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The dynamics of vegetation grazed by a food-limited population of Soay sheep on St Kilda

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Abstract

1. The population of Soay sheep on the island of Hirta in the Outer Hebrides has been the subject of continuous study for more than 35 years. This paper focuses on the botanical aspects of the plant-herbivore interaction, showing how the vegetation affects and is affected by the sheep.

2. Grazing impacts on biomass and spatial structure varied across plant communities, with *Holcus/Agrostis* grasslands affected most and Wet Heath least, consistent with the hypothesis that herbivore impacts are proportional to plant productivity.

3. Within plant communities, the negative relationships between sheep numbers and plant abundance (sward height, gap/tussock cover and biomass) were significant in March but not significant in August, as expected if sheep numbers are limited by food supply in winter.

4. In most species, flower stem density declined with increasing sheep numbers. There were no examples where unpalatable plants showed increased flowering (e.g. from competitor release under selective grazing).

5. Plant production in temporary grazing exclosures (above ground net primary production) was greatest in *Holcus/Agrostis* grassland (12.6t/ha dry matter/year), lower in *Nardus* grassland (5.1t/ha/yr) and least in *Plantago* sward (1.3t/ha/yr) associated with differences in historical nutrient supply and microclimate.

6. The net effect of grazing on plant species richness was positive: a few highly palatable species were excluded, but small-scale coexistence of grazing tolerant species was enhanced by defoliation.

7. The Soay sheep population fluctuated from 908 (in 1988) to 2208 (in 2009), increasing by an average of 39 extra animals per year over the period 1985-2011. Between 2011 and 2020, the population fluctuated less widely and showed no trend.

8. Population change ($\ln(N(t+1)/N(t))$) was inversely density dependent but positively correlated with plant production in *Holcus/Agrostis* grassland which increased during the study.

9. This plant-herbivore interaction is highly resilient, and though some species (*Festuca rubra* and *Ranunculus acris*) declined in the *Holcus/Agrostis* grassland, there was no significant upward trend in the abundance of unpalatable plant species.

10. *Synthesis*. Implications for future studies and analyses of plant-herbivore data. Concentrating on estimating primary productivity and herbivore offtake, rather than simply measuring change in plant biomass, is likely to provide greatly improved explanatory power for understanding herbivore population dynamics.

1 INTRODUCTION

The motivation behind this study was to understand the dynamics of a plant-herbivore interaction: to work out the impact of food supply on population change in the herbivore, and to quantify the effects of grazing on primary production and botanical composition of the vegetation (Crawley 1983). This interaction is still poorly understood because there have been so few long-term field studies that paid equal attention to the plants and their herbivores. The population of Soay sheep on the island of Hirta in the St Kilda Archipelago is an ideal model system for this kind of study, because the sheep have no vertebrate predators like foxes or buzzards, no competitors like rabbits or voles, and there is no immigration or emigration of the keystone herbivore (Clutton-Brock & Pemberton 2004), so that grazing impacts on plant communities can be attributed unequivocally to the sheep. When sheep numbers are high, intraspecific competition for food is the most important determinant of herbivore mortality (Grenfell et al., 1998). This creates a system of plant-herbivore dynamics that is as simple as is likely to be found anywhere in the world (Crawley, 1983).

The population dynamics of Soay sheep on Hirta can be characterised as follows (Clutton Brock & Pemberton, 2004). At low density, the population increases exponentially for 1 or 2 years ($\lambda \approx 1.4$ per year). Once population reaches the point at which there is insufficient forage to meet demand over winter, there is substantial mortality for 1 year ($\lambda \approx 0.6$) with deaths concentrated in the yearling and senescent age groups (Bonenfant,et al., 2009). The deterministic core of these dynamics involves overcompensating density dependent competition for food during winter (Grenfell et al., 1998). The two principal stochastic elements are weather affecting primary production (e.g. the date of the start of grass growth in spring, and temperature during the rapid growth phase), and weather affecting over-winter mortality of the sheep (e.g. higher than average rainfall combined with chilling winds, causing greater heat loss through heavy, wet fleeces; Coulson et al., 2001). It is clear that well-fed, pre-senescent Soay sheep with moderate to low parasite burdens are not killed by harsh winter weather. The animals are hardy to winter weather conditions substantially more severe than are ever experienced on Hirta. It is the three-way interaction between poor body-condition as a result of protracted low food intake, high parasite burden, and enhanced heat-loss in winter that kills animals in large numbers and accounts for the most severe declines in population size. There is no evidence that gut parasites cause the observed sharp declines in population density, but animals with high parasite burdens are more likely to die during population crashes (Hayward et al., 2009). The focus of this paper is on year-to-year changes in the impacts of grazing on plant performance: sward height, gap and tussock structure, biomass and flowering, community composition and species richness, and above-ground net primary production.

