussocks decreased with increased sheep

346   stocking densities (Figure 3), due to a smaller tussock area and associated dense vegetation C

347   pool. Under commercial sheep stocking, the contribution of tussocks and inter-tussocks to

348   total vegetation C was equal. Average vegetation C, including tussocks and inter-tussocks,

349   was 3.50 ($\pm$ 0.46) Mg C ha^{-1} ($\pm$ 1 SE) higher in ungrazed swards than in swards subject to

350   commercial sheep grazing. After 7 years without grazing, *M. caerulea* swards have the

351   potential to accumulate 38 % more C than a commercially grazed sward and 27 % more C

352   than a sward under low sheep stocking density. Prior to the establishment of this experiment

353   the land was stocked at low sheep density; increasing to commercial sheep stocking would

354   have resulted in an estimated net loss of 2.16 ($\pm$ 0.96) Mg C ha^{-1} ($\pm$ 1 SE) from the *M.*

355   *caerulea* sward over 7 years.

356

357   LANDSCAPE-SCALE C STOCKS

358   In this experiment the area covered by *M. caerulea* sward at the landscape-scale did not differ

359   under commercial sheep grazing compared to low-intensity sheep grazing (z_6 = 0.32, p =

360   0.946) or no grazing (z_6 = 1.36, p = 0.359) treatments. However, there was inherent variation

361   in its abundance between plots (ranging between 34.1 $-$ 88.7 % cover; Supplementary

362   information Table S1). Scaling the *M. caerulea* sward C by the actual cover of *M. caerulea*

363   sward within each plot, C stocks were 3.83, 5.01 and 6.85 Mg C ha^{-1} for commercial sheep

364   grazing, low sheep grazing and no grazing, respectively. The mean percentage reduction in the

365   C stock of *M. caerulea* under commercial sheep grazing compared to no grazing was similar

366   when accounting for the actual *M. caerulea* sward cover at the whole landscape-scale (46 $\pm$ 16

367   % $\pm$ 1 SD) as at the sward scale as described above (38 $\pm$ 16 %).
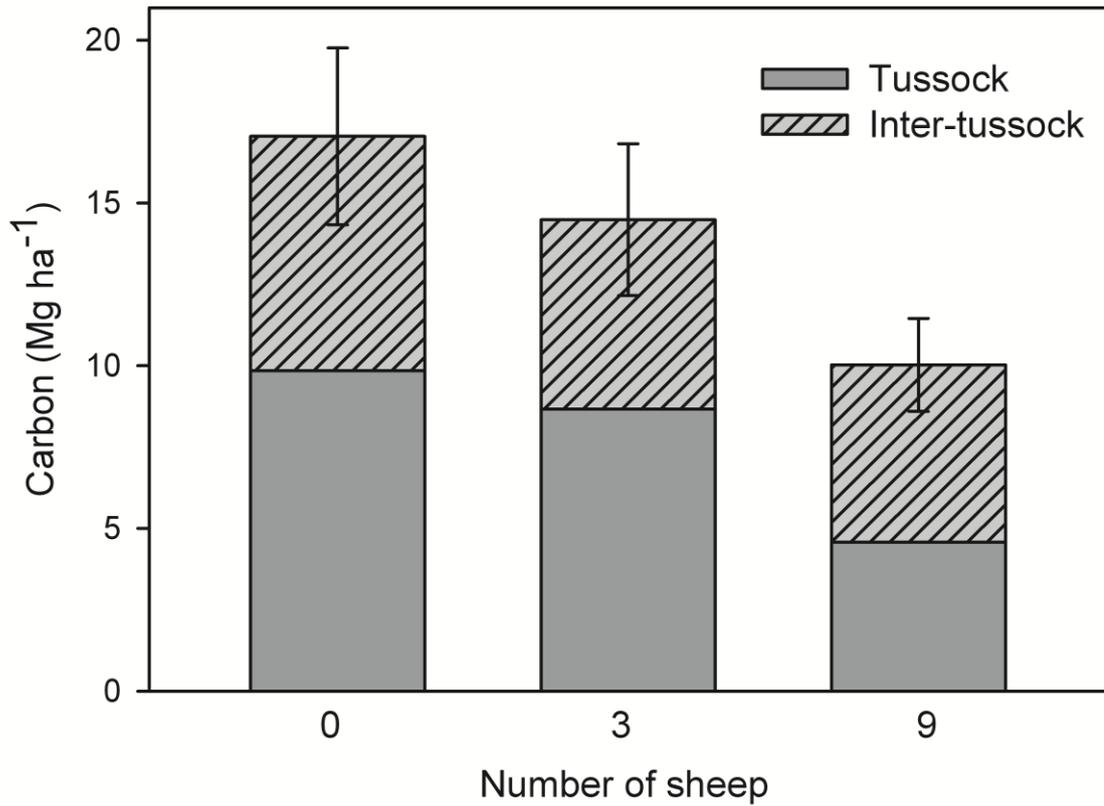
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Figure 3 Total carbon content of *Molinia caerulea,* tussocks (dark grey) and inter-tussock (hashed light grey) in three sheep grazing treatments (ewes plot[-1]) at the sward scale. Sheep Sheep grazing treatments of 0, 3 and 9 ewes plot[-1] are the equivalent of 0, 0.9 and 2.7 ewes ha^{-1}, respectively. Carbon estimates have been adjusted by tussock area in each grazing treatment. Bars are means $\pm$ 1 SE, $n = 4$ per treatment.

