Impacts of grazing abandonment on ecosystem service provision: Coastal grassland as a model system

Hilary Ford [a,b,*], Angus Garbutt [a], Davey L. Jones [b], Laurence Jones [a]

[a] Centre for Ecology & Hydrology, Environment Centre Wales, Deiniol Road, Bangor, UK
[b] School of Environment, Natural Resources and Geography, Bangor University, Environment Centre Wales, Deiniol Road, Bangor, UK

ABSTRACT

A coastal grassland was used as a model system to examine how grazing management, un-grazed (for six years), rabbit grazed or fully grazed (ponies 0.2 ha^{-1}, cattle 0.05 ha^{-1} and rabbits 45 ha^{-1}), affected biodiversity and ecosystem service provision, by measuring an extensive suite of biophysical variables as proxies for ecosystem services. For 'supporting services', nutrient cycling was greatest in un-grazed grassland but primary productivity did not differ. The 'provisioning service' of food production was only provided by fully grazed grassland. For grazing effects on 'regulating services' total carbon (C) stock did not differ and effects on pest regulating invertebrates and pollinator abundance were variable. The potential for flood control was considered greatest in the un-grazed grassland; with faster water infiltration than in the fully grazed grassland. The 'cultural service' of environmental appreciation was considered higher in fully grazed grassland due to significantly greater plant species richness, more forb species and more forbs flowering than in un-grazed grassland.

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1. Introduction

Grassland management for multiple ecosystem services often results in potential conflicts or trade-offs (MacLeod and McIvor, 2006). This is important as many ecosystem services are delivered by semi-natural grasslands (Bullock et al., 2011; Table 1); "supporting services" (primary productivity and nutrient cycling); "provisioning services" (food production, preservation of the genetic diversity of wild species and fresh water supply); "regulating services" (maintenance of an equable climate, water storage, pest regulation and pollination) and "cultural services" (conservation status, environmental appreciation and recreation). In managed grasslands, the basic trade-off is between intensive management to maximise food production and extensive management resulting in lower production, but increased biodiversity and a wider range of cultural services (Power, 2010). Semi-natural, low productivity grasslands, traditionally used for low intensity cattle and sheep farming, have declined by 90% in the UK since 1945, converted to intensive production by drainage and fertilisation (Bullock et al., 2011). In many parts of Europe they now face a further threat, with managed grazing of these habitats being 'abandoned' in both the uplands and lowlands due to the removal of

European Union (EU) subsidies (Strijker, 2005). Policy makers have signed up to halt biodiversity loss and degradation of ecosystem services within the EU by 2020 and to adopt an integrated approach to land use management (Kleijn et al., 2011). It is therefore vital to assess how abandonment of low productivity grazing land impacts on biodiversity, ecosystem function and potential consequences for ecosystem service provision.

The effects of removing large herbivores (i.e. cattle, sheep or horses) are well understood for grassland biodiversity and ecosystem function, but the implications for wider ecosystem service provision have been poorly quantified, or not quantified at all, especially for multiple services (Power, 2010). Grazing removal decreases plant diversity (Pykälä, 2003), increases invertebrate and small mammal abundance and diversity (Morris, 2000; Schmidt et al., 2005), and can either increase or decrease bird abundance and diversity dependent on feeding and nesting sward requirements (Vickery et al., 2001). Where large grazers are removed smaller grazers, particularly rabbits, may define habitat characteristics, keeping patches of grassland fairly open, preventing declines in plant diversity but allowing soil to become less compact (Isermann et al., 2010), creating a habitat with characteristics of both grazed and un-grazed grassland, with likely mixed effects upon ecosystem services. Voles and other small mammals are usually present, even within 'un-grazed' areas and have different effects on vegetation and nutrient cycling characteristics to large herbivores (Bakker, 2003). Cessation of cattle grazing where rabbits are not present leads to the development of a plant community dominated by highly competitive tall grasses or shrubs (Janišová et al., 2011)

* Corresponding author at: Centre for Ecology & Hydrology, Environment Centre Wales, Deiniol Road, Bangor, UK. Tel.: +44 7854 758788.
E-mail addresses: hilaryfordnz@hotmail.com (H. Ford), ag@ceh.ac.uk (A. Garbutt), d.jones@bangor.ac.uk (D.L. Jones), lj@ceh.ac.uk (L. Jones).

Table 1
Ecosystem services (S = supporting, P = provisioning, R = regulating, C = cultural) with list of proxy measurements.

Ecosystem service	Proxy measurement
Primary productivity (S)	Annual net primary productivity (above ground)
Nutrient turnover (S)	N mineralisation rate
	Detritivore feeding rate
	Root turnover rate
Food production (P)	Number of cattle per hectare
Genetic diversity (P)	Plant species richness
Equable climate (R)	C stock
Flood control potential (R)	Water infiltration rate
Pest regulation (R)	Invertebrate biodiversity, spider and predatory beetle abundance
Pollination (R)	Nectar feeder biodiversity and abundance
Conservation (C)	Abundance of RDB or nationally scarce invertebrates
Aesthetic appreciation (C)	Plant biodiversity, vegetation structure, grass:forb ratio & flowering

with reduced soil compaction and possible implications for several variables linked to ecosystem service provision.