The early literature on plant-herbivore dynamics focused on the role of large, mobile, polyphagous herbivores in preventing succession from grassland to woodland by selectively eliminating the seedlings of woody plants (Tansley, 1935). Subsequent work distinguished systems where the herbivores were food limited, and impacts on vegetation might be expected to be large (Sinclair, 1975) from cases where herbivore populations were regulated top-down by their predators, parasites or diseases, and impacts on vegetation might be expected to be less (Oksanen 1983, Carpenter et al., 1985). It is now generally agreed that large herbivores exert a major influence on grassland ecosystem structure and function (Milchunas & Lauenroth, 1993), and that this impact increases with plant productivity (Chase et al., 2000). In particular, grazing-induced differences in plant richness are seen to depend upon the extent to which selective grazing reduces the biomass of the dominant species: when the dominant is palatable, resources are freed up, thereby facilitating competitor-release of previously suppressed species and increasing species richness (Koerner et al., 2018). Dominant species tend to be more palatable, and hence more strongly suppressed by grazing in grasslands with higher productivity (Bakker et al. 2006, Lezama, et al. 2014), and the consequent increase in light intensity at ground level promotes higher plant species richness (Borer et al., 2014).

The consensus is that plant species adapted to resource-rich environments have intrinsically faster growth rates than species adapted to resource-poor environments. Endara & Coley (2011) summarize their three principal findings: 1) fast-growing species have shorter leaf lifetimes than slow-growing species; (2) fast-growing species have lower amounts of constitutive defences than slow-growing species; and (3) fast-growing species support higher herbivory rates than slow-growing species. This means that species adapted to resource-poor environments grow inherently more slowly, invest more in constitutive defences and support lower herbivory than species from more productive habitats (Endara & Coley 2011).

The theory underlying plant-herbivore dynamics centres on the positive correlation between palatability and competitive ability (Pacala & Crawley 1992, Ishii & Crawley 2011): those plant species that do best in the absence of herbivory (perhaps because they devote a large fraction of their resources to growth and a small fraction to defence) do less well in the presence of herbivory because well-defended, unpalatable species become relatively more competitive following selective defoliation of their more palatable neighbours. It is possible, too, that highly palatable plants can be resistant of, or tolerant to, grazing (Archibald et al. 2019). Long term studies of plant-herbivore interactions in natural systems are exemplified by work in the Serengeti savanna, concentrating on energy flows and nutrient cycling (McNaughton 1985) and on the complex interactions between herbivores of different body-sizes and feeding preferences, sometimes competitive, sometimes facultative (McNaughton 1984). The interplay of selective grazing, animal preferences and effects on plant competitive ability typically resulted in moderate to heavy grazing stimulating plant productivity up to twice the levels in ungrazed control plots. It was clear that high grazing pressure constituted strong selection on the plants for compensatory growth following defoliation (McNaughton, 1979). One of the most distinctive features of this plant-herbivore system was the prevalence of grazing lawns, where frequent grazing limited invasion by tall species that might shade out short-grass growth forms and prevented build-up of senescent leaf material that would reduce the attractiveness of the sward to grazers (Hempson et al., 2015). Close grazing leads to improved food quality through the creation of higher leaf to stem ratios, higher foliar nitrogen levels, enhanced digestibility, stimulation of foliar regrowth rates and upregulation of photosynthesis following defoliation, all tending to drive the age structure of foliage towards younger, more nutritious leaves (Anderson et al., 2013).

Illius & O'Connor (1999) studied the interaction between temporal and spatial heterogeneity in a semiarid rangeland system where ungulate herbivores were limited by food availability during the dry season. Temporal heterogeneity was driven by highly variable rainfall, with droughts causing frequent episodic mortality in herbivore populations. Spatial heterogeneity was reflected in the location of dry-season access to drinking water for the herbivores and ground water to maintain green plant biomass. Animal numbers were regulated in a density-dependent manner by the limited forage available in what they call 'key resource areas', which are utilized during the unfavourable season. Illius & O'Connor (2000) emphasized the importance of spatial and temporal variation in the action of regulating density-dependence in herbivore dynamics: this is as true for the Soay sheep on Hirta as it was in their semi-arid rangeland system. There is a direct parallel in the importance of spatial heterogeneity. On Hirta, the 'key resource area' is the *Holcus/Agrostis* grassland (Regan et al., 2016). Temporal heterogeneity, however, is of a different kind. In semi-arid rangeland, the principal cause of destruction of green plant biomass was drought, but on Hirta the principal cause of destruction of green plant biomass is defoliation by sheep. But the net result is that the action of density dependent herbivore mortality varies dramatically from year to year in both systems. On Hirta, it acts typically once in every 2 or 3 years (see above).

Grazing-induced changes in species composition and diversity may reflect predictable responses by plant life forms characterized by different functional traits like growth form, defoliation tolerance and plant palatability (Díaz et al. 2007), leading to a trade-off between a plant's ability to exploit nutrients and tolerate herbivory in different locations. For instance, herbivores can greatly increase light availability and alter soil available nitrogen depending on the vegetation quality, grazing intensity, and nutrient supply, and such modifications of resources may cause associated changes in plant species richness, composition, and vegetation structure through a variety of different mechanisms (Anderson et al., 2007).

Some of the most dramatic effects of herbivores on plant communities followed the intentional introduction of large mammalian herbivores onto remote oceanic islands that lacked any history of grazing. The initial abundance of essentially undefended plants led to a boom in animal numbers, then a massive crash once the native vegetation had been destroyed (Klein, 1968; van Vuren & Coblentz, 1987). Subsequently, it has become clear that plant species in systems with a history of grazing exhibit a variety of resilience mechanisms that allow reversible shifts in floristic composition with changes in grazing intensities (Cingolani et al., 2005).