373 The RothC estimate of SOC in 2009 (114.3 Mg C ha^{-1}), based on mixed forest equilibrium

374 followed by a century and a half of low sheep stocking, were within the standard error of SOC

375 measured in 2009 (Figure 4, year 0). Following this accurate prediction of soil C stocks after

376 150 years of low-intensity sheep grazing and using measured *M. caerulea* inputs, the model

377 was run forward for a further 100 years under the different grazing scenarios. In the absence of

378 grazing, the system was predicted to accumulate 14.36 Mg C ha^{-1} of SOC, whereas

379 commercial sheep grazing was predicted to result in a SOC loss of 23.11 Mg C ha^{-1} (Figure 4).

380 Maintenance of low sheep grazing management resulted in accrual of 13.62 Mg C ha^{-1} over

381 100 years, this amount being similar to lower estimates of SOC accrual with no grazing. Thus,

382 commercial sheep grazing was the only grazing treatment predicted to reduce SOC. Within the

383 model, changes in the Humified Organic Matter (HUM) pool had the largest influence on total

384 SOC (Figure 5). Predicted HUM in the ungrazed treatment was 25.34 Mg C ha^{-1}, or 23 %,

385 higher than under commercial stocking densities, but only 9.71 Mg C ha^{-1}, or 10 %, higher

386 than under low sheep grazing. Resistant Plant Material (RPM) and Decomposable Plant

387 Material (DPM) are plant inputs into SOC, but also become part of SOC. RPM was a smaller

388 SOC pool than HUM, comprising on average 19 % compared to 79 % of the total SOC across

389 all grazing treatments. However, RPM showed a larger percentage difference between grazing

390 treatments than HUM after 100 years; predicted RPM C pools in the ungrazed treatment were

391 38 % greater than commercial sheep stocking and 15 % greater than low sheep stocking

392 scenarios. The combined predicted DPM and Microbial Biomass (BIO) pools only comprised

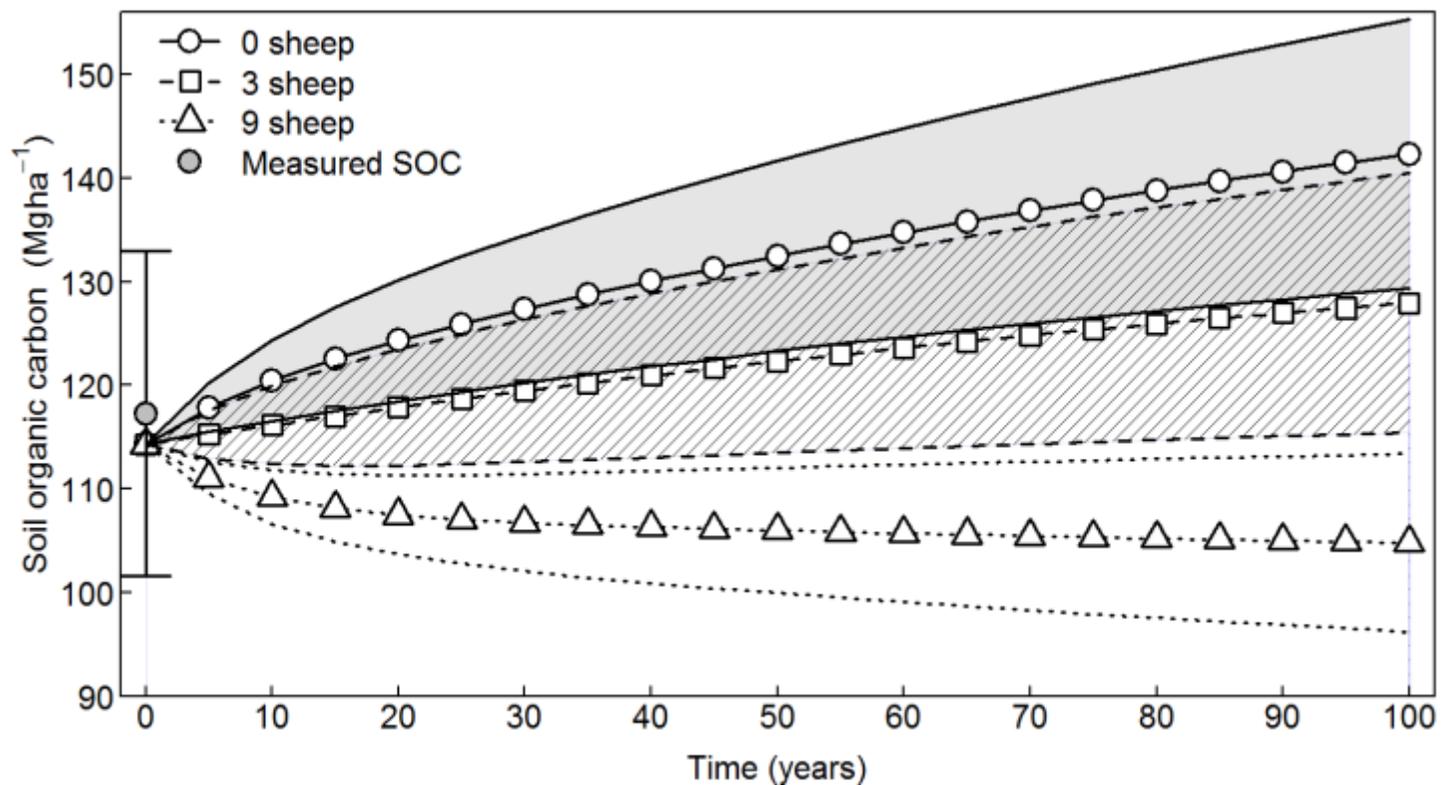393 an average of 2 % of the total SOC stocks across all treatments.