Above-ground primary productivity (ANPP), a key supporting service, may increase or decrease with grazing intensity (De Mazancourt et al., 1998; Leriche et al., 2003). Nutrient turnover, another supporting service, also shows variable effects with grazing management (Bakker, 2003; Bardgett et al., 1998; Van Wijnen et al., 1997). Coastal grasslands, particularly those adjacent to crop fields, may potentially provide invertebrates for the twinned regulating services of pest control and pollination (Everard et al., 2010; Losey and Vaughan, 2006). However, effects of grazing intensity on these services are difficult to predict. Invertebrate pest regulators, such as spiders and beetles, are often more abundant on un-grazed grassland (Morris, 2000) but pollinators may be most abundant on grazed grassland due to a likely increase in floral resources (Potts et al., 2003; Sjödin et al., 2008). Soil moisture and temperature changes may also affect the regulating service of equable climate, via impacts upon C storage and greenhouse gas emissions (Luo and Zhou, 2006). The cultural service of aesthetic appreciation is likely to be higher in grazed grasslands due to expected greater plant diversity and abundance and diversity of forbs (Pykälä, 2003).

To date, where links have been drawn between grazing intensity, impact upon ecosystem characteristics, and multiple ecosystem service provision, these have been largely based on literature reviews (Bullock et al., 2011; Kemp and Michalk, 2007). There have been few habitat case studies where these effects have been quantified within an ecosystem services framework. The novelty of this study lies in using a wide range of habitat measurements across different grazing intensities as proxies for specific ecosystem services (Table 1). A managed grazing experiment within a low fertility grazed coastal grassland was used as a model system to examine how grazing affects ecosystem service provision, following the framework of the Millennium Ecosystem Assessment (MA, 2005) and the UK National Ecosystem Assessment (Bullock et al., 2011). The three grazing treatments used were 'fully grazed' (i.e. extensively cattle, pony and rabbit grazed), 'rabbit grazed' and 'ungrazed' (i.e. abandoned). The overarching hypothesis of this study is that 'changes in grazing will differentially affect individual services, and will alter the balance of supporting, provisioning, regulating and cultural ecosystem service provision of semi-natural grassland.

2. Materials and methods

2.1. Study site and experimental design

Fixed sand dune grasslands are low-productivity semi-natural grasslands, and a UK Biodiversity Action Plan (BAP) priority habitat. Newborough Warren is a calcareous coastal sand dune grassland, located in NW Wales (53°8′59″N, 4°21′1″W), noted for its high biodiversity and designated as a National Nature Reserve, Site of Special Scientific Interest and Special Area of Conservation under the EC Habitats and Species Directive 1992. The 389 ha site is managed by Countryside Council for Wales (CCW). Managed grazing was introduced in 1987; stocking levels have varied but the site is now grazed by ponies (Equus ferus caballus; 0.2 ha^{-1}), cattle (Bos taurus; 0.05 ha^{-1}) and rabbits (Oryctolagus cuniculus; 45 ha^{-1}), designed to maximise plant diversity. Rare breed cattle, Belted Galloways and Dexters are stocked within the fully grazed study area for 18 months before being 'finished' on improved pasture and sold for meat (Graham Williams, pers. commun.). The predominant vegetation in the experimental area is fixed dune Festuca rubra - Galium verum grassland. In 2003, three replicate experimental blocks, each containing three 10 m × 10 m experimental units, one fully grazed unit (unfenced), one rabbit grazed unit (fenced with 10 cm × 10 cm mesh to exclude large grazers) and one un-grazed unit (fenced with 10 cm × 10 cm mesh and an additional 2.7 cm × 3.7 cm mesh buried 20 cm underground to prevent rabbit access) were set up. Experimental blocks are separated from each other by hundreds of metres and by low dunes. Prior to construction of grazing exclosures the vegetation was a uniform 4–6 cm height. Small mammals such as field voles (Microtus agrestis) and invertebrate herbivores were assumed to be present within all experimental units. All biophysical measurements avoided a 1 m buffer zone adjacent to the fences for rabbit grazed and un-grazed exclosures. Fully grazed units are denoted as PR1–PR3 (PR stands for pony & rabbit grazed); rabbit grazed units as R1–R3 and un-grazed units as U1–U3.

2.2. Soil characteristics

Soil moisture content and temperature were recorded within each experimental unit, at six locations, once a month from June to September 2009. Soil conductivity was measured in direct volts using a Delta T Theta Meter HH1 across 6 cm depth and converted to percentage soil moisture content using a calibration suitable for mineral soils. Soil temperature was measured in the top 11 cm using a digital thermometer. Samples to determine bulk density and soil organic matter content were collected during September 2009 using three intact soil cores of 3.8 cm diameter and 15 cm depth from each experimental unit. Cores were dried at 105 °C for 72 h and the dry mass divided by the volume of the core to calculate bulk density. Loss-on-ignition, at 375 °C for 16 h was used to estimate organic matter content. pH was determined using a Corning pH meter 220. Water infiltration rate was measured using three single ring infiltrometers (Carroll et al., 2004) per experimental unit. This method was used as vertical percolation flux dominates water flow in sandy soil. These 10 cm diameter × 20 cm length cylinders were hammered 5 cm into the ground and briefly filled with water to pre-saturate the ground. Water was again poured into the infiltrometers up to 5 cm from the top. The time taken for the water

to move 5 cm down the infiltrometer was recorded and converted into a water infiltration rate in mm min^{-1}.