In his paper, we address several important gaps in our current understanding. For example, little is known about the numerical responses of herbivore populations to changes in plant productivity brought about by year-to-year variation in growing conditions. Likewise, the long-term consequences of changes in herbivore numbers on the biomass of coexisting plant species are poorly documented. The paper is structured around 7 interrelated hypotheses:

1. Grazing impacts will differ across plant communities, with bigger impacts where plant production is higher, resulting in exclusion of the most highly palatable plant species.

2. Grazing will reduce flowering of palatable species and will increase flowering of unpalatable species if they benefit sufficiently from competitor-release under selective defoliation.

3. Plant species richness will decline with increasing biomass, both within and between plant communities, and sheep grazing will increase small-scale plant species richness by reducing total biomass.

4. Net above-ground plant production, assessed using temporary grazing exclosures, will vary across plant communities with soil nutrient supply and microclimate.

5. Long-term herbivore exclusion will lead to increased growth of the most palatable plant species, leading to competitive exclusion of less palatable species and a decline in plant species richness.

6. Because the numbers of Soay sheep are limited by food supply during winter, herbivore impacts measured in March will be greater than in August. This means that plants experience relatively low grazing pressure during the growing season.

7. Sheep population change will be positively correlated with plant production but negatively correlated with plant biomass.

2 METHODS

Since 1985 the Soay sheep population of the island Hirta, St Kilda has been the subject of intensive study (Fig. S E 1). The study site and the methods involved in assessing sheep numbers (both on the whole island and in the Village Bay study area) are described in Clutton-Brock & Pemberton (2004). The population is unmanaged with no offtake and no veterinary interventions. The spatial distribution of grazing pressure across the different plant communities within the study site was detailed by Regan et al. (2016) who showed that grazing was concentrated on more palatable grassland dominated by *Agrostis capillaris* and *Holcus lanatus*. Their data involved a synthesis of all of the location data (at hectare scale) over the lifetime of an animal, collected during the 20-30 detailed censuses of the study population each year.

2.1 Study Site

From 1990-1992, plant data were collected from *Holcus/Agrostis* grasslands at locations 1-4 on Transects A-C (Fig. 1). In August 1993 the study area was extended, with data collected on 5 transects (A-E) starting close to sea level and extending uphill to c. 200m altitude and encompassing other plant communities including Wet Heath, Heather, *Nardus* grassland and *Plantago* Sward (see below). Six sampling locations were chosen within each transect by stratified random sampling (two between the sea and The Street, two between The Street and the Head Dyke, and two outside the Head Dyke). These same locations were used in each subsequent year to minimize the impact of spatial heterogeneity in grassland structure and botanical composition.