Figure 4 RothC modelled changes in SOC (to a depth 15 cm) in three grazing treatments (ewes plot[-1]). Sheep grazing treatments of 0, 3 and 9 ewes plot[-1] are the equivalent of 0, 0.9 and 2.7 ewes ha^{-1}, respectively. The model input was from derived from mean vegetation C stocks in the three grazing treatments ± 95% CI. The range of 95% CI for each grazing treatment is white for commercial sheep-grazing, hashed-bars for low-intensity sheep-grazing and light-grey shading for no livestock. Mean SOC measured in 2009 (year 0) is shown by a grey filled circle with error bars ±1 SE, $n = 16$.
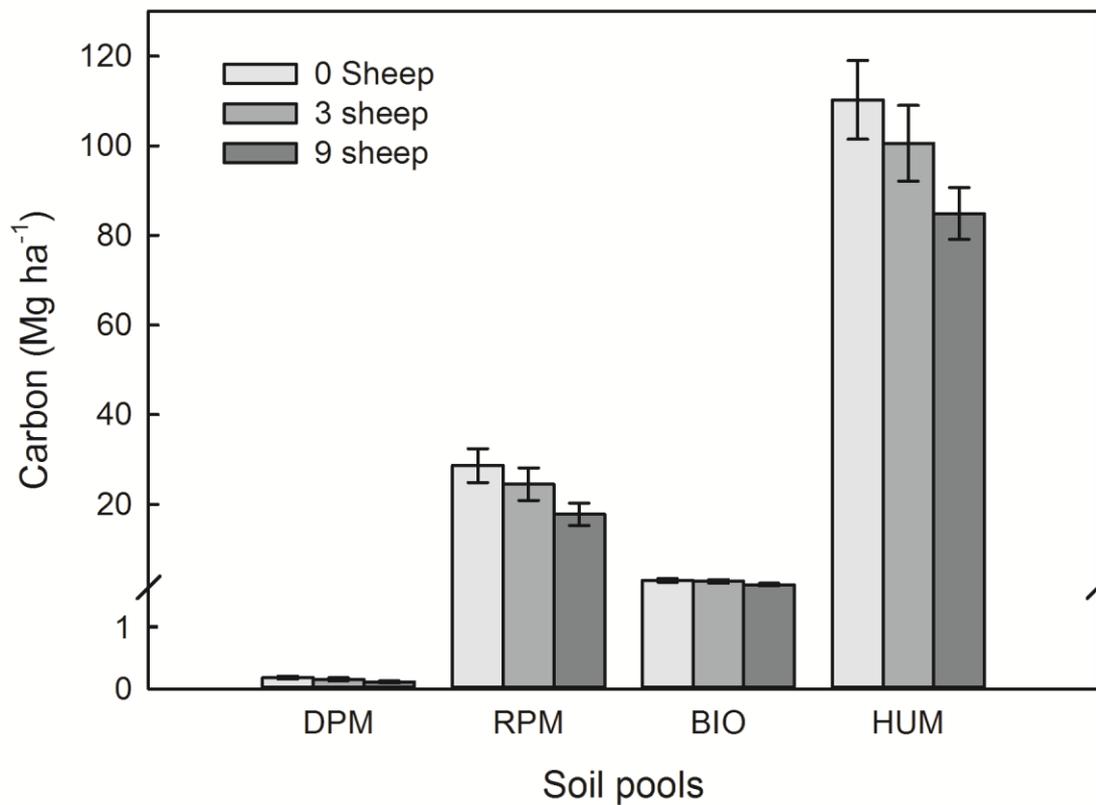
Figure 5 RothC modelled SOC pools after 100 years in three sheep grazing treatments (ewes plot[-1]). Sheep grazing treatments of 0, 3 and 9 ewes plot[-1] are the equivalent of 0, 0.9 and 2.7 ewes ha^{-1}, respectively. Modelled RothC SOC pools include: Decomposable Plant Material (DPM), Resistant Plant Material (RPM), Microbial Biomass (BIO), Humified Plant Matter (HUM) and Inert Organic Matter (IOM) not shown. A break in the y-axis at 1.5 Mg C ha^{-1} has been used to make DPM pools visible. The model input was derived from mean vegetation C stocks in the three grazing treatments ± 95% CI.

DISCUSSION

Our study demonstrated the influence of livestock grazing on plant C storage and, by taking into account the spatial heterogeneity of the vegetation, enabled both spatial and temporal scaling of our findings. The distribution of C in upland grasslands is spatially heterogeneous and assessing the impact of livestock on plant C stocks requires sampling that accounts for this. Our approach identified potentially dense C stores in the form of *M. careulea* tussocks, similar to grass tufts and tussocks in other grazed grassland systems (Milchunas and others 1989; Burke and others 1999; Stewart and Metherell 1999). Moreover, our study shows that the influence of livestock on the abundance of these structures has important implications for potential SOC accumulation and C management. In this system, the complete removal of livestock resulted in the largest C accrual in *M. careulea* swards, yet this was closely followed by C accrual under low-level sheep grazing. In the longer term, SOC was predicted to accumulate through the continued input of *M. careulea* C under no livestock and low-level sheep grazing, while commercial sheep grazing was predicted to result in a mean loss of SOC over 100 years.