Plant available nitrogen (N) was measured by N mineralisation assays (Rowe et al., 2011) calculated from three 15 cm depth soil cores per unit, taken in September 2009. Soil cores were taken using plastic corers, capped at both ends to minimise soil disruption and stored intact at 4 °C. Accumulated inorganic N was flushed from the cores by spraying with a solution of similar ionic concentration to UK rain over 7 d until 150 ml of leachate had been collected. Cores were incubated at 10 °C for 28 d, homogenised and a sub-sample extracted using 1 M KCl for the analysis of ammonium and nitrate content (Rowe et al., 2011). Net nitrification and ammonification rates were calculated over these 28 d, assuming that all previous inorganic N had been removed during the 7 d flushing period, and were expressed as mg N g^{-1} dry wt d^{-1}. Litter breakdown via mesofaunal detritivores was measured in autumn using ten bait lamina (Terra Protecta GmbH, Germany) per unit (in two lines of five, 50 cm apart).

2.3. Vegetation characteristics

During July, vegetation height was measured at five points within five 1 m × 1 m quadrats per experimental unit with a custom made drop disc of 20 cm diameter, 10 g mass. Within two quadrats from each unit above-ground live vegetation and plant litter was collected from a 25 cm × 50 cm area cut to ground-level. One root core of 5 cm diameter and 10 cm depth was also taken per quadrat and washed to remove all soil. Above-ground vegetation, litter and roots were all dried at 80 °C for 24 h and weighed to give indicators of above-ground shoot biomass, litter biomass and below-ground root biomass, respectively. C stock (t C ha^{-1}) was measured for four pools: soil, roots, plant litter and shoots, derived from biomass using the following conversions: Soil C as 0.55 of soil organic matter; root C is 0.44 of root biomass (dry wt) and plant litter and shoot C is 0.42 of biomass (dry wt) in comparable UK fixed dune grasslands (unpublished data). ANPP, peak biomass from three grazer excluded areas per experimental unit, was recorded as a direct measure of primary productivity. During February 2009, vegetation was cut to ground level in three 50 cm × 50 cm areas per experimental unit. Each cut area was protected from pony, cattle and rabbit grazers by an 8 cm mesh gabion (50 cm × 50 cm × 50 cm) and vegetation allowed to re-grow until peak biomass at the end of August when areas were re-cut within a central 25 cm × 25 cm area. Vegetation was dried at 80 °C for 72 h then weighed and converted to kg dry wt m^{-2} yr^{-1} to provide a measure of ANPP. Autumnal fine root turnover was estimated by modifying the method of Lukac and Godbold (2010). In mid September 2010 four nylon 1 mm root turnover mesh strips (Normesh, UK), 2.5 cm wide × 15 cm long, were placed in vertical cuts made in the soil with 2.5 cm overlap at the bottom and 2.5 cm emerging from the soil, 50 cm apart, across a 2 m transect in each unit. After 28 d the mesh strips were removed along with a slightly wider and deeper intact soil core. Cores were pushed out and divided in two along the mesh line, the number of fine roots penetrating each mesh depth zone (0–2.5; 2.5–5; 5–7.5; 7.5–10 cm) were counted by eye as a proxy for fine root turnover.

2.4. Biodiversity of plants and invertebrates

Plant percentage cover, species richness and number of species flowering were recorded during July in five 1 m × 1 m quadrats from each experimental unit. For functional group analysis, plant percentage cover data was standardised to 100% and divided into six broad phylogenetic functional groups: lichen, moss, forbs, sedges, grass and shrubs.

Pitfall traps were used to sample ground dwelling invertebrates for 26 d in May and 28 in July. Six pitfall traps per experimental unit

were set up in two lines of three, 2 m apart. Each trap consisted of a plastic cup (80 mm diameter × 105 mm deep) a third full with a 50/50 mix of ethylene glycol and water, to preserve invertebrates, with a drop of washing up liquid to break the surface tension. Each trap was pushed into a hole made by a soil auger until they were level with the soil surface. A rain hat was placed over each trap and set at 3 cm from the ground. A wire basket of 5 cm mesh size was also placed over each rain hat and pegged down to prevent interference by grazers. Most invertebrates caught in pitfall traps were identified to species level, apart from Diptera and parasitic Hymenoptera, and assigned to a functional group: predatory, zoophagous (predatory and scavenging), phytophagous (herbivore or granivorous), detritivore (feed on detritus and associated decomposer community of fungi and bacteria), or an additional category 'not assigned'.

Nectar feeding invertebrates were sampled by bait-less pan traps, six per experimental unit (2 blue, 2 white, 2 yellow), for 72 h during June and again in July 2009. In each experimental unit two triangles, 5 m apart, consisting of one pan trap of each colour, 1.5 m apart, was set up. Traps of the same colour were pooled to give three samples per experimental unit. Each trap consisted of 203 mm diameter shallow bowls sprayed yellow, blue or white, half filled with water containing a drop of washing detergent to break the surface tension. Wire baskets of 5 cm mesh size were placed over all traps to prevent damage by grazing animals. The contents of the pitfalls and pan traps were preserved in 70% Industrial strength methylated spirits (IMS) or ethanol.

