OPTIMISING CARBON STORAGE WITHIN A SPATIALLY HETEROGENEOUS UPLAND GRASSLAND THROUGH SHEEP GRAZING MANAGEMENT

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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;

Garnett and others 2001; Frogbrook and others 2009). Therefore, to calibrate grazing as a C management tool, we must consider the relationship between grazing and spatially heterogeneous C stores.

Livestock grazing is a well-known driver of heterogeneity; altering plant species composition, canopy structure and biomass distribution (Bakker and others 1984; Berg and others 1997; Derner and others 1997; Adler and others 2001). Despite the fundamental role of plant C input in soil C accumulation, little attention has been paid to the spatial heterogeneity of vegetation C stores found in many grazed systems. In grasslands, tufts or tussocks formed by many grass species are potentially dense C stores, containing a high C content per unit ground area. The number per unit area and size of these tussocks may be influenced by grazing. For example, on a steppe plateau, grazing has been shown to reduce litter accumulation and subsequently soil particulate C under tussocks (Milchunas and others 1989; Burke and others 1999). In the steppe plateau in the previous study, the low organic content of the soil facilitates the detection of grazing influencing soil C accumulation, whereas in temperate organic soils such effects may be more subtle and difficult to detect (Marriot and others 1997; Ward and others 2007; Medina- Roldán and others 2012). However, the effect of grazing on tussocks and plant C storage can often be detected and quantified, with findings from such studies suggesting that grazing could be used to manage above-ground C stocks. In a study of temperate upland grasslands, high sheep grazing intensities reduced C stocks of the tussock foliage and roots; however, this was offset by increased C stocks in the inter-tussock foliage and roots (Stewart and Metherell 1999). The latter study highlights the importance of accounting for the scale of observation when determining the influence of grazing on spatial heterogeneity (Augustine and Frank 2001; Gillson 2004; Bråthen and others 2007).

The UK uplands (areas generally > 200 m a.s.l. where farming becomes less profitable due to the limited productivity of the land; Orr and others 2008; Reed and others 2009) are extensively grazed by livestock or deer. These systems typically have spatially heterogeneous vegetation and organic and peaty soils, which are estimated to hold almost 30 % of the UK national stock of soil C in the top 15 cm of the profile (Carey and others 2008). Therefore it is vital that these extensively grazed uplands are managed appropriately to avoid the loss of stored C from the soil and vegetation.

Approximately 10 % of the UK uplands are covered by *Molinia caerulea* (L.) Moench. (purple moor grass) dominated vegetation (Bunce and Barr 1988). Given the large national extent of *M. caerulea*-dominated vegetation (c. 6000 km^2), it should be represented in C budget modelling for the uplands, particularly in relation to land-use change. *M. caerulea*, a deciduous grass, forms dense tussocks consisting of compact aggregations of shoot-bases. In between these tall growing, dense tussocks the 'inter-tussock' plant communities are short and usually species poor (Rodwell 1991). The above-ground and below-ground productivity of *M. caerulea* exceeds that of most other common upland plant species, including the widespread *Calluna vulgaris* (Aerts 1989; Aerts and others 1992); thus *M. caerulea* is an ideal management target for C sequestration (Gogo and others 2010) and can be managed using livestock grazing. Light artificial defoliation has been shown to reduce shoot-base and root biomass of *M. caerulea* (Latusek 1983; Thornton 1991) and *M. caerulea* cover has been shown to reduce under extensive cattle grazing (Grant and others 1996). Sheep only consume *M. caerulea* in spring before the new leaves become tough and unpalatable (Hunter 1962; Taylor and others 2001) and cover was unaffected by sheep grazing from mid-late summer onward (Fraser and others 2011). There has been little research undertaken with regards to how year-round sheep grazing affects the abundance of *M. caerulea* and the structure of its sward, despite the prevalence of both sheep and *M. caerulea* in extensively-grazed landscapes (SAC 2008). Addressing this question is integral for gaining a predictive understanding of whether grazing management can be used to optimise C storage in upland grasslands dominated by *M. caerulea*.

Most grazing experiments are too short to provide a definitive understanding of the soil C storage potential (Tanentzap and Coomes 2012). This problem of limited experimental duration can be addressed by the use of soil organic matter (SOM) turnover models. One such model, RothC, divides SOM into a number of conceptual pools of C, each of which is defined by its lability. Soil C input comes from plant material, which is divided into decomposable (DPM) and resistant (RPM) plant material, with their ratio depending on the origin of the plant material. Plant material as DPM and RPM becomes incorporated into SOC and decomposes at different rates into microbial biomass (BIO) and humus (HUM), thereby releasing CO_2 (Coleman and Jenkinson 1999). BIO and HUM then decompose at different rates producing more CO_2, BIO and HUM. The partitioning of the products of decomposition depends on the soil clay content, whereas decomposition rates are modified by temperature and soil moisture and whether vegetation cover is present or absent. The model also includes a pool of inert soil organic matter (IOM). The RothC model has been applied to numerous sites worldwide under various types of agricultural management (e.g. Smith and others 1997; Zimmermann and others 2007). Following its thorough validation in upland grasslands and pastures, it has been effectively used as a predictive tool for these systems (Guo and others 2007; Liu and others 2011).