EFFECT OF GRAZING ON SPATIALLY HETEROGENEOUS PLANT C STOCKS

The main mechanism by which livestock grazing influences the C cycle is considered to be the consumption of plant biomass (Reeder and others 2004; Soussana and others 2004; Welker and others 2004). Our study of an upland grassland system suggests that other mechanisms may play a key role. We have shown that C stocks can be spatially heterogeneous, with tussocks representing C 'hot spots'. Sheep grazing affects C storage by influencing the abundance of tussocks within the sward, reducing tussock area by up 30% compared to ungrazed swards. Commercial sheep grazing reduced the C held in *M. caerulea* swards by reducing their abundance, yet if biomass removal was the main mechanism of

21

419   impact, we would have expected commercial sheep densities would primarily have reduced

420   *M. caerulea* tussock size. This would occur through shoot removal subsequently affecting the

421   size of the shoot-bases, which are the overwintering storage organs (Latusek 1983; Thornton

422   1991; Taylor and others 2001), and it is the size and number of these shoot-bases that

423   determine tussock size (Grant and others 1996). However, the fact that it is the number of

424   tussocks which has declined suggests that other mechanisms are important, such as trampling

425   (Billotta and others 2007), severe defoliation causing all of a tussock's shootbases to die at the

426   same time, and a reduction in flowering (Thornton 1991; Grant and others 1996).

427

428   In the longer term, the loss of C due to heavy grazing of *M. caerulea* might be expected to

429   become smaller as a result of grazer-induced changes in plant species composition, with less

430   palatable species replacing *M. caerulea*. This could mitigate any loss of plant C stocks

431   attributed to grazing (Tanentzap and Coomes 2012). However, in this system, the area of the

432   landscape covered by the *M. caerulea* sward was not noticeably smaller after 7 years of sheep

433   grazing compared to no grazing. Furthermore, controlled grazing studies in the same type of

434   upland vegetation have shown that heavy grazing favours more palatable grasses such as

435   *Agrostis* and *Holcus* spp. (Grant and others 1996; Taylor and others 2001). These swards do

436   not form tussocks, and have a small plant C storage potential, similar to *M. caerulea* inter-

437   tussocks (data not shown). Thus, the change in plant species composition that is likely to

438   occur under prolonged heavy grazing at Glen Finglas would result in continued loss of C,

439   though perhaps at relatively slower rates than initial loss caused by the reduction in number of

440   *M. caerulea* tussocks.

441

PREDICTING HOW GRAZING AFFECTS SOIL C STORAGE

Empirical evidence of grazing-induced changes in plant C inputs influencing SOC pools is difficult to detect due to high heterogeneity of soil physiochemical properties within the landscape and slow turnover rates of SOC. RothC predicted changes in soil organic matter fractions should correspond to chemically measured SOC pools (Zimmermann and others 2007). Modelled DPM and RPM SOC pools should equate to litter and fermentation layers in the soil profile. DPM and RPM are inputs of plant-derived material into RothC, but also become SOC pools themselves as dead plant-derived material with a high lability. Following our predictions; high intensity sheep grazing reduced the DPM and RPM pools, which supports empirical studies that find less C in litter and fermentation pools in grazed uplands (Ward and others 2007; Medina- Roldán and others 2012). On the other hand, the predicted reduction in the slower turnover SOC pool Humified Organic Matter (HUM) under high sheep grazing intensity (Fig. 5) is not evident in empirical studies (Marriot and others 1997; Garnett and others 2001; Ward and others 2007; Frogbrook and others 2009; Medina- Roldán and others 2012). In our RothC predictions, differences in HUM pools made the largest contribution to grazing-induced changes in total SOC. In order to support these predictions more grazing experiments of decades' duration are required (Smith and others 1997).

Models of C dynamics in the uplands require more data from multiple stocking densities in a single landscape (Worrall and others 2009). RothC predicted a large difference in SOC between scenarios of no grazing and commercial sheep grazing, with the former accumulating more SOC. However, predictions for low sheep grazing densities were similar to those for no sheep grazing. This clearly indicates that as far as accumulation of SOC is concerned, it is not grazing vs. no grazing that matters, but the intensity of sheep grazing. Similarly lowering sheep grazing pressure and reducing shoot off-take prevents SOC loss in steppe plateau

467 pastures; identified using CENTURY organic turnover model with estimated plant C inputs

468 (Wang and others 2008). Here we similarly identified that low sheep grazing pressure is

469 optimal for SOC storage in temperate upland grasslands, but in this case we used measured

470 plant C inputs, which may provide a better basis for modelling.

471

472 USING LIVESTOCK GRAZING TO MANAGE UPLAND C STORAGE

473 The measured benefits for plant C stores of stopping or reducing sheep grazing on *M.*

474 *caerulea* swards (3.5 Mg C ha^{-1} after 7 years) are smaller than the benefits of other plant C

475 sequestration strategies, such as short rotation forestry (21.5 - 22.5 Mg C ha^{-1} in 3 years;

476 Deckmyn and others 2004) or plantation of bio-energy crops, such as *Miscanthus x giganteus*

477 (17 Mg C ha^{-1} in 10 years; Clifton-Brown and others 2007; Dondini and others 2009).