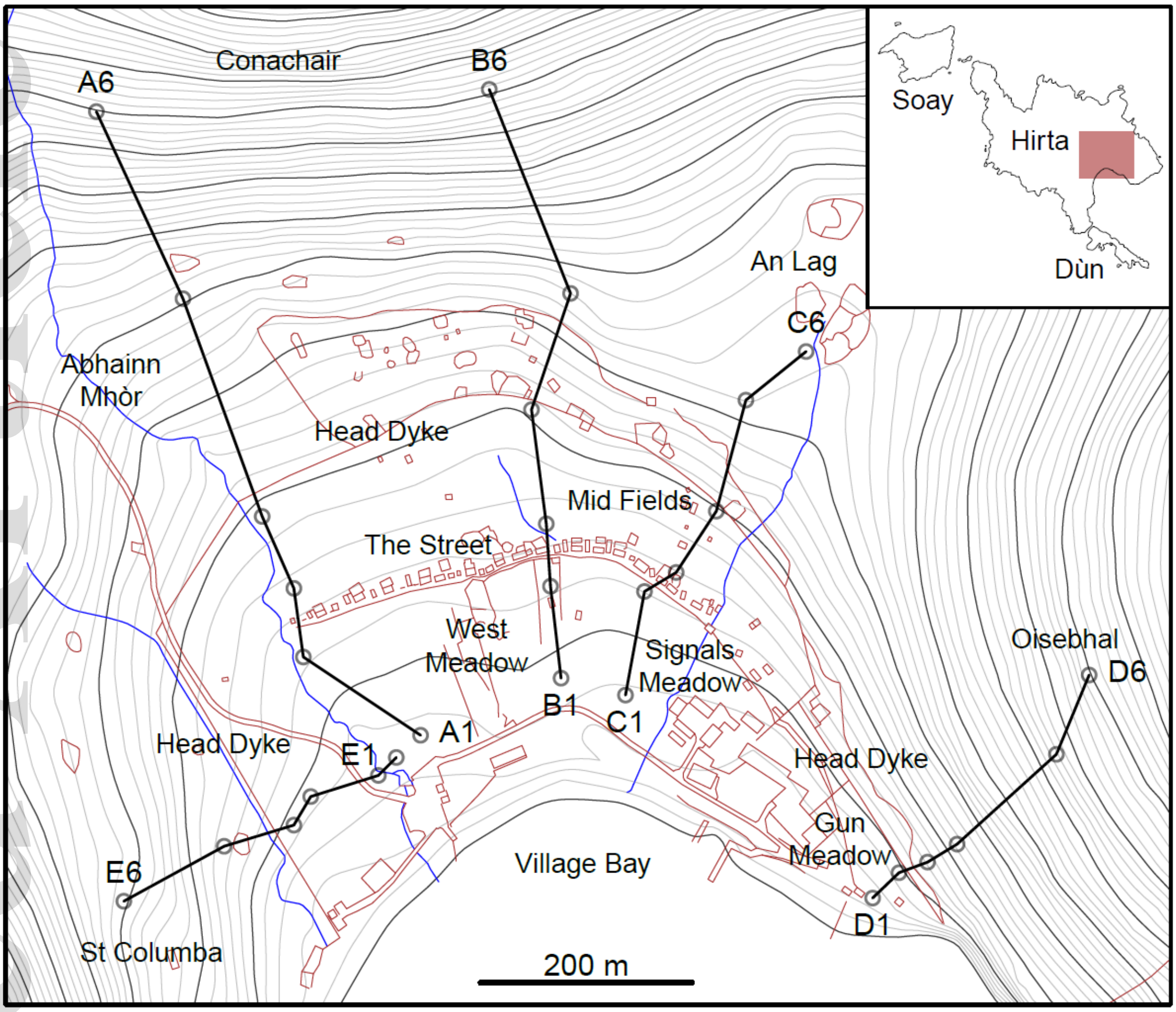

Fig. 1. The study area, showing the locations of places named in the text. Each of the 5 Transects (A-E) has 6 Locations, numbered 1 at the seaward end and 6 at the upland end. The inset shows the location of the study area within Hirta. The Head Dyke is a dry-stone wall (shown as a dark red line) running in a n-shape from east of St Columba, north of Mid Fields and ending above the sea to the east of Gun Meadow. The pale contour lines are 5m apart and the dark contours 25m apart.

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The 30 sampling locations were each allocated to one of five plant communities on the basis of multivariate analysis of their botanical compositions (Supplementary Information section A): *Holcus/Agrostis* grassland (14 locations, illustrated in Supplementary Information section E Figs

2-4, henceforth abbreviated to Figs S E 2-4); *Plantago* sward (4; Figs S E 7-9); *Nardus* grassland (2; Figs. S E 5-6); Wet Heath (4; Figs. S E 12-13) and Heather (6). The Heather locations were further subdivided into Short (B5 & C5; Fig. S E 11), Tall (B6, D5 & D6; Fig. S E 10) and *Calluna/Molinia* (A6, Fig. S E 14, an un-replicated vegetation type within the study area).

The soils beneath the *Holcus/Agrostis* grassland have elevated levels of soil nutrients as a result of centuries of fertilization for crop production. The chief ingredients in these composts were ashes from burning peat, human urine and faeces, straw and faeces from domestic animals, along with the bones, wings, and entrails of harvested sea-birds. Seaweed was of minor importance, being relatively scarce on St Kilda (Meharg et al, 2006).

2.2 Sward Height

Using a sward-stick (Hodgson et al., 1981) at each point, the slider was lowered until the window first touched plant biomass (living or dead) and sward height was recorded to the nearest 0.5 centimeter. This is a measure of local maximum plant height and was taken only under conditions that were sufficiently calm that wind-flattening of the vegetation was negligible. From 1990 to 1992, sward height data were collected from locations 1-4 on transects A, B and C (Fig. 1).

From August 1993 to August 2017, we took 25 sward height measurements in March and in August each year at each sampling point (25 heights x 6 locations x 5 transects = 750 sward heights per visit). A 2m-long wooden stick (the rod) was marked out with 20 units each 10cm apart. The rod was thrown within the sampling location (‘randomized’), then rotated about its central point to follow the contours, and 25 sward heights were recorded, 10cm apart, along its length (starting at the western end, and sliding the rod eastwards to accommodate the final 5 measurements).

Sward height (cm) has dimension L (length) and biomass has dimensions of mass per unit area (i.e. L3/L2 = L) so, other things being equal, sward height ought to be a linear predictor of biomass. This relationship between sward height and total biomass holds true across all plant communities, fitting best for the most productive *Holcus/Agrostis* grasslands ($r^2 = 0.675$; Fig. S D 2) and least well for tall, tussocky heather ($r^2 = 0.385$).

2.3 Gap and Tussock Cover

Much of the time the sward is highly heterogeneous at a scale of 20 cm x 20 cm, with pronounced, closely grazed gaps and more or less conspicuous tussocks (illustrated in S E Figs. 18, 19), so it is essential to quantify the relative cover of gaps and tussocks if an accurate estimate of total biomass is to be obtained. The rod (see above) was thrown 3 times at each sampling location and rotated about its centre to lie along the contours. A row of 10 adjacent 20 cm x 20 cm quadrats was placed along its length. Then for each quadrat in turn, three observers were obliged to agree on a classification of the vegetation inside the quadrat. A tussock was relatively tall vegetation, often (particularly in March) containing substantial dead organic matter. A gap was a close-grazed sward, often with a high percentage cover of *Trifolium repens*. If a quadrat was clearly intermediate between a gap and a tussock, it was defined as 'Indeterminate', but observers were encouraged to categorize as few quadrats as reasonable as 'Indeterminate'. Thus, a total of 30 scores was distributed over the 3 categories 'Gap', 'Tussock' and 'Indeterminate' for each of 6 locations on each of 5 transects on each visit (from August 1993 and March 1994 onwards).