We used a long-term, fully-replicated grazing experiment, established at a landscape-scale (each plot is 3.3 ha) in central Scotland, to address the following three aims: (1) to determine the effect of different sheep stocking densities on C stocks in *M. caerulea* swards; (2) to describe the C stored in this grazed vegetation at three spatial scales (tussock, sward and landscape), thereby accounting for spatial heterogeneity at each scale; and (3) to use resulting data as vegetation C inputs to the RothC model to predict the long-term impact of different sheep stocking densities on soil organic C (SOC) accumulation. Using this unique approach of accounting for heterogeneous vegetation C coupled with model simulations of soil C, we aim to identify an optimal grazing density for long-term C storage in an upland landscape that has spatially heterogeneous vegetation, soil and grazing pressure.

MATERIALS AND METHODS

STUDY AREA AND EXPERIMENTAL SETUP

The study was carried out on the Glen Finglas estate (4039 ha) in central Scotland (56°16´N 4°24´W), an upland area (200 - 500 m a.s.l.) receiving a mean 1344 mm of annual rainfall and with mean January and July temperatures of 2.6 ºC and 14.3 °C, respectively (1982-2000 average from Loch Venachar at ca. 5 km distance; UK Meteorological Office 2012). Glen Finglas has organic soils, including blanket peats, peaty gleys and humus iron podzols with 60 % of the area having soil with a C concentration greater than 40% to a depth of 15 cm (Soil Survey of Scotland 1984; SIFSS, 2013). The vegetation is a fine-grained mosaic of the following dominant types, as classified by the British National Vegetation Classification (NVC) communities (Rodwell 1991, 1992): M23 (*Juncus effusus-acutiflorus–Galium palustre* rush-pasture), M25 (*Molinia caerulea–Potentilla erecta* mire), U4 (*Festuca ovina–Agrostis capillaris–Galium saxatile* grassland) and U5 (*Nardus stricta–G. saxatile* grassland). The defining characteristic of the vegetation at the study site is the presence of tussocks, which primarily consist of *M. caerulea.* Swards are grazed by black-faced sheep and Luing cattle with no burning management of the grassland vegetation, typical of many upland areas of Scotland. Before the study was initiated, there was a low grazing pressure by black-faced sheep (0.7 ewes ha^{-1}) across the estate.

In 2003, a landscape-scale grazing experiment was established across three sites, spaced approximately 4.1 km apart within Glen Finglas, each containing two replicate blocks. Each block is composed of four 3.3 ha fenced plots containing different grazing treatments, randomly assigned to: (a) ‘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); (b) ‘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 (c) no livestock. Sheep remained in the plots throughout the year and were only removed for normal farm operations and during periods of severe weather.

TUSSOCK-SCALE CARBON SAMPLING

In November 2009, *M. caerulea* tussocks and inter-tussocks were sampled in the two different sheep grazing treatments and the ungrazed treatment, replicated across four of the six blocks; one site (two blocks) was not sampled due to the near absence of *M. caerulea* in some plots. Within plots, sampling locations were selected at random from long-term vegetation survey points (Dennis and others 2004) that were defined under the British National Vegetation Classification (NVC) as M25 *Molinia caerulea – Potentilla erecta* mire (Rodwell 1991).

The distribution of C in plant parts was determined for one tussock and one inter-tussock area (< 2 m apart) per plot (24 samples, namely: 3 grazing treatments × 4 blocks × tussock/ inter-tussock). A 20 cm × 20 cm turf to a soil depth of 5 cm was collected to quantify C within standing dead litter, shoot-bases and shallow roots (0 – 5 cm). Deep roots (5 - 15 cm) were collected directly below the turf using a 4.2 cm diameter bevel-ended corer. All turfs and root cores were stored at 4 °C prior to sorting.

Standing dead grass litter (predominately *M. caerulea*), hereafter termed ‘shoots’, were sorted from each turf. Shoot-bases and shallow roots were sub-sampled from a 5 cm × 5 cm area of the turf. Roots were recovered using a 0.5 mm sieve through repeated cycles of washing, sedimentation and decanting. All above- and below-ground biomass was oven-dried for 48 hrs at 80 ºC and weighed (± 0.01 g). Plant component samples were homogenized by stainless steel ball-milling (F.Kurt Retsch GMbH & Co. KG, MM200, Germany; Smith *et al.* 2013a), to generate a standard 5 mg sub-sample for elemental C analysis (Carlo-Erba NA 1500 Series 2, USA).

SWARD-SCALE VEGETATION SAMPLING

To determine the effect of grazing on the structure of the *M. caerulea* sward, plots of all three sheep grazing treatments (ungrazed, low and commercial) were subdivided into four equal parts and a 2 m × 10 m quadrat was randomly laid out within each part, at least 3 m away from any fence, following random cardinal directions. Stream trenches, rocky terrain and areas dominated by *J. acutiflorus/effusus* and *Pteridium aquilinum* were avoided. Sampling was undertaken in April 2007, before new young shoots broke through the *M. caerulea* leaf litter.

Within all 48 quadrats (3 grazing treatments × 4 blocks × 4 replicate quadrats) records were made of each individual tussock. These included a record of other plant species found in each *M. caerulea* tussock and two measures of tussock diameter, one at the widest point and the other perpendicular to it. The surface area of each tussock was calculated using the equation for the area of an ellipse: πab ($a = \frac{1}{2}$ largest diameter and $b = \frac{1}{2}$ perpendicular diameter), hereafter termed ‘tussock size’. Total tussock area was the sum of all tussock areas within a quadrat, and inter-tussock area was the remaining quadrat area. A mean tussock and inter-tussock area was obtained for each plot. Carbon held in the *M. caerulea* sward was then determined by multiplying the mean tussock and inter-tussock area by the quantities of C in the tussock and inter-tussocks, respectively. These plot-specific measures of *M. caerulea* sward C were then averaged for each sheep grazing treatment (ungrazed, low and commercial).