478 Likewise, predicted SOC accumulation following cessation of sheep grazing was small over a

479 time span of 100 years (14.36 Mg C ha^{-1}) compared to *Miscanthus* plantations (130 – 160 Mg

480 C ha^{-1} of SOC in 30 years; Dondini and others 2009). Nevertheless, C gains from reducing or

481 a cessation of sheep grazing in this upland landscape are obtained without significant

482 engineering (Reed and others 2009). Equally, the diverse upland landscape allows multiple C

483 management practices to be pursued where locally appropriate, which often enhances the

484 social and cultural value of uplands (Morgan-Davies and Waterhouse 2008; Dandy and Van

485 der Wal 2010).

486

487 Uplands are managed for multiple purposes; culturally, as a source of rural employment and

488 for the goods and services they provide (Orr and others 2008; Reed and others 2009).

489 Appropriate upland C management must be weighed against such wider land use objectives.

490 Using evidence from the Glen Finglas grazing experiment, C storage can be weighed against

491 the abundance of characteristic species, as is increasingly being discussed for the uplands (e.g.

492 Van der Wal and others 2011). For instance, at Glen Finglas ungrazed *M. caerulea* swards are

493 poor foraging habitat for the meadow pipit (*Anthus pratensis*) (Vandenberghe and others

494 2009). However, both breeding and foraging success of this typical upland bird species was

495 greatest under low density sheep grazing compared to either commercial or no sheep grazing

496 (Evans and others 2005; Prior and others 2011). Field vole (*Microtus agrestis*) abundance

497 (Evans and others 2006), and nocturnal moth and other arthropod abundance and diversity are

498 negatively affected by increasing sheep grazing intensity (Dennis and others 2008; Littlewood

499 2008). This suggests that optimal management to both sequester C and sustain biodiversity in

500 *M. caerulea*-dominated upland landscapes may be to reduce sheep grazing intensity, as

501 opposed to a cessation of sheep grazing altogether.

502

512 **REFERENCES**

513 Adler PB, Raff DA, Lauenroth WK. 2001. The effect of grazing on the spatial heterogeneity

514   of vegetation. Oecologia 128: 465 – 479.

515

516 Aerts R. 1989. Aboveground biomass and nutrient dynamics of *Calluna vulgaris* and *Molinia*

517   *caerulea* in a dry heathland. Oikos 56: 31-38

518

519 Aerts R, Bakker C, De Caluwe H. 1992. Root turnover as determinant of the cycling of C, N,

520   and P in a dry heathland ecosystem. Biogeochemistry 15: 175-190.

521

522 Augustine DJ, Frank DA. 2001. Effects of migratory grazers on spatial heterogeneity of soil

523   nitrogen properties in a grassland ecosystem. Ecology 82: 3149-3162.

524

525 Bakker JP, De Leeuw J, Van Wieren SE. 1984. Micro-patterns in grassland vegetation

526   created and sustained by sheep-grazing. Vegetatio 55: 153-161.

527

528 Bates DM, Maechler M. 2010. lme 4. Linear mixed-effects models using S4 classes.

529   http://lme4.r-forge.r-project.org/,last accessed 21st March 2013.

530

531 Berg G, Esselink P, Groeneweg M, Kiehl K. 1997. Micropatterns in *Festuca rubra-*

532   dominated salt-marsh vegetation induced by sheep grazing. Plant Ecol 132: 1-14.

533

534 Billotta GS, Brazier RE, Haygarth PM. 2007. The impacts of grazing animals on the quality

535   of soils, vegetation and surface waters in intensively managed grasslands. Adv Agron 94:

536   237-280.

537

538 Bråthen KA, Ims RA, Yoccoz NG, Fauchald P, Tveraa T, Hausner VH. 2007. Induced shift

539   in ecosystem productivity? Extensive scale effects of abundant large herbivores.

540   Ecosystems 10: 773-789.

541

542 Bunce RGH, Barr CJ. 1988. The extent of land under different management regimes in the

543   uplands and the potential for change, in: Usher, M.B., Thompson, D.B.A. (Eds.), Ecological

544   Change in the Uplands. pp. 415-426. Special Publication 7 of the British Ecological

545   Society. Blackwell Scientific Publications, Oxford, UK.

546

547 Burke IC, Lauenroth, WK, Vinton MA, Hook PB, Kelly RH, Epstein HE, Aguiar MR, Robles

548   MD, Aguilera MO, Murphy KL, Gill RA. 1999. Plant-soil interactions in temperate

549   grasslands. Biogeochemistry 42: 121-143.

550

551 Carey PD, Wallis S, Chamberlain PM, Cooper A, Emmett BA, Maskell LC, McCann T,

552   Murphy J,Norton LR, Reynolds B, Scott WA, Simpson IC, Smart SM, Ullyett JM. 2008.

553   Countryside Survey: UK Results from 2007. NERC/Centre for Ecology & Hydrology,

554   105pp. (CEH Project Number: C03259).

555

556 Cichini K, Schwienbacher E, Marcante S, Seeber GUH, Erschbamer B. 2011. Colonization of

557   experimentally created gaps along alpine successional gradient. Plant Ecol 212:1613–1627.

558

559 Clifton-Brown J, Breuer J, Jones MB. 2007. Carbon mitigation by the energy crop,

560   *Miscanthus.* Glob Change Biol 13: 2296–2307.

561

562   Coleman K, and Jenkins D. 1999. RothC-26.3. A Model for the Turnover of Carbon in Soils.

563   Model Description and Windows Users Guide. IACR. Rothamsted, Harpenden.

564

565   Conant RT, Paustian K, Elliott ET. 2001. Grassland management and conversion into

566   grassland: Effects on soil carbon. Ecol Appl, 11: 343-355.