2.5. Analysis

The effect of grazing on each measured variable was analysed using an ANOVA on linear mixed effects model (lme) output in R (R Development Core Team, 2011) e.g. lme (temperature ~ grazing, random = ~1|block/grazing). This approach was used to enable the raw data to be analysed accounting for replication at the level of the experimental unit or block (n = 3). Variables were log, square root, or arcsine square root transformed as appropriate to improve model fit. Results of best model fit were presented here based on lowest Akaike information criterion (AIC) number and quantile probability plot (qqnorm) with most normal distribution. Where ANOVA results showed a significant grazing effect, differences between pairs of grazing treatments (PR & R; PR & U), were reported directly from the lme summary output. As the remaining treatment pair (R & U) could not be 'read' directly from the lme summary, the difference between values for R and U in relation to PR was divided by the standard error to give a number (#) for the following calculation '2 × (1 − pt(#,d.f. = 4))' This gives a probability value for the difference between R and U for a two-tailed test where d.f. = 4.

3. Results

3.1. Soil and vegetation characteristics

Soil temperature was significantly higher on the fully grazed than the un-grazed grassland. Vegetation height was significantly different between all treatment pairs with the lowest sward height in the fully grazed, intermediate in the rabbit grazed and highest in the un-grazed grassland (Table 2). Root biomass was significantly greater in the rabbit grazed than the un-grazed grassland. Plant litter was significantly higher in the un-grazed and rabbit grazed compared to the fully grazed grassland. Water infiltration rate, was significantly higher in the un-grazed and rabbit grazed than fully grazed grassland. Soil pH, moisture content, bulk density, organic matter content and above-ground shoot biomass were not

Table 2
Soil and vegetation characteristics, grazing treatment means ± standard deviations with bold letters indicating significant differences at $^*p < 0.05$ or $^{***}p < 0.001$, ns = non-significant.

	Fully grazed	Rabbit grazed	Un-grazed	ANOVA
Soil				
pH	6.21 ± 0.37	6.16 ± 0.45	6.01 ± 0.33	ns
Moisture content (%)[a]	13.02 ± 8.12	8.28 ± 2.62	6.26 ± 5.42	ns
Temperature (°C)[a]	18.08 ± **2.90 a**	17.20 ± **0.39 ab**	16.93 ± **2.20 b**	*
Bulk density (g cm^{-3})	1.01 ± 0.07	1.02 ± 0.09	0.93 ± 0.10	ns
Organic matter content (%)	3.11 ± 0.71	3.23 ± 0.64	3.57 ± 0.92	ns
Infiltration rate (mm min^{-1})	6.60 ± **1.94 a**	22.74 ± **14.7 b**	37.27 ± **28.8 b**	*
Vegetation				
Vegetation height (cm)	5.27 ± **1.03 a**	19.43 ± **7.68 b**	37.63 ± **7.94 c**	***
Root biomass (kg dry wt m^{-2})	1.24 ± **0.55 ab**	1.22 ± **0.36 a**	0.71 ± **0.26 b**	*
Litter biomass (kg dry wt m^{-2})	0.12 ± **0.03 a**	0.22 ± **0.08 b**	0.28 ± **0.04 b**	*
Shoot biomass (kg dry wt m^{-2})	0.83 ± 0.29	0.80 ± 0.29	0.59 ± 0.25	ns
ANPP (kg dry wt m^{-2} y^{-1})	0.34 ± 0.09	0.35 ± 0.07	0.34 ± 0.10	ns

[a] Mean values of 4 months data, June–September.

significantly different between grazing treatments. Total C stock did not differ significantly with grazing. As separate C pools 'soil' and 'shoots' (above-ground live biomass) were not significantly different between grazing treatments (Fig. 1). Root C stock was significantly greater for rabbit grazed than un-grazed grassland, contributing around 20% of the total C pool. Plant litter C stock was significantly greater in un-grazed and rabbit grazed than grazed grassland.

ANPP and soil organic matter content (soil surface organic layer ~6 cm thick) did not differ significantly with grazing treatment (Table 2). Net nitrification rate was significantly higher in the un-grazed than the fully grazed grassland but net ammonification rate did not differ significantly with grazing treatment (Fig. 2). Mesofaunal feeding rate was significantly greater for rabbit grazed in depth zone 1 and for un-grazed in depth zone 2 and 3 compared to fully grazed grassland (Fig. 3). Fine root turnover at 0–2.5 cm was significantly greater in un-grazed and rabbit grazed than fully grazed grassland (Fig. 4).

3.2. Biodiversity

Cumulative plant species richness, for un-grazed, rabbit grazed and fully grazed plots was 45, 49 and 61 species (per 15 m^2), respectively. At the experimental unit level, fully grazed grassland was significantly more species rich, particularly for forbs, than un-grazed grassland (Table 3). Graminoids were equally species rich regardless of grazing intensity. Forb cover was significantly higher in fully and rabbit grazed grassland than in un-grazed habitat. In contrast, grass cover was significantly lower in fully grazed than rabbit or un-grazed grassland (Fig. 5). Total number of species
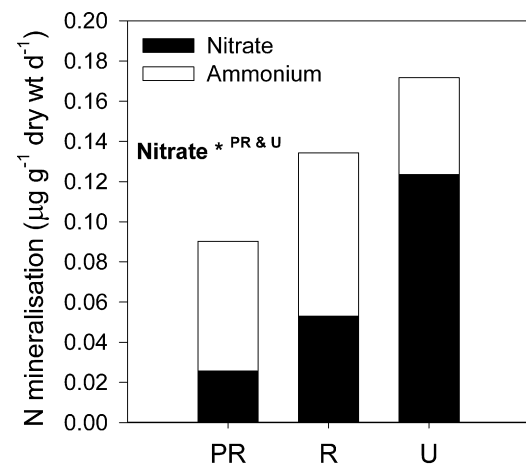