LANDSCAPE-SCALE COVER OF M. CAERULEA-DOMINATED COMMUNITIES

The total plot-area dominated by *M. caerulea* was derived from long-term point survey data (Dennis and others 2004). Within each plot 81 points, ca. 20 m apart, were described using the

National Vegetation Classification (NVC; Rodwell 1992) in September 2009. Points identified as representing M25, *Molinia caerulea – Potentilla erecta* mire, were used to map the *M. caerulea*-dominated area in a Geographic Information Systems (GIS) package (ESRI® ArcGIS^{TM} 9.3). *M. caerulea*-dominated points were transformed into an estimated area for each plot using inverse-distance interpolation. The quantity of C held in *M. caerulea* sward for the relevant plot was then combined with the estimated *M. caerulea*-dominated area within each plot to generate a landscape estimation of C stocks under the different grazing treatments.

STATISTICAL ANALYSIS

Measured parameters from 2092 tussocks dominated by *M. caerulea* were used in the statistical analysis. All statistical analysis was conducted in R using the lme4 package (version 2.10.1, R Development Core Team 2009; Bates and Maechler 2010). Differences in total tussock area, number of tussocks and average tussock size were explored for all stocking treatments (ungrazed, low, and commercial) using a linear mixed-effect model with residual maximum likelihood estimations (REML). The number of tussocks was analysed using a Poisson error structure, and average tussock size was $\log_{10}$ transformed to achieve a normal distribution. The random structure was defined as plot nested within block nested within site. To justify the inclusion of grazing treatments in the model we used a likelihood ratio deletion test (LRT), comparing a model with and without (null) grazing treatments (Pinheiro and Bates 2000). Statistical significance of the different grazing treatments was obtained through formulating contrast statements between each grazing treatment within the same model structure (see Hothorn and others 2008; Cichini and others 2011). Untransformed *M. caerulea* sward cover as a percentage of each plot was analysed using a similar linear mixed-effect model structure without plot in the random structure.

MODELLING SOIL ORGANIC CARBON

RothC (Coleman and Jenkinson 1999) was used to calculate soil organic C (SOC) dynamics. To achieve this RothC was used in three stages; first, to establish the historic SOC for the original, forested land (pre 1860s) before the site was transformed to grassland; second, to estimate SOC at the time of tussock carbon measurements in 2009, after a century and a half of light grazing; and third, to predict the long-term (100 years) impact of the different experimental grazing treatments. To estimate SOC under the historic forest vegetation cover at Glen Finglas, RothC was run to equilibrium for a mixed forest, with an annual C input (from plant material) of 2.95 Mg C ha^{-1} and a DPM/RPM (Decomposable Plant Material/Resistant Plant Material) ratio of 0.25. These values were taken from Coleman and Jenkinson (1999) and are commonly used for the equilibration of models starting with deciduous forest cover (Smith and others 1997). Glen Finglas has been grazed by livestock since the 1860s (Sanderson 1998), so to establish SOC content in different soil pools at the point of measurement (2009) the model was run for 149 years using plant inputs from the low sheep stocking treatment, assuming traditional management in the uplands. The annual C input was an average of the sward-scale (including tussock and inter-tussock) *M. caerulea* C stock of 7.87 Mg C ha^{-1} with a measured DPM/RPM ratio of 1.5; this value is similar to that for improved grasslands in Coleman and Jenkinson (1999). The amount of RPM, the lignin and lignin-like plant material, used to calculate the previous DPM/RPM ratio, was determined using a sulphuric-acid digestion method (Woodin and others 2009) and was averaged for both roots and above-ground (shoot-base and leaf) tissue from the low intensity sheep grazing treatment. The DPM was calculated as (Total Dry Material – RPM). Inert Organic Matter (IOM), the biologically inert SOC pool, was set at zero due to a lack of radiocarbon data essential to quantify this pool. Changes in IOM estimates are likely to result in only small errors in predicting SOC (Fallon and others 2000). The SOC of experimental plots was measured in 2009 (16 soil cores, 4.2 cm diameter, 15 cm deep; adjusting bulk density for stone content > 1 mm and determining C via elemental analysis) to validate the model estimate. An overall average SOC, across all grazing treatments, was used for validation as the treatments had not been established long enough to have generated detectable differences in SOC between them.

RothC was then run from 2009 for 100 years following three scenarios, commercial sheep stocking, low sheep stocking, and no livestock, using the average tussock and inter-tussock C stock measured in each grazing treatment as the annual inputs of plant residues, again with a DPM/RPM ratio of 1.5. Predicted confidence intervals (CI) were generated using the upper and lower 95% CI of plant C stocks as inputs for each grazing treatment. The meteorological data used to drive RothC to equilibrium were precipitation data from Glen Finglas 1982 – 2000 (UK Meteorological Office 2012) and average temperature data from two Scottish upland sites Glensaugh and Invercauld 2010 -2011 (Artz and others unpublished). This alternative source of upland temperature data was used due to a lack of annual measurements for Glen Finglas and was assumed not to influence predicted treatment effects from RothC. As a multipool model, RothC is relatively insensitive to differences in temperature compared to other single C pool models (Jones and others 2005).