2.4 Gap and Tussock Biomass

Biomass samples of 1 gap and 1 tussock were collected from each of 6 locations on each of 5 transects in March and August each year. At each sample location, the rod was thrown (as above) and 8 suitable gaps and 8 suitable tussocks were flagged, as close to the rod as possible. One randomly chosen gap and tussock was then carefully cut using sharp kitchen scissors to exactly 20 cm x 20 cm, leaving a stubble of c. 0.5cm and taking care not to include any soil, wool or faeces in the sample bag. Within 24 hours, each sample was carefully sorted into dead organic matter (all species combined), bryophyte (all species combined) and vascular plants (sorted separately to species).

After sorting, each biomass-component was placed in a separate paper bag and dried at 80'C for at least 24 hours. Once dry, the samples were weighed to 2 decimal places of a gram. Very light samples were recorded as 0.01g.

Samples of heather (*Calluna vulgaris*) were obtained from 20 cm x 20 cm quadrats cut at ground level using secateurs from August 1993 onwards (Fig. S E 20). These were sorted from other live and dead plant material and then clipped, using sharp, fine scissors into woody and live green leaf material that were bagged, dried and weighed separately. In short heather, green and woody heather biomass components were separated from March 1996 onwards (total *Calluna* biomass was measured at B5 and C5 from 1993 to 1995). Tall heather tussocks might have > 100g dry weight of woody material in a 20 cm x 20 cm sample. Short heather was typically a closely matted, carpet-like sward with horizontal woody shoots appressed closely to the soil amounting to c. 13g/ 20 cm x 20 cm of woody material.

2.5 Estimating Species Biomass

The estimated dry weight of plant species *i* at Transect = *j* and Location = *k* is W_{ijk} and was calculated by weighting its dry mass in the gap sample MG_{ijk} by the relative abundance of gaps ($G_{jk}/(G_{jk}+T_{jk})$) at this location, and adding this to its dry mass in the tussock sample MT_{ijk} weighted by the relative abundance of tussocks ($T_{jk}/(G_{jk}+T_{jk})$):

$$W_{ijk} = \frac{G_{jk}}{(G_{jk} + T_{jk})}.MG_{ijk} + \frac{T_{jk}}{(G_{jk} + T_{jk})}.MT_{ijk}$$

Because there are no sorted samples from indeterminate quadrats, we implicitly assume that biomass there is the average of the relevant gap and tussock samples.

2.6 Flower Stem Density

We assessed flower stem densities in August from 1994 onwards, using larger 40 cm x 40 cm quadrats. Each transect was walked from its seaward end (Fig. 1), and 30 quadrats were assessed in each of 3 zones: formerly cultivated land between the sea and The Street; less intensively cultivated ground between The Street and the Head Dyke; and uncultivated heath, uphill beyond the Head Dyke. Each quadrat was thrown uphill from the last one. For each vascular plant species, the total number of flowering stems was recorded. There are 90 samples from each of 5 transects (450 samples in all) each year.

2.7 Vascular Plant Species Richness

Vascular plant species richness was calculated from the August biomass samples, combining data from individual gaps and tussocks (each measuring 20 cm x 20 cm; above), and averaged across sampling locations for each plant community in each year. August data were used for computing species richness because in March many of the herbaceous species were still underground. At this very small spatial scale, the size of individual plants has an important influence on the total number of individuals and hence the number of species represented (Crawley & Harral, 2001). Larger-scale (hectare) species richness is tabulated in S A Table 1.

2.8 Above-ground Net Primary Production (ANPP)

To estimate primary production and grazing offtake it is necessary to exclude the sheep for a period of several months. We used temporary exclosures (pyramids, 1.5m x 1.5m at ground level; illustrated in Fig. S E 17) which were moved to fresh positions within their sample locations twice per year, in March and in August, having excluded the sheep for 7 months (August to March) and 5 months (March to August) respectively. We had two replicate exclosures in each of 4 locations: West Meadows and Mid Fields (both in formerly cultivated ground now dominated by *Holcus/Agrostis* grassland), St Columba (*Nardus* grassland) and Gun Meadow (*Plantago* sward; grid references of the locations are in S C Table 1). The data were gathered from 2000 to 2017.

The exclosures were centred above gaps (rather than tussocks or indeterminate swards). At the end of the fenced period, the pyramid was removed and plant biomass in the central 20 cm x 20 cm quadrat was carefully plucked between thumb and forefinger. Plucking continued until the vegetation inside the quadrat was the same height as the grazed vegetation in the matched quadrat outside the pyramid. This sample is referred to as 'Pluck down' and is a non-negative estimate of grazing offtake (estimates based on the difference in total biomass outside and inside the pyramid can lead to nonsensical negative estimates of offtake because of spatial heterogeneity in sward density; Sala, & Austin 2000). Next, the residual biomass was cut down to leave a 0.5 cm stubble and placed in a separate labelled bag. The outside quadrat was harvested as for a normal gap sample (above). It is important to note that the residual stubble inside a pyramid after several months of protection from sheep grazing is different from the stubble after cutting an outside sample. The former is a sparse and etiolated collection of upright stems, while the latter is a densely woven carpet of grazed and trampled shoots. A comparison of the mass of inside and outside stubbles is therefore not a useful metric.