Fig. 2. Effect of grazing (PR = fully grazed, R = rabbit grazed, U = un-grazed) on N mineralisation. Bold text indicates significant differences between grazing treatments for each component, $^*p < 0.05$.
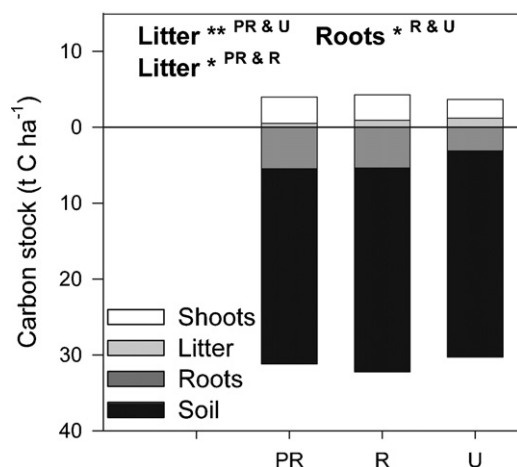

Fig. 1. Effect of grazing (PR = fully grazed, R = rabbit grazed, U = un-grazed) on C stock. Bold text indicates significant differences between grazing treatments for each component, $^*p < 0.05$, $^{**}p < 0.01$.
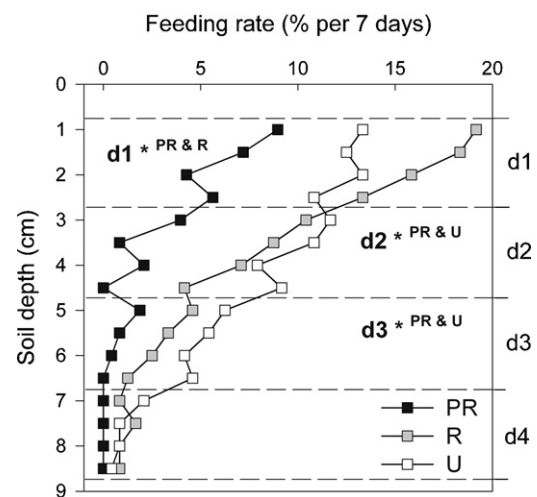

Fig. 3. Effect of grazing (PR = fully grazed, R = rabbit grazed, U = un-grazed) on below-ground mesofaunal feeding rate in autumn. Bold text indicates significant differences between grazing treatments for each depth zone (d1–d4), $^*p < 0.05$.

Table 3
Plant species richness and flowering, grazing treatment means ± standard deviations with bold letters indicating significant differences at *$p < 0.05$, ns = non-significant.

Variable	Fully grazed	Rabbit grazed	Un-grazed	ANOVA
Mean species richness (spp per 1 m × 1 m)				
All species	22.93 ± **4.04 a**	18.93 ± **4.51 ab**	16.20 ± **2.27 b**	*
Graminoid (grasses & sedges)	7.33 ± 1.50	7.20 ± 0.86	6.60 ± 0.83	ns
Forb	11.13 ± **2.45 a**	7.80 ± **2.81 ab**	5.47 ± **1.36 b**	*
Number of species flowering				
All species	10.53 ± **3.36 a**	8.93 ± **2.15 a**	6.33 ± **1.84 b**	*
Graminoid	4.40 ± 1.50	5.67 ± 0.98	4.60 ± 1.24	ns
Forb	6.13 ± **2.20 a**	3.27 ± **1.83 ab**	1.73 ± **1.22 b**	*
Percentage species flowering				
Graminoid	59.89 ± **16.8 a**	79.02 ± **11.6 b**	69.40 ± **16.4 ab**	*
Forb	54.36 ± **14.6 a**	41.92 ± **15.1 ab**	32.29 ± **21.2 b**	*
Forb/forb + graminoid pc.				
Forb percentage	21.25 ± **0.07 a**	16.65 ± **0.08 a**	6.90 ± **0.05 b**	*

flowering, particularly forbs, and percentage of forb species flowering were all significantly greater in fully grazed than un-grazed habitat.

Of nearly ten thousand invertebrates sampled from pitfalls, 40% were predatory spiders of 62 species and 3% predatory and

Fig. 4. Effect of grazing (PR = fully grazed, R = rabbit grazed, U = un-grazed) on number of new fine roots produced per month, as a proxy for potential fine root turnover. Bold text shows significant differences between grazing treatments for each soil depth *$p < 0.05$.

Fig. 5. Effect of grazing (PR = fully grazed, R = rabbit grazed, U = un-grazed) on plant functional groups (adjusted to 100%). Bold text shows significant differences between grazing treatments for each plant group, *$p < 0.05$, **$p < 0.01$.

zoophagous beetles, mainly carabids and Staphylinidae of 43 species. Pan traps sampled 14 bee species. Predatory Coleoptera were more abundant (ANOVA; $F = 5.2$, d.f. = 4, $p < 0.05$) and species rich (ANOVA; $F = 13.2$, d.f. = 4, $p < 0.01$) in fully grazed than un-grazed grassland. Araneae were also significantly most abundant (ANOVA; $F = 9.72$, d.f. = 4, $p < 0.05$) and species rich (ANOVA; $F = 9.72$, d.f. = 4, $p < 0.05$) on fully grazed land. Nectar feeders, as a proxy for pollinators, did not differ significantly in either abundance or species richness with grazing intensity.