RESULTS

TUSSOCK AND INTER-TUSSOCK SCALE PLANT C DISTRIBUTION

Total C stored in *M. caerulea* tussocks was reduced by commercial sheep stocking (Figure 1), while values from low sheep stocking and ungrazed plots were similar. Treatment effects on plant C pools were due to the influence of grazing on vegetation biomass: the C concentrations in *M. caerulea* shoots, shoot-bases and roots were unaffected by grazing treatment. *M. caerulea* shoot-bases comprised the largest tussock C pool, which was approximately 50 % or 11 Mg C ha^{-1}, smaller under commercial sheep grazing compared to low and ungrazed treatments. There was no effect of grazing on the C pools of the shallow or deep roots under tussocks. Quantities of C in inter-tussock vegetation were 81.0 ± 8.7 %

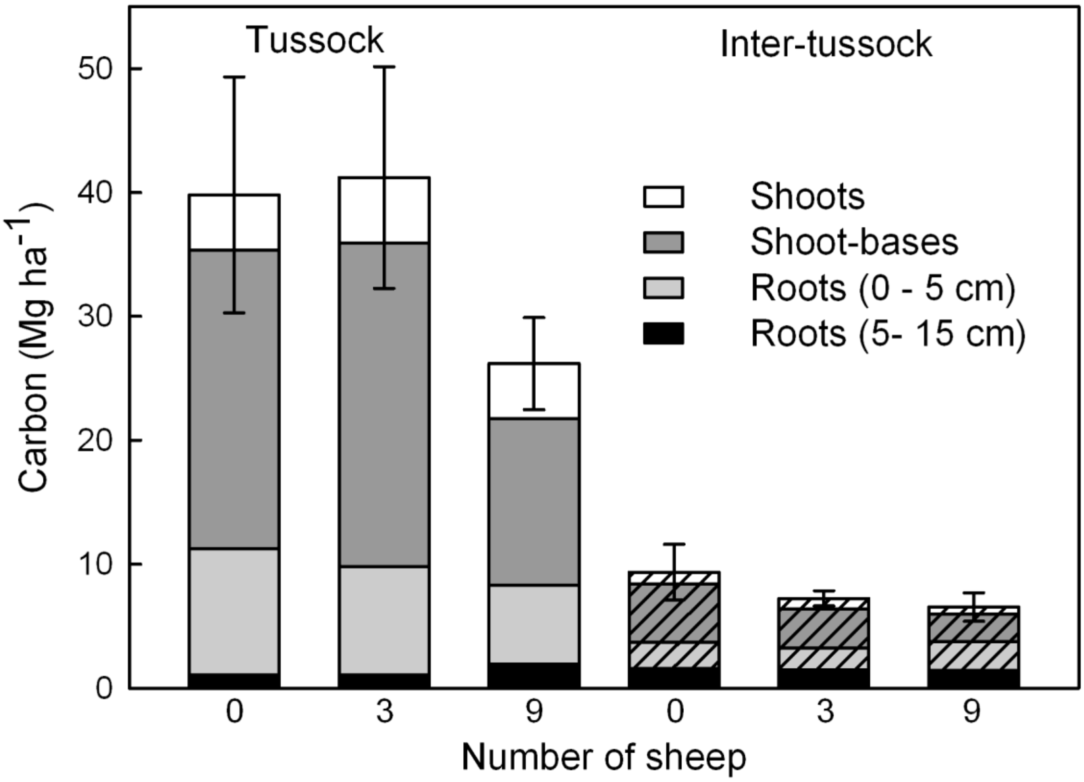

Figure 1 *Molinia caerulea* carbon pools within tussock (solid bars) and inter-tussock (hashed-bars) in three sheep grazing treatments (ewes plot^{-1}). Sheep grazing treatments of 0, 3 and 9 ewes plot^{-1} are the equivalent of 0, 0.9 and 2.7 ewes ha^{-1}, respectively. Error bars are only for the total,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

(mean ± 1 SD) less than in tussock vegetation across all grazing treatments, but the influence of grazing on plant C pools followed a similar pattern to tussocks (Figure 1).

SWARD SCALE TUSSOCK AND INTER-TUSSOCK AREA AND C STOCKS

Overall livestock grazing treatments significantly explained variation in total tussock area, ($\chi2(2)=6.419$, $p=0.04$), the number of tussocks ($\chi2(2)=12.205$, $p=0.002$), but not average tussock size ($\chi2(2)=0.2878$, $p=0.866$) when compared to a null model without treatments. Within the *M. caerulea* sward, the total area of tussocks under commercial sheep stocking densities was significantly lower ($z_{36} = 2.54$, $p = 0.030$), covering 30 % less area than in ungrazed plots (Figure 2). Low sheep stocking reduced total tussock area in comparison to the ungrazed treatment, but not significantly so ($z_{36} = 1.61$, $p = 0.242$), due to large variability in total tussock area within plots.

The significantly lower tussock area in grassland subject to commercial grazing was due mainly to the low number of tussocks rather than these being smaller in size. The number of tussocks was significantly lower only under the commercial sheep grazing intensity compared to other treatments; average densities were 2.0 ± 0.46 tussocks per m^2 (mean ± 1 SD) under high grazing, compared to 2.5 ± 0.49 tussocks per m^2 under low ($z_{36} = 3.22$, $p = 0.004$) and 2.7 ± 0.42 tussocks per m^2 under ungrazed ($z_{36} = 4.41$, $p = <0.001$) treatments. The size of established tussocks varied greatly, averaging 0.085 ± 0.069 m^2 (mean ± 1 SD) across all treatments, and was not significantly influenced by any grazing treatment, even under commercial sheep grazing compared to low ($z_{36} = 0.06$, $p = 0.998$) and ungrazed ($z_{36} = 0.49$, $p = 0.874$) treatments.