567

568   Dandy N, Van der Wal R. 2011. Shared appreciation of woodland landscapes by land

569   management professionals and lay people: an exploration through field-base interactive

570   photo-elecitiation. Landscape Urban Plan 102: 43-53.

571

572   Dawson JJC, Smith P. 2007. Carbon losses from soil and its consequences for land-use

573   management. Sci Total Environ 382: 165-190

574

575   Deckmyn G, Muys B, Garcia Quijano J, Ceulemans R. 2004. Carbon sequestration following

576   afforestation of agricultural soils: comparing oak/beech forest to short-rotation poplar

577   coppice combining a process and a carbon accounting model. Glob Change Biol 10: 1482–

578   1491

579

580   Dennis P, Elston D, Evans D, Evans S, Gordon I, Grant M, Kunaver A, Marquiss M, Mayes,

581   B, McCracken D, Pakeman R, Pearce-Higgins J, Redpath S, Skartveit J, Stephen L, Benton

582   T, Bryant D, 2004. Effects of grazing management on upland bird populations:

583   disentangling habitat structure and arthropod food supply at appropriate spatial scales

584   (GRUB), Scottish Executive Environment & Rural Affairs Department, pp 1-57.

585

586 Dennis P, Skartveit J, McCracken DI, Pakeman RJ, Beaton K, Kunaver A, Evans D. 2008.

587   The effects of livestock grazing on foliar arthropods associated with bird diet in upland

588   grasslands of Scotland. J Appl Ecol 45: 279-287.

589

590 Derner JD, Briske DD, Boutton TW. 1997. Does grazing mediate soil carbon and nitrogen

591   accumulation beneath C4, perennial grasses along an environmental gradient? Plant Soil

592   191: 147 -156.

593

594 Dondini M, Hasting, Saiz G, Jones MB, Smith P. 2009. The potential of *Miscanthus* to

595   sequester carbon in soils: comparing field measurements in Carlow, Ireland to model

596   predictions. Glob Change Biol Bioenergy 1: 413–425.

597

598 Evans DM, Redpath SM, Evans SA, Elston DA, Dennis P. 2005. Livestock grazing affects

599   the egg size of an insectivorous passerine. Biol Letters 1: 322-325.

600

601 Evans DM, Redpath SM, Elston DA, Evans SA, Mitchell RJ, Dennis P. 2006. To graze or not

602   graze? Sheep, voles, forestry and nature conservation in the British uplands. J Appl Ecol 43:

603   499-505.

604

605 Fallon P, Smith P, Coleman K, Marshall S. 2000. How important is inert organic matter for

606   predictive soil carbon modelling using the Rothamsted carbon model? Soil Bio Biochem 32:

607   433-436.

608

609 Frank DA, McNaughton SJ, Tracy BF. 1998. The ecology of the Earth's grazing ecosystems:

610   Profound functional similarities exist between the Serengeti and Yellowstone. Bioscience

611   48: 513-521.

612

613 Fraser MD, Theobald VJ, Dhanoa MS, Davies OD 2011. Impact on sward composition and

614   stock performance of grazing Molinia-dominant grassland. Agri Eco Environ 144:102-106.

615

616 Frogbrook ZL, Bell J, Bradley RI, Evans C, Lark RM, Reynolds B, Smith P,

617 Towers W. 2009. Quantifying terrestrial carbon stocks: examining the spatial variation in

618   two upland areas in the UK and a comparison to mapped estimates of soil carbon. Soil Use

619   and Manage 25: 320–332.

620

621 Garnett MH, Ineson P, Stevenson AC, Howard DC. 2001. Terrestrial organic carbon storage

622   in a British moorland. Glob Change Biol 7: 375-388.

623

624 Gillson L. 2004. Evidence of hierarchical patch dynamics in an east African savanna?

625   Landscape Ecol 19: 883-894.

626

627 Gogo S, Laggoun-Défarge F, Delarue F, Lottier N. 2010. Invasion of a sphagnum-peatland

628   by *Betula spp.* and *Molinia caerulea* impacts organic matter biochemistry: implications for

629   carbon and nutrient cycling. Biogeochemistry 106: 53-69.

630

631 Grant SA, Maxwell TJ. 1988. Hill vegetation and grazing by domesticated herbivores: the

632   biology and definition of management options, in; Usher, M.B., Thompson. D.B.A. (Eds):

633   Ecological Change in the Uplands. pp. 201-214. Special Publication no. 7 of the British

634   Ecological Society. Blackwell Scientific Publications, Oxford, UK.

635

636   Grant SA, Torvell L, Common TG, Sim EM, Small JL. 1996. Controlled grazing studies on

637   *Molinia* grassland: effects of different seasonal patterns and levels of defoliation on *Molinia*

638   growth and responses of swards to controlled grazing by cattle. J Appl Ecol 33: 1267-1280.

639

640   Guo LB, Gifford RM. 2002. Soil carbon stocks and land use change: a meta-analysis. Glob

641   Change Biol 8: 345-360.

642

643   Guo L, Fallon P, Coleman K, Zhou B, Li Y, Lin E, Zhang F. 2007. Application of the RothC

644   model to the results of long-term experiments on typical upland soils in northern China. Soil

645   Use Manag, 23: 63-70.

646

647   Hothorn T, Bretz F, Westfall, P. 2008. Simultaneous Inference in General Parametric Models.

648   Biometrical Journal 50: 346-363.

649

650   Hunter RF. 1962. Hill sheep and their pasture: a study of sheep grazing in South-East

651   Scotland. J Ecol, 50: 651-680.

652

653   Jones C, McConnell, Coleman K, Cox P, Fallon P, Jenkinson D, Powlson, D. 2005. Global

654   climate change and soil carbon stocks; predictions from two contrasting models for turnover

655   of organic carbon in soil. Glob Change Biol 11: 154 -166.