These pyramid samples were not sorted (dead organic matter and bryophytes were scarce in the new growth from the gap communities, and grasses greatly outweighed herbs in all cases). The samples were relatively bulky and were oven-dried for at least 48 hours.

For the new location of the pyramid, 8 suitable gaps were flagged and one of these was chosen at random to be fenced. Using a steel 20 cm x 20 cm quadrat, 15 cm nails were secured in the turf at each of the 4 corners (these locate the sample once the grass has grown up over the coming months). Outside the new exclosure, two gaps were selected. One of these was harvested at this point (labelled as 'Initial') and the other was left intact (to be cut and labelled as 'Outside' when the pyramid was analyzed on the next visit).

All 4 pyramids in Mid Fields and West Meadow were vandalized prior to August 2004, so there was no estimate of plant production from *Holcus/Agrostis* grassland for the period March to August 2004. We have estimated a value by interpolation using mean pluck-down from St Columba during this interval in 2004 (12.55g) to select the year with the closest value on St Columba (this was 2013, with a value of 12.50g) and used the mean from Mid Fields and West Meadow in 2013 as the interpolated value for 2004 (28.66g).

Pilot trials over the period 1997-2003 with temporary grazing exclosures on Conachair (in Heather) and on An Lag (in Wet Heath) produced estimates of offtake by the sheep calculated as "inside dry matter minus outside dry matter". In Heather, 10 of these estimates were positive, but 14 were negative, and in Wet Heath, 7 were positive but 15 were negative. These data clearly did not provide reliable estimates of primary production, typically because of small-scale spatial heterogeneity in biomass leading to negative estimates of offtake (Tuke, 2001; Jones, 2003), so sampling from these plant communities was stopped, and none of these data were used in the present paper.

2.9 Population dynamics of the sheep

We measured sheep population change from August in year (t) to August in year (t+1) based on difference between successive whole-island counts (N(t) and N(t+1)) as

$$delta = \ln(N(t+1)/N(t))$$

Positive values indicate an increase and negative values a decline in population. The explanatory variables were sheep density (N(t)), plant abundance (sward heights or biomass), plant production

(**2.8** above) and various weather measurements downloaded from the Met Office archive for Stornoway in the Outer Hebrides which is the closest weather station to St Kilda, lying 135km to the north-east: https://www.metoffice.gov.uk/pub/data/weather/uk/climate/stationdata/stornowaydata.txt

2.10 Long-term exclusion of sheep

Dotted about the study area are small storehouses known as cleitean (or cleits; Fig. S E 15). These beehive-like structures were built by the islanders to store and dry their seabirds, crops, peat and fishing gear. They have corbelled drystone walls and stone slabbed roofs that were originally covered in turf. Most of the cleits have angled walls that allow the sheep to climb up and graze their roofs. A few, however, are sufficiently steep-walled to exclude the sheep, and these support a flora (illustrated in Fig. S E 16a & b) that is similar to inaccessible cliff ledges on Hirta and on the ungrazed island of Dun (Crawley 2017). We selected 4 cleits with the least grazed roofs for analysis in March and August 2017 (locations and grid references in Table S C 2). Two sample quadrats of 20 cm x 20 cm were cut and sorted (as in **2.4** above) from each roof, and from the grazed sward 10m uphill from the base of each cleit (thus avoiding the heavily trampled and dunged ground close to the cleit, which the sheep use for shelter). These data provide 4 independent contrasts of grazed versus non-grazed swards for two seasons in the same 12-month period.

2.11 Statistical Analysis

To keep the analysis as simple as possible, the data are represented as annual means by averaging across the sampling locations for each of 25 years. Temporal variation within each sampling location in the *Holcus/Agrostis* grassland is illustrated in box-and-whisker plots of live biomass in August (Fig. S D 14a). The data were positively skewed at all the locations, but the mean values were normally distributed. Spatial variation within each year in the *Holcus/Agrostis* grassland is illustrated in box-and-whisker plots of live biomass in August (Fig. S D 14b). Again, the means were normally distributed. Because the focus was on between-year effects, there was no need to use hierarchical mixed effects to model the within-year spatial variation.

We have concentrated on effects and their standard errors, rather than on significance testing, and we present effect sizes whether or not $p < 0.05$. The significance of temporal trends was assessed by linear regression of the annual average of each response variable against year (e.g. for sheep numbers Fig. 2, $n = 35$, $d.f. = 33$). The importance of effects in a regression is reported as the ratio of the fitted values of the response variable calculated at the maximum and minimum measured values of the explanatory variable (see Fig. S D 10 for details).

To improve homogeneity of variance, analyses were carried out separately in each of the plant communities, and within plant communities, homogeneity of variance was further improved by treating gaps and tussocks as separate categories (**2.3**, above). Where a response variable differed substantially across plant communities in mean or variance (or both), we carried out comparisons within each plant community separately, using Welch Two Sample t-test to adjust for slight differences in variance between samples by reducing degrees of freedom (Wilcox, 2003). The standard error of the difference between the means of two samples *a* and b is obtained in R using `t.test(a,b)$stder` (R Core Team, 2019).

In scatter plots, a fitted regression line is shown only if the relationship has $p < 0.05$. In such cases, the confidence envelope for the slope is shown as dashed lines (fitted value +/- 95% confidence interval of the predicted slope = Student's t x s.e. slope).