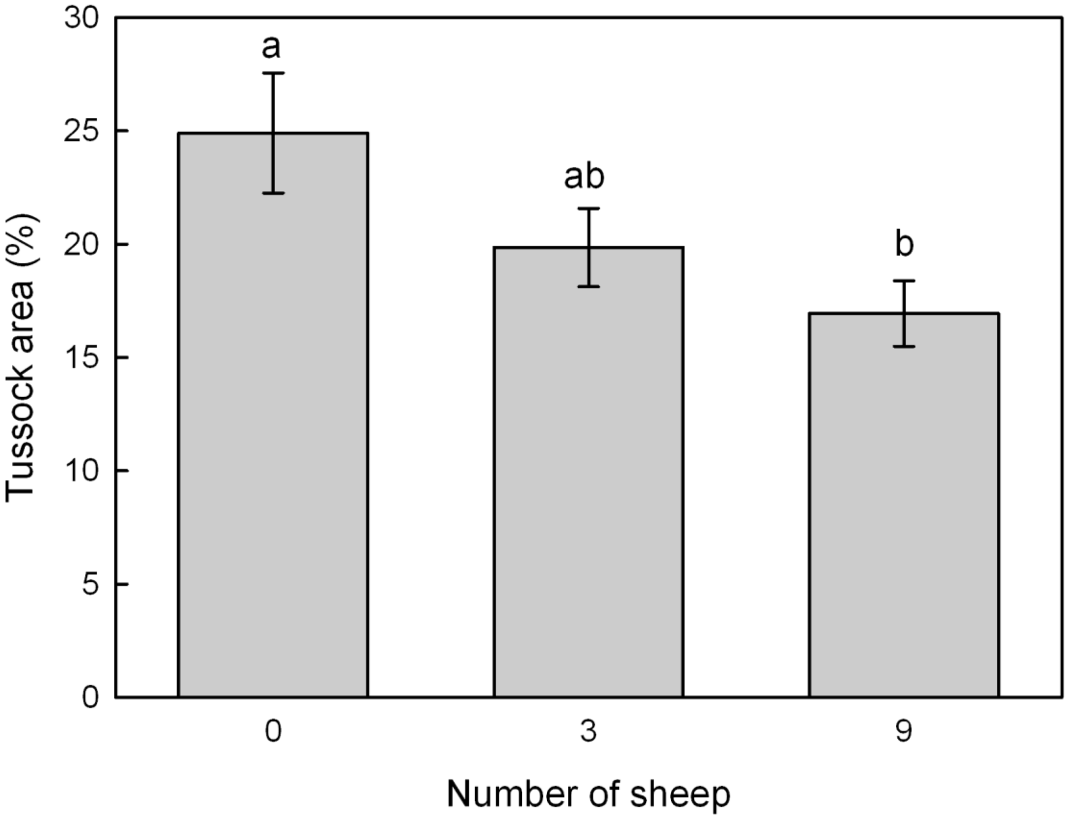

Figure 2 Total tussock area within 2 m × 10 m transects in three sheep grazing treatments (ewes plot^{-1}). Sheep grazing treatments of 0, 3 and 9 ewes plot^{-1} are the equivalent of 0, 0.9 and 2.7 ewes ha^{-1}, respectively. Different letters above bars represent a significance difference ($P<0.05$),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

At the sward scale, the C stocks of *M. caerulea* tussocks decreased with increased sheep stocking densities (Figure 3), due to a smaller tussock area and associated dense vegetation C pool. Under commercial sheep stocking, the contribution of tussocks and inter-tussocks to total vegetation C was equal. Average vegetation C, including tussocks and inter-tussocks, was 3.50 (± 0.46) Mg C ha^{-1} (± 1 SE) higher in ungrazed swards than in swards subject to commercial sheep grazing. After 7 years without grazing, *M. caerulea* swards have the potential to accumulate 38 % more C than a commercially grazed sward and 27 % more C than a sward under low sheep stocking density. Prior to the establishment of this experiment the land was stocked at low sheep density; increasing to commercial sheep stocking would have resulted in an estimated net loss of 2.16 (± 0.96) Mg C ha^{-1} (± 1 SE) from the *M. caerulea* sward over 7 years.

LANDSCAPE-SCALE C STOCKS

In this experiment the area covered by *M. caerulea* sward at the landscape-scale did not differ under commercial sheep grazing compared to low-intensity sheep grazing ($z_6 = 0.32$, $p = 0.946$) or no grazing ($z_6 = 1.36$, $p = 0.359$) treatments. However, there was inherent variation in its abundance between plots (ranging between 34.1 – 88.7 % cover; Supplementary information Table S1). Scaling the *M. caerulea* sward C by the actual cover of *M. caerulea* sward within each plot, C stocks were 3.83, 5.01 and 6.85 Mg C ha^{-1} for commercial sheep grazing, low sheep grazing and no grazing, respectively. The mean percentage reduction in the C stock of *M. caerulea* under commercial sheep grazing compared to no grazing was similar when accounting for the actual *M. caerulea* sward cover at the whole landscape-scale (46 ± 16 % ± 1 SD) as at the sward scale as described above (38 ± 16 %).