656

657 Latusek E 1983. The autecology of *Molinia caerulea* (L.) Moench with particular reference

658   to grazing. Unpublished PhD thesis, Manchester Polytechnic, Manchester, UK.

659

660 Littlewood N. 2008. Grazing impacts on moth diversity and abundance on a Scottish upland

661   estate. Insect Conserv Diver 1: 151–160.

662

663 Liu DL, Chan KY, Conyers MK, Li G, Poile GK 2011. Simulation of soil organic carbon

664   dynamics under different pasture managements. Geoderma 165: 69 -77..

665

666 Marriott CA, Hudson G., Hamilton D, Neilson R, Boag B, Handley LL, Wishart J,

667   Scrimgeour CM, Robinson D. 1997. Spatial variability of soil total C and N and their stable

668   isotopes in an upland Scottish grassland. Plant Soil 196: 151-162.

669

670 Martinsen V, Mulder J, Austrheim G, Mysterud A. 2011. Carbon storage in low-alpine

671   grassland soils: effects of different grazing intensities of sheep. Eur J Soil Sci 62: 822 – 833.

672

673 McNaughton SJ, Wallace LL, Coughenour MB. 1983. Plant adaptation in an ecosystem

674   context: effects of defoliation, nitrogen, and water on growth of an African C4 Sedge.

675   Ecology 64: 307-318.

676

677 Medina-Roldán E, Paz-Ferreiro J, Bardgett RD. 2012. Grazing exclusion affects soil and

678   plant communities, but has no impact on soil carbon storage in an upland grassland. Agri

679   Eco Enviro 149:118-123.

680

681 Milchunas DG, Lauenroth WK, Chapman PL, Kazempour MK. 1989. Effects of grazing,

682   topography, and precipitation on the structure of a semi-arid grassland. Vegetatio 80: 11-23.

683

684 Milchunas DG, Lauenroth WK. 1993. Quantitative effects of grazing on vegetation and soils

685   over a global range of environments. Ecol Monographs 63: 327-366.

686

687 Morgan-Davies C, Waterhouse A. 2008. Hill and upland areas: Livestock farming changes

688   and stakeholder preferences. Aspects Appl Biol 85: 49-56.

689

690 Orr HG, Wilby RL, Hedger MM, Brown I. 2008. Climate change in the uplands: A UK

691   perspective on safeguarding regulatory ecosystem services, Climate Res 37: 77-98.

692

693 Ostle NJ, Levy PE, Evans CD, Smith P. 2009. UK land use and soil carbon sequestration.

694   Land Use Policy 26: 274-283.

695

696 Piñeiro G, Paruelo JM, Oesterheld M, Jobbágy, EG. 2010. Pathways of grazing effects on soil

697   organic carbon and nitrogen. Rangeland Ecol Manage 63:109 –119.

698

699 Pinheiro JC, Bates DM. 2000. Mixed Effects Models in S and S-PLUS. Springer-Verlag,

700   New York.

701

702 Prior GL, Evans DM, Redpath S, Thirgood SJ, Monaghan P. 2011. Birds bias offspring sex

703   ratio in response to livestock grazing. Biol Letters 7: 958 – 960.

704

705   R Development Core Team.2009. R: A language and environment for statistical computing.

706   R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL

707   http://www.R-project.org.

708

709   Reed MS, Bonn A, Slee W, Beharry-Borg N, Birch J, Brown I, Burt TP, Chapman D,

710   Chapman PJ, Clay GD, Cornell SJ, Fraser EDG, Glass JH, Holden J, Hodgson JA,

711   Hubacek K, Irvine B, Jing N, Kirkby MJ, Kunin WE, Moore O, Moseley D, Prell C,

712   Price,MF, Quinn CH, Redpath S, Reid C, Staglo S, Stringer LC, Termansen M, Thorpp S,

713   Towers W, Worrall F.2009. The future of the uplands. Land Use Policy 26: 204–216.

714

715   Reeder JD, Schuman GE, Morgan JA, Lecain DR. 2004. Response of organic and inorganic

716   carbon and nitrogen to long-term grazing of the shortgrass steppe. Environ Manage 33: 485-

717   495.

718

719   Rodwell JS. 1991. British Plant Communities. Volume 2: Mires and Heaths. Cambridge

720   University Press, Cambridge.

721

722   Rodwell JS. 1992. British Plant Communities. Volume 3: Grasslands and Montane

723   Communities. Cambridge University Press, Cambridge.

724

725   Sanderson N, 1998. Glen Finglass historic landscape survey, Woodland Trust, Hythe, UK. p1

726   – 104.

727

728   Scottish Agriculture College (SAC) 2008. Rural Policy Centre, Farming's retreat from the

729   hills, Outlook for 2009. p1-32.

730

731   Smith P, Smith JU, Powlson DS, McGill WB, Arah JRM, Chertov OG, Coleman K, Franko

732   U, Frolking S, Jenkinson DS, Jensen LS, Kelly RH, Klein-Gunnewiek H, Komarov AS, Li C,

733   Molina JAE, Mueller T, Parton WJ, Thornley JHM, Whitmore AP. 1997. A comparison of the

734   performance of nine soil organic matter models using datasets from seven longterm

735   experiments. Geoderma 81: 153–225.