The percentage cover data for gaps and tussocks (**2.3**, above) were analysed using linear models without arc-sine transformation, because the averages across locations exhibited constant variance and normally distributed errors. Likewise, the count data of species richness in the sorted biomass samples (**2.7**, above) were averaged across locations before analysis, and did not require transformation or the use of generalised linear models.

For modelling annual change in sheep population, we use the response variable *delta* (defined above). We tested the effects of three successive estimates of primary production: period one (p1) = March(t) to August(t) chosen to influence body condition going into the rut, p2 = August(t) to March(t+1) to represent over-winter grass growth, and p3 = March(t+1) to August(t+1) to reflect grass growth during lactation and early lamb growth. Models were compared using `AIC` (R Core Team, 2019).

The method for quantifying population fluctuation is to calculate the standard deviation of the logarithm of population size after any trend in population size has been removed (Williamson

1976). Detrending is achieved by adding the residuals from the linear regression to the arithmetic mean population size.

3 RESULTS

3.1 Sheep population

The total sheep population (males plus females, lambs plus yearlings plus adults) counted in August over the years 1985 to 2020 is shown in Fig. 2.

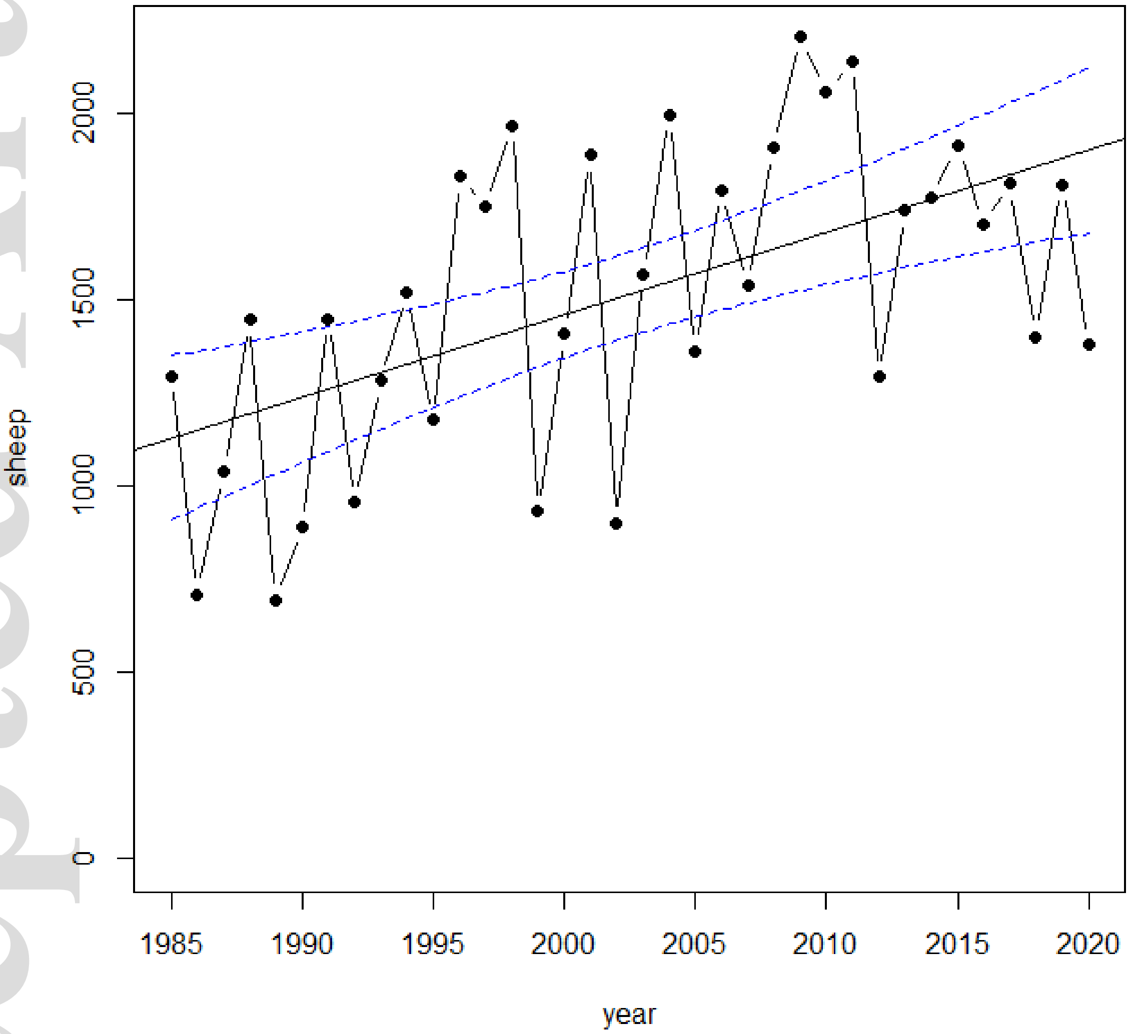

Fig. 2. Time series of the whole-island count in August each year 1985-2020. The fitted line shows an average increase of 22.04 extra sheep per year over the time period as a whole (s.e. = 5.53, $p < 0.001$).