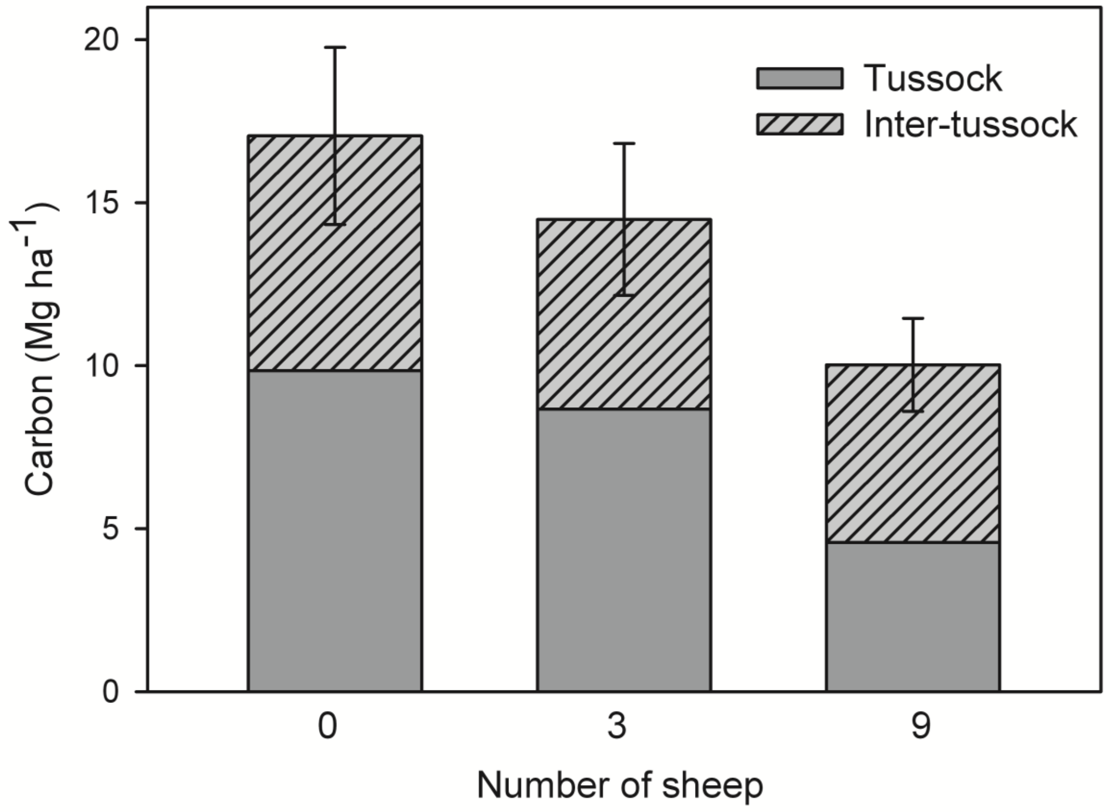

Figure 3 Total carbon content of *Molinia caerulea*, tussocks (dark grey) and inter-tussock (hashed light grey) in three sheep grazing treatments (ewes plot^{-1}) at the sward scale. Sheep Sheep grazing treatments of 0, 3 and 9 ewes plot^{-1} are the equivalent of 0, 0.9 and 2.7 ewes ha^{-1}, respectively.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

PREDICTING SOIL ORGANIC C STORAGE

The RothC estimate of SOC in 2009 (114.3 Mg C ha^{-1}), based on mixed forest equilibrium followed by a century and a half of low sheep stocking, were within the standard error of SOC measured in 2009 (Figure 4, year 0). Following this accurate prediction of soil C stocks after 150 years of low-intensity sheep grazing and using measured *M. caerulea* inputs, the model was run forward for a further 100 years under the different grazing scenarios. In the absence of grazing, the system was predicted to accumulate 14.36 Mg C ha^{-1} of SOC, whereas commercial sheep grazing was predicted to result in a SOC loss of 23.11 Mg C ha^{-1} (Figure 4). Maintenance of low sheep grazing management resulted in accrual of 13.62 Mg C ha^{-1} over 100 years, this amount being similar to lower estimates of SOC accrual with no grazing. Thus, commercial sheep grazing was the only grazing treatment predicted to reduce SOC. Within the model, changes in the Humified Organic Matter (HUM) pool had the largest influence on total SOC (Figure 5). Predicted HUM in the ungrazed treatment was 25.34 Mg C ha^{-1}, or 23 %, higher than under commercial stocking densities, but only 9.71 Mg C ha^{-1}, or 10 %, higher than under low sheep grazing. Resistant Plant Material (RPM) and Decomposable Plant Material (DPM) are plant inputs into SOC, but also become part of SOC. RPM was a smaller SOC pool than HUM, comprising on average 19 % compared to 79 % of the total SOC across all grazing treatments. However, RPM showed a larger percentage difference between grazing treatments than HUM after 100 years; predicted RPM C pools in the ungrazed treatment were 38 % greater than commercial sheep stocking and 15 % greater than low sheep stocking scenarios. The combined predicted DPM and Microbial Biomass (BIO) pools only comprised an average of 2 % of the total SOC stocks across all treatments.