Pan traps sampled *Colletes cunicularius* a Red Data Book (RDB3) listed sand mining bee, and pitfalls sampled the carabid beetle *Amara lucida*, Staphylinidae *Mycetoporus piceolus* and *Mycetoporus punctus*, Linyphiidae *Mecopisthes peusi* and the ground bug *Megalonotus praetextatus*, all nationally scarce invertebrates associated with coastal dune habitat (Alexander et al., 2005). Certain species were only found as one or two isolated individuals, *C. cunicularius*, *A. lucida*, *M. punctus* and *M. praetextatus*, and therefore cannot be linked to habitat type. The rove beetle *M. piceolus* was more abundant in the un-grazed grassland; in contrast the small spider *M. peusi* was more numerous in the grazed grassland. Full results for invertebrate abundance and diversity are presented in Table A1.

4. Discussion

Most European semi natural grasslands, including coastal grasslands, have suffered a decline in traditional grazing, with marginal grasslands being 'abandoned' or replaced by 'conservation grazing' to address conservation priorities such as plant diversity or provision of habitat for breeding birds (GAP, 2012). The relationships between grazing impacts on biophysical measures in this study and probable impacts on ecosystem services are summarised in Fig. 6, supplemented by additional information from the literature for some services. We acknowledge that for some of these services, particularly the cultural services, they are proxies of 'potential' ecosystem services, rather than 'realised' ecosystem services. From the results of this study, it is clear that different grazing regimes favour different ecosystem services, and management decisions necessitate trade-offs in delivery of those ecosystem services, or changes in the way grazing management is applied. Here, the widely held view that low intensity grazing is always the 'best' management option for the conservation of semi-natural grasslands is challenged.

4.1. Supporting services

Primary productivity and nutrient cycling are key supporting services of semi-natural grasslands. These underlie regulating services such as equable climate by greater plant biomass leading to
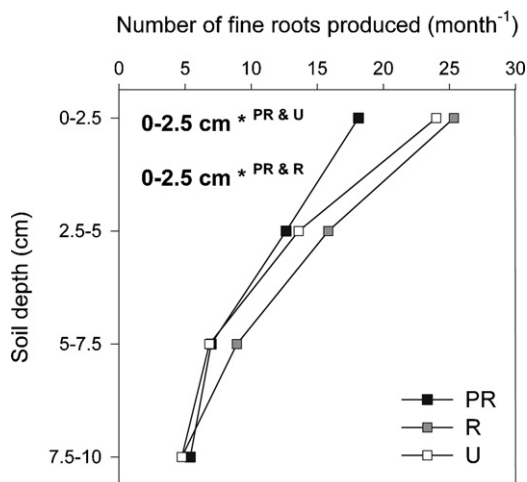
Effects of grazer removal

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CULTURAL SERVICE          REGULATING SERVICE
ENVIRONMENTAL             PEST CONTROL & POLLINATION (+/-)
APPRECIATION (-)
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1 VEGETATION
Vegetation height ↑***
Plant species richness ↓* Forb % cover ↓* Grass % cover ↑* Forb % flowering ↓*
ANPP *ns* Shoot biomass & C stock *ns*
Litter biomass & C stock ↑*
Root biomass ↓*

Predatory invertebrates ↑#
Pollinators ↓#

2 SOIL
Bulk density *ns* Daytime temperature ↓* Soil moisture *ns* Water infiltration rate ↑*

SUPPORTING SERVICE
PRIMARY PRODUCTIVITY (=)

SUPPORTING SERVICE
NUTRIENT CYCLING (+)

Organic matter *ns* Soil C stock *ns*

REGULATING SERVICE
FLOOD CONTROL (+)

3 OTHER
Methane from cattle ↓#
Cattle for meat ↓#

Detritivore feeding rate ↑* Plant available nitrate ↑*

REGULATING SERVICE
EQUABLE CLIMATE (=/+)

PROVISIONING SERVICE
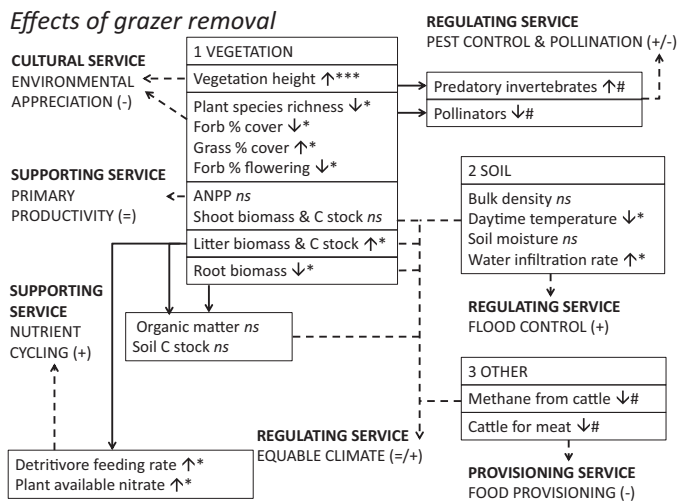FOOD PROVISIONING (-)
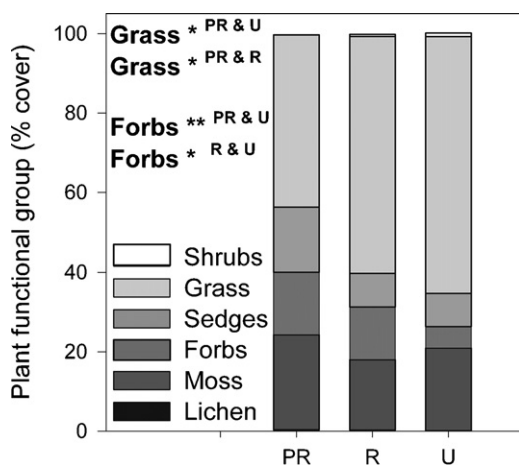
Fig. 6. Effects of pony and cattle removal from coastal grassland on measured variables and potential ecosystem service delivery. Significant increase or decrease in variables indicated by up (↑) or down (↓) arrows (*$p < 0.05$, ***$p < 0.001$, ns = not significant), # for expected results from the literature. Direct links between variables (solid lines), indirect links to ecosystem services (dashed lines) with positive (+), equal (=) or negative (−) effects on ecosystem services are also shown.