736

737   Soil Indicators For Scottish Soils (SIFSS) 2013. The James Hutton Institute. Available from

738   http://sifss.hutton.ac.uk/index.php , last accessed 28 June 2013.

739

740   Soil Survey of Scotland. 1984. Organisation and methods of the 1:250 000 scale soil survey

741   of Scotland. Macaulay Institute for Soil Research, Aberdeen.

742

743   Soussana J, Loiseau P, Vuichard N, Ceschia E, Balesdent, J., Chevallier, T., Arrouays, D.

744   2004. Carbon cycling and sequestration opportunities in temperate grasslands. Soil Use

745   Manage, 20, 219-230.

746

747   Stewart DPC, Metherell AK. 1999. Carbon (^{13}C) uptake and allocation in pasture plants

748   following field pulse-labelling. Plant Soil 210: 61-73.

749

750   Tanentzap AJ, Coomes DA. 2012. Carbon storage in terrestrial ecosystems: do browsing and

751   grazing herbivores matter? Biol Rev 87: 72–94.

752

753   Taylor K, Rowland AP, Jones HE 2001. *Molinia caerulea* (L.) Moench, J Ecol 89: 126-144

754

755 Thompson DBA, MacDonald AJ, Marsden JH, Galbraith CA. 1995. Upland heather

756   moorland in Great Britain: A review of international importance, vegetation change and

757   some objectives for nature conservation. Biol Conserv 71: 163-178.

758

759 Thornton B, 1991. Effect of nutrition on the short-term response of *Molinia caerulea* to

760   defoliation. Ann Botany 68: 569-576

761

762 UK Meteorological Office. MIDAS Land Surface Stations data (1853-current),

763   [Internet].NCAS British Atmospheric Data Centre, 2006, Date of citation. Available from

764   http://badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dataent_ukmo-midas, last accessed

765   26th June 2012.

766

767 Vandenberghe C, Prior G, Littlewood NA, Brooker R, Pakeman RJ. 2009. Influence of

768   livestock grazing on meadow pipit foraging behaviour in upland grassland. Basic Appl Ecol

769   10: 662-670

770

771 Van der Wal R, Bonn A, Monteith D, Reed M, Blackstock K, Hanley N, Thompson D, Evans

772   M, Alonso I. 2011. Mountains, moorlands and heaths. Pp. 105-159, in: The UK National

773   Ecosystem Assessment Technical Report. UK National Ecosystem Assessment, UNEP-

774   WCMC, Cambridge.

775

776 Ward SE, Bardgett RD, McNamara NP, Adamson JK, Ostle NJ. 2007. Long-term

777   consequences of grazing and burning on northern peatland carbon dynamics. Ecosystems

778   10: 1069-1083.

779

780   Wang Y, Guangsheng Z, Bingrui J. 2008. Modeling SOC and NPP responses of meadow

781   steppe to different grazing intensities in Northeast China, Eco Mod 217:72-78.

782

783   Welker JM, Fahnestock JT, Povirk KL, Bilbrough CJ, Piper RE. 2004. Alpine grassland CO_2

784   exchange and nitrogen cycling: grazing history effects, Medicine Bow Range, Wyoming,

785   U.S.A. Arc Antarct Alp Res 36: 11-20.

786

787   Woodin SJ, Van der Wal R, Sommerkorn M, Gornall JL. 2009. Differential allocation of

788   carbon in mosses and grasses governs ecosystem sequestration: A ^{13}C tracer study in the

789   high arctic. New Phytol 184: 944-949.

790

791   Worrall F, Evans MG, Bonn A, Reed MS, Chapman D, Holden J. 2009. Can carbon

792   offsetting pay for upland ecological restoration? Sci Total Environ 408: 26 -36.

793

794   Zimmermann M, Leifeld J, Schmidt MWI, Smith P, Fuhrer J. 2007. Measured soil organic

795   matter fractions can be related to pools in the RothC model. Eur J Soil Sci 58: 658–667.

SUPPLEMENTARY INFORMATION

Table S1 Plot scale estimates of *M. caerulea* cover in September 2009 from long-term British National Vegetation Classification records (Dennis and others 2004). Grazing treatments are as follows: (9) 'Commercial' stocking, 9 sheep per plot reflecting a typical commercial stocking rate of 2.7 ewes ha^{-1} for nutrient-poor rough upland grassland (Thompson and others 1995); (3) 'Low' stocking, 3 sheep per plot or one-third the commercial rate at 0.9 ewes ha^{-1}, similar to stocking rates prior to the experiment; and (0) no livestock. Grazing treatment were assigned randomly to plots within two replicate blocks across three sites.

Plot number	Number of sheep	*M. caerulea* sward area (ha)	Plot Area (ha)	*M. caerulea* sward % area
1	9	2.862	3.258	87.9
2	9	2.210	3.157	70.0
3	9	1.099	3.225	34.1
4	9	1.923	3.340	57.6
5	3	2.814	3.285	85.7
6	3	2.418	3.334	72.5
7	3	1.783	3.058	58.3
8	3	1.406	3.329	42.2
9	0	2.792	3.279	85.2
10	0	2.779	3.277	84.8
11	0	1.395	3.323	42.0
12	0	2.486	3.234	76.9