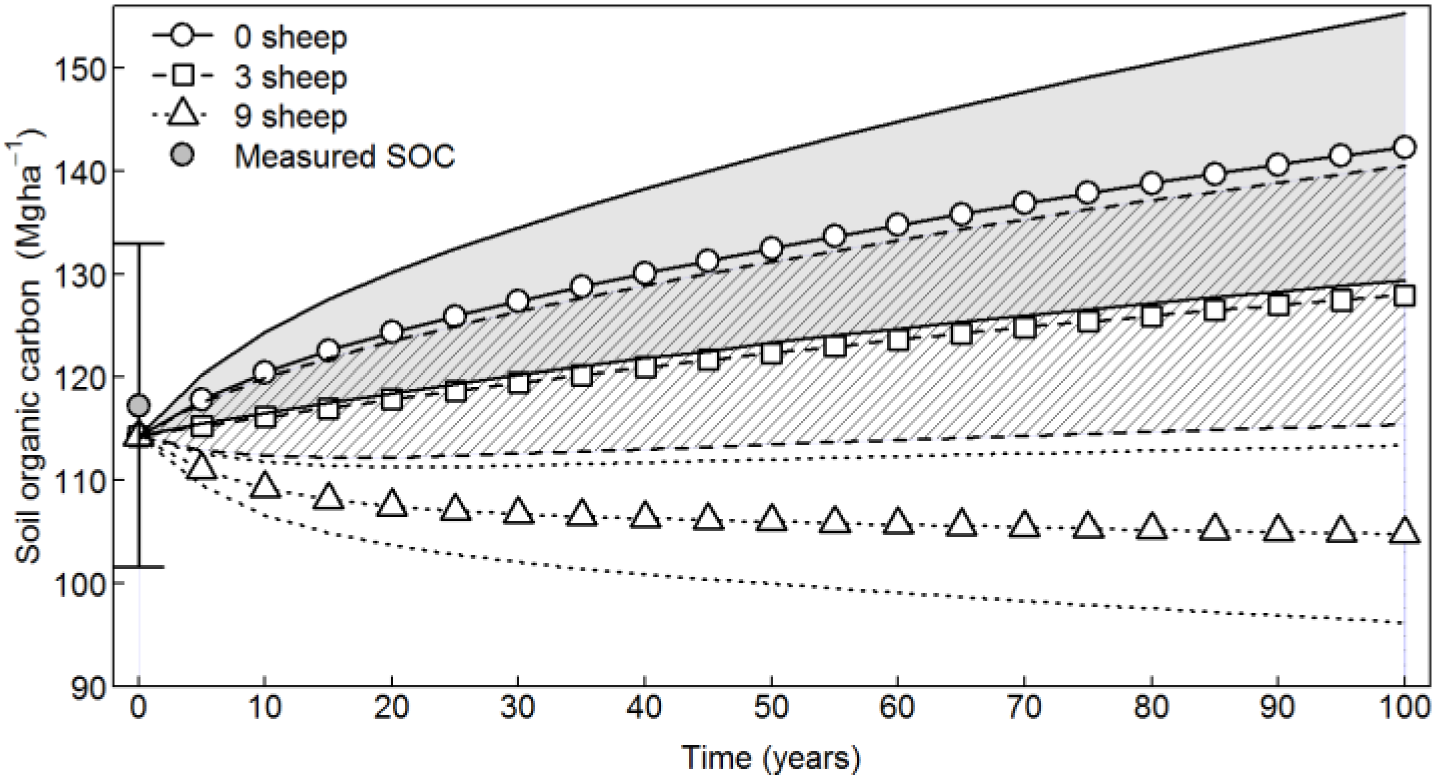

Figure 4 RothC modelled changes in SOC (to a depth 15 cm) in three grazing treatments (ewes plot^{-1}). Sheep grazing treatments of 0, 3 and 9 ewes plot^{-1} are the equivalent of 0, 0.9 and 2.7 ewes ha^{-1}, respectively. The model input was from derived from mean vegetation C stocks in the three grazing 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.