higher C sequestration rates (Soussana et al., 2004), and provisioning services such as forage production and quality (Bullock et al., 2011). Nutrient cycling is important as it determines plant available N, a limiting factor for plant primary productivity (Bardgett et al., 2011). Decomposition may influence N cycling positively or negatively, dependent on the C:N ratio of organic substrate available to microbes (Bardgett, 2005). Generally, faster decomposition rates will be detrimental for C storage as soil respiration will increase (Luo and Zhou, 2006). Classic theory suggests that more intensively grazed land will be dominated by faster bacterial nutrient cycling and un-grazed or lightly grazed grassland by slower fungal cycling (Bardgett et al., 1998; McNaughton et al., 1997). However, in this study one aspect of nutrient cycling, net nitrification rate, was greatest in un-grazed grassland, supporting an opposing view that grazing by large herbivores can decrease nutrient cycling (Bakker, 2003; Van Wijnen et al., 1997). This may be because cattle distribute N unevenly via their faeces and urine whereas smaller mammals such as voles, present within un-grazed units, return nutrients to plants more uniformly (Rotz et al., 2005). In addition, as the plant litter inputs, mesofaunal feeding rate and root turnover rate were greater in un-grazed and rabbit than fully grazed grassland more nutrients may be returned to the soil via decomposition in these grazing regimes.

4.2. Provisioning services

It can be argued that the low intensity grazed coastal grassland is more important than other grassland management types for the provisioning service of food supply, with good quality beef or lamb produced at low stocking levels (Wood et al., 2007). This service would be lost upon removal of grazing. However, as grazing abandonment is not a static state, with natural succession shrubs and trees will dominate and non-commercial food sources such as nuts and berries may become important to some people, but these benefits are difficult to quantify (Everard et al., 2010). Genetic diversity of wild species may be enhanced by the use of rare breeds of cattle for conservation grazing and seed from semi-natural grassland used to create species-rich grasslands under agri-environmental schemes (Bullock et al., 2011). This service may be enhanced by extensive grazing management to maximise plant biodiversity.

Fresh drinking water supply, via recharge of aquifers under grassland is another key provisioning service. This service is also provided by both chalk aquifers underlying semi-natural grasslands and vast swathes of UK upland grasslands that are major water catchments (Holland et al., 2011; Koo and O'Connell, 2006). In this study water infiltration rates increased when large herbivores were removed, regardless of the presence or absence of rabbits, as large grazers are responsible for soil compaction (Elliott and Carlson, 2004). Even though the study coastal grassland is largely level, in sloping habitats it is likely that high water infiltration rates will improve water storage and reduce run-off (Marshall et al., 2009). It may therefore be proposed that rabbit grazed or un-grazed grasslands should be promoted on hillsides where water storage is important for land managers. If primary succession continues in the un-grazed or 'abandoned' grassland, shrubs are likely to dominate and the pattern of water infiltration and water storage may be reversed, with greater water storage in the grazed grassland due to lower evapo-transpiration rates (Chartier et al., 2011).

4.3. Regulating services

Regulating services include maintenance of an equable climate, control of flooding and water quality and pest regulation and pollination. Semi-natural grasslands play an important part in maintenance of an equable climate as they are a valuable C store, according to current evidence emit little nitrous oxide and have lower methane emissions than intensively managed grasslands due to lower stocking levels (Bullock et al., 2011; Jones and Donnelly, 2004; Soussana et al., 2004). There is currently little consensus on the role of grazing in grassland C sequestration. Light, moderate or heavy grazing can all increase soil C, depending on grassland type (Kemp and Michalk, 2007). Conversely extensive grazing or no grazing may also increase C storage (Campbell et al., 1997; Soussana et al., 2004) and lead to increased C storage. This study found that total C stock from four combined pools, soil, roots, litter and shoots, did not differ with grazing intensity but that root C was greatest in fully and rabbit grazed, while litter C was greatest in rabbit and un-grazed grassland. As root-derived C contributed more to total C stock than litter or shoot-derived C and root-derived C has a residence time of 2.5 times that of litter or shoot derived C (Rasse et al., 2005) there is potential for greater C storage in the grazed grassland.

Water storage within grassland groundwater also maintains regulating functions such as moderating overland flow, reducing flooding and improving water quality by reducing nutrients and pathogenic bacteria than often contaminate surface waters (Bullock et al., 2011; Kemp and Michalk, 2007). The decreased infiltration rates due to compaction caused by grazing of cattle or other large herbivores leads to higher runoff and N contamination via faeces or urine (Cheng-Zhang and Squires, 2010; Rotz et al., 2005). By contrast, grazing abandonment increases infiltration rates with significant potential as a tool to manage flood risk (Carroll et al., 2004).