The most remarkable feature of the time-series is that we have never observed two successive years of decline in population size. Over the time period as a whole, the sheep population increased by an average of 22 extra animals per year (Fig. 2). From 1985 to 2011, however, the increase was much steeper than this (average annual increase = 39.4 animals, s.e. = 8.22) while in recent years, the population has fluctuated less widely and has shown no significant trend (see Fig. S D 1 for details). The effects of this varying population of herbivores on different measures of plant abundance are described in the following sections: sward height, % gap cover, % tussock cover, gap mass, tussock mass and overall biomass.

3.2 Sward Height

In the *Holcus/Agrostis*, the most extensive community, dominant at 14 of the 30 sampling locations, there was no relationship between summer sward height and current sheep numbers, but after a winter of grazing, there was a significant negative relationship between sward height in March(t+1) and sheep numbers in August(t) (Fig. S D 3). Again, in the closely-cropped carpet of the *Plantago* sward there was no significant effect of sheep numbers on mean sward height measured in August(t), but in March(t+1) there was a significant negative relationship (Fig. S D 4). In both *Nardus* grassland and Wet Heath there was no relationship between sheep numbers and mean sward height at either season (Fig. S D 5). In the Heather community, dominated as it is by woody perennials, there was no effect of sheep numbers on mean height of the canopy in August(t) or March(t+1).

There were large seasonal effects, with a significantly taller sward in August than in March in all plant communities, except Heather (Table S D 1); these differences were greatest in *Holcus/Agrostis* grassland (3.17-fold taller in August), then in *Nardus* grassland (2.20-fold), *Plantago* sward (1.87-fold) and Wet Heath (1.68-fold).

3.3 Gap and tussock cover

Gaps were more abundant in March than in August, and in years when the sheep population was larger. The opposite pattern was observed for tussocks; they were more abundant in August than in March, and in years when the sheep population was lower. Across the 5 plant communities, gaps and tussocks were most pronounced in the *Holcus/Agrostis* grassland and showed the largest seasonal fluctuations and the most pronounced responses to changes in sheep numbers in March, but not August (Fig. 3). At the other extreme, there were few (and often no) tussocks in *Plantago* sward or Short Heather in either season, independent of sheep numbers. There were no significant effects of sheep numbers on tussock cover in any of the other plant communities, and there was a significant positive effect of sheep numbers on gap cover only in Wet Heath in August (effect = 0.0249, s.e.= 0.00698, p = 0.0017).

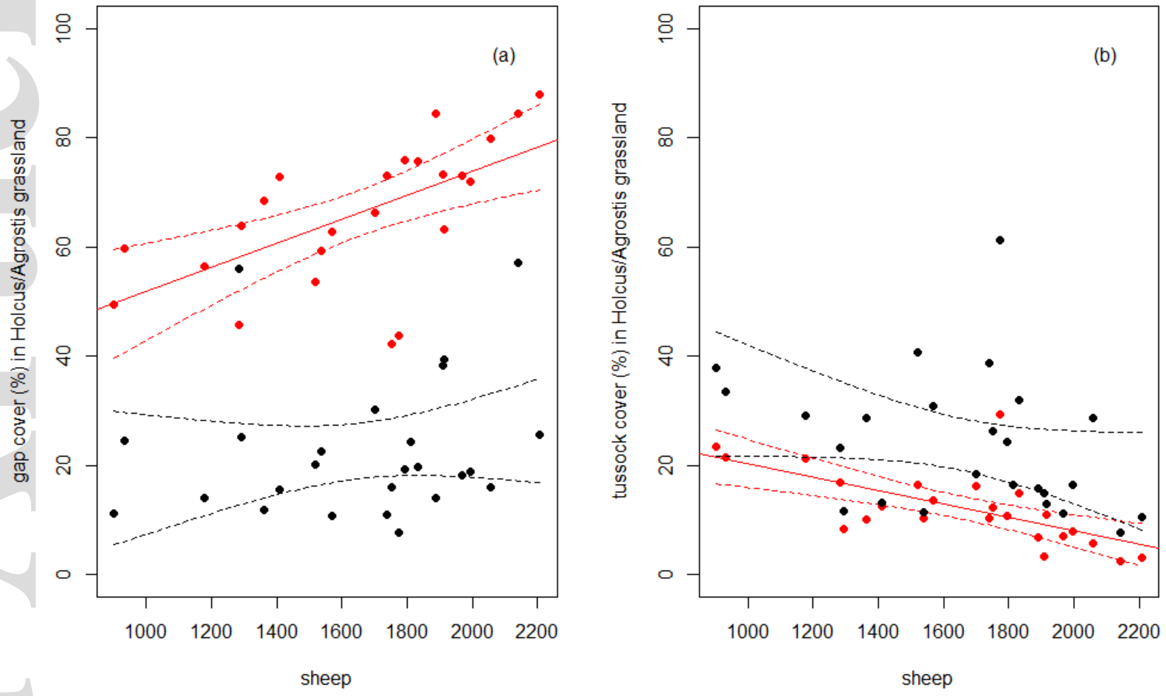

Fig. 3 (a) Gap cover (mean %) in *Holcus/Agrostis* grassland in March(t+1) (red symbols) and August(t) (black symbols) as a function of sheep numbers in August(t). Significant regression lines are shown with their confidence envelopes; non-significant relationships show only the confidence envelopes. In March the relationship was significant (red lines; effect = 0.022, s.e. = 0.0061, p = 0.0016), but not in August (effect = 0.0066, s.e