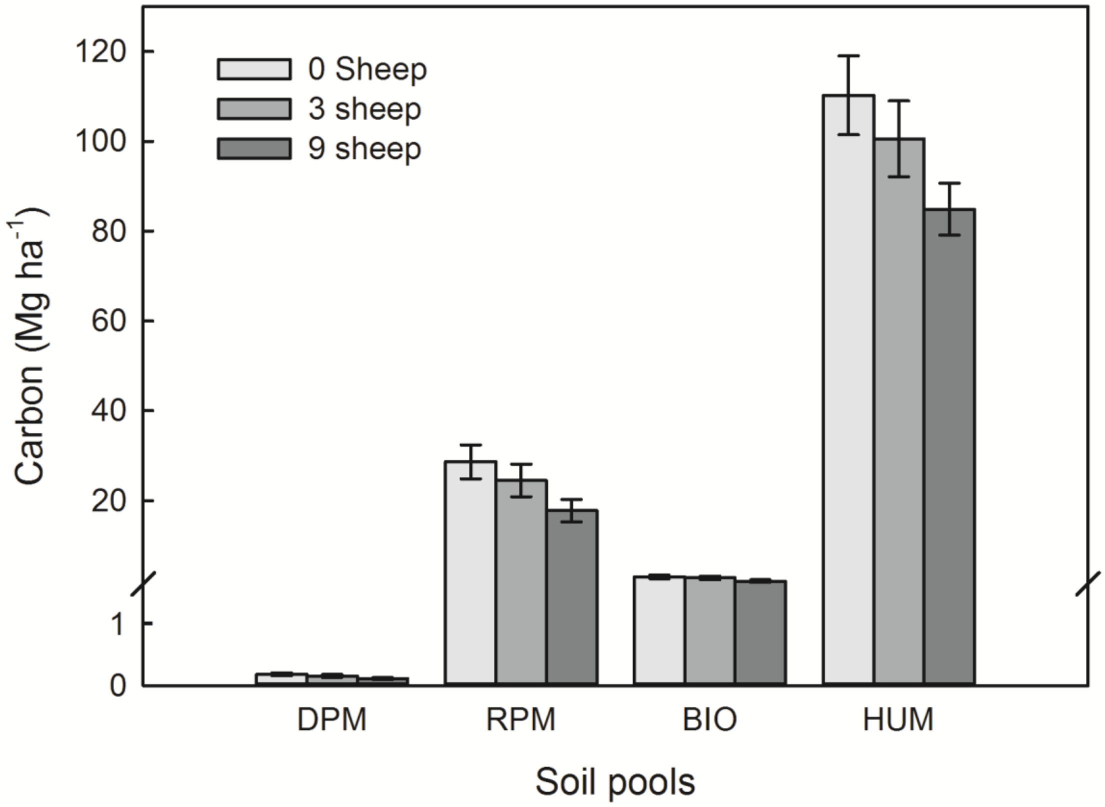

Figure 5 RothC modelled SOC pools after 100 years in three sheep grazing treatments (ewes plot^{-1}). Sheep grazing treatments of 0, 3 and 9 ewes plot^{-1} are the equivalent of 0, 0.9 and 2.7 ewes ha^{-1}, respectively. Modelled RothC SOC pools include: Decomposable Plant Material (DPM), Resistant Plant 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 impact, we would have expected commercial sheep densities would primarily have reduced *M. caerulea* tussock size. This would occur through shoot removal subsequently affecting the size of the shoot-bases, which are the overwintering storage organs (Latusek 1983; Thornton 1991; Taylor and others 2001), and it is the size and number of these shoot-bases that determine tussock size (Grant and others 1996). However, the fact that it is the number of tussocks which has declined suggests that other mechanisms are important, such as trampling (Billotta and others 2007), severe defoliation causing all of a tussock's shootbases to die at the same time, and a reduction in flowering (Thornton 1991; Grant and others 1996).

In the longer term, the loss of C due to heavy grazing of *M. caerulea* might be expected to become smaller as a result of grazer-induced changes in plant species composition, with less palatable species replacing *M. caerulea*. This could mitigate any loss of plant C stocks attributed to grazing (Tanentzap and Coomes 2012). However, in this system, the area of the landscape covered by the *M. caerulea* sward was not noticeably smaller after 7 years of sheep grazing compared to no grazing. Furthermore, controlled grazing studies in the same type of upland vegetation have shown that heavy grazing favours more palatable grasses such as *Agrostis* and *Holcus* spp. (Grant and others 1996; Taylor and others 2001). These swards do not form tussocks, and have a small plant C storage potential, similar to *M. caerulea* inter-tussocks (data not shown). Thus, the change in plant species composition that is likely to occur under prolonged heavy grazing at Glen Finglas would result in continued loss of C, though perhaps at relatively slower rates than initial loss caused by the reduction in number of *M. caerulea* tussocks.

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 pastures; identified using CENTURY organic turnover model with estimated plant C inputs (Wang and others 2008). Here we similarly identified that low sheep grazing pressure is optimal for SOC storage in temperate upland grasslands, but in this case we used measured plant C inputs, which may provide a better basis for modelling.

USING LIVESTOCK GRAZING TO MANAGE UPLAND C STORAGE

The measured benefits for plant C stores of stopping or reducing sheep grazing on *M. caerulea* swards (3.5 Mg C ha^{-1} after 7 years) are smaller than the benefits of other plant C sequestration strategies, such as short rotation forestry (21.5 - 22.5 Mg C ha^{-1} in 3 years; Deckmyn and others 2004) or plantation of bio-energy crops, such as *Miscanthus x giganteus* (17 Mg C ha^{-1} in 10 years; Clifton-Brown and others 2007; Dondini and others 2009). Likewise, predicted SOC accumulation following cessation of sheep grazing was small over a time span of 100 years (14.36 Mg C ha^{-1}) compared to *Miscanthus* plantations (130 – 160 Mg C ha^{-1} of SOC in 30 years; Dondini and others 2009). Nevertheless, C gains from reducing or a cessation of sheep grazing in this upland landscape are obtained without significant engineering (Reed and others 2009). Equally, the diverse upland landscape allows multiple C management practices to be pursued where locally appropriate, which often enhances the social and cultural value of uplands (Morgan-Davies and Waterhouse 2008; Dandy and Van der Wal 2010).

Uplands are managed for multiple purposes; culturally, as a source of rural employment and for the goods and services they provide (Orr and others 2008; Reed and others 2009). Appropriate upland C management must be weighed against such wider land use objectives. Using evidence from the Glen Finglas grazing experiment, C storage can be weighed against the abundance of characteristic species, as is increasingly being discussed for the uplands (e.g.

Van der Wal and others 2011). For instance, at Glen Finglas ungrazed *M. caerulea* swards are poor foraging habitat for the meadow pipit (*Anthus pratensis*) (Vandenberghe and others 2009). However, both breeding and foraging success of this typical upland bird species was greatest under low density sheep grazing compared to either commercial or no sheep grazing (Evans and others 2005; Prior and others 2011). Field vole (*Microtus agrestis*) abundance (Evans and others 2006), and nocturnal moth and other arthropod abundance and diversity are negatively affected by increasing sheep grazing intensity (Dennis and others 2008; Littlewood 2008). This suggests that optimal management to both sequester C and sustain biodiversity in *M. caerulea*-dominated upland landscapes may be to reduce sheep grazing intensity, as opposed to a cessation of sheep grazing altogether.

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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