Invertebrate abundance and diversity, particularly of large predatory spiders, carabids and staphylinids is often higher in un-grazed grasslands (Ford et al., 2012a; Morris, 2000), with potential implications for pest regulation where semi-natural grasslands border arable fields. Our results show the opposite, with greatest abundance and diversity of predatory invertebrates in the fully grazed grassland. As catch size was consistently greatest in fully grazed, intermediate in rabbit grazed and smallest in un-grazed it is likely that increased structural complexity of vegetation in the rabbit grazed and un-grazed treatments resulted in reduction of catch (Melbourne, 1999), therefore these results may not capture true abundance and diversity of predatory invertebrates. Nectar feeders and therefore pollinators, including bumble bees,

hoverflies and butterflies, tend to be driven by floral abundance, floral richness, availability of nectar resources and sward structure (Potts et al., 2003; Sjödin et al., 2008), all factors influenced by grazing intensity. Grazing also affects soil microbial diversity, with clear effects on microbial composition in both sand dunes and salt-marsh (Ford et al., 2012b), although the implications for ecosystem services provision are unclear.

4.4. Cultural services

Proof of the importance of coastal grasslands to cultural services includes the conservation status of coastal grasslands as a UK Biodiversity Action Plan (UK BAP) listed priority habitat with some important plants, nationally scarce invertebrates (Alexander et al., 2005), birds such as RDB3 skylarks (*Alauda arvensis*) and BAP listed priority amphibian, natterjack toad (*Epidalea calamita*). Environmental appreciation and recreation are also key cultural services in semi-natural grasslands and coastal sand dunes in particular attract significant numbers of tourists (Bullock et al., 2011; Jones et al., 2011). Aesthetic appreciation of the environment is likely to improve with reduction in grass in favour of increased abundance of flowering plants (Mitteager et al., 2006; Paar et al., 2008). In this study plant species richness, particularly for forbs, and flower abundance were significantly greater in fully than in un-grazed habitat. Tall grasses were more dominant in the un-grazed areas, indeed *Arrhenatherum elatius*, a negative indicator species of fixed dune grassland, was present only within rabbit grazed and un-grazed grassland. Plassmann et al. (2010) also found that the number of positive indicator species was lower in un-grazed grassland. Therefore a tentative conclusion could be drawn that aesthetic appreciation is greater in extensively grazed than un-grazed grassland.

4.5. Grazing management for conservation

Mixed grazing is often recommended as grazing with both horses and cattle can lead to enhanced control of competitive grass species, opening up gaps for other plant species and increases in structural diversity compared to cattle grazing alone (Loucougaray et al., 2004). Welsh mountain ponies graze on poor quality forage and avoid flowering heads, with potential positive results for plant diversity, flowering and aesthetics, as argued in this study. Sheep will graze a sward shorter than either cattle or ponies and may select high quality plant parts such as flowers, pods and young shoots (Rook et al., 2004), making them less suitable for conservation grazing. Despite the majority of north–west European grassland managers promoting low intensity grazing by ponies and/or cattle, Newton et al. (2009), in a systematic review of grazing management, found that the presence of grazers consistently lead to a decline in 'tussocky' vegetation with negative effects on reptile and invertebrate habitat. Rotational grazing, where animals are moved at regular time intervals allowing vegetation time to 'recover', often has favourable effects on plant, bird and invertebrate diversity (Söderström et al., 2001; Wrage et al., 2011). It is also recognised that un-grazed vegetative buffer zones adjacent to riparian or arable fields, can allow spatial co-delivery of multiple ecological services, although these are rarely quantified (Olson and Wäckers, 2007). Where large grazers are removed rabbit grazing may define habitat characteristics, keeping patches of grassland fairly open, with a lower mean sward height than un-grazed grassland, preventing major declines in plant or forb diversity but allowing soil to become less compact (Isermann et al., 2010) with greater infiltration rates, results mirrored by this study. However, rabbits are often dependent on large herbivores to maintain the short vegetation they prefer, and these effects may not persist.

4.6. Ecosystem service tradeoffs

In the light of abandonment of low productivity grazing land throughout Europe, in addition to biodiversity measures of 'success' in conservation, ecosystem service measures and trade-offs need to be taken into account when choosing an appropriate grassland management scheme. Results from this case study and the wider scientific literature indicate that extensively cattle grazed or mixed pony/cattle grazed grassland should be conserved for the ecosystem services of plant genetic diversity, food provision, cultural environmental appreciation and potential pollination services. Un-grazed grassland should be conserved for the ecosystem services of invertebrate biodiversity, water storage and flood control (particularly on hill-side slopes), nutrient cycling and the potential for pest regulation. Rabbit grazed grasslands provide slightly lower plant biodiversity and cultural services than grazed grasslands but similar water infiltration dynamics to un-grazed grasslands. Grazing management should depend on the conservation objectives for a particular habitat but should take into account likely trade-offs with other ecosystem services. Perhaps grassland managers, whilst maintaining extensively grazed areas, could trial the introduction of rabbit grazed or un-grazed 'buffer strips' next to water courses, natural boundaries or arable fields, to minimise biodiversity and ecosystem service trade-offs.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2012.09.003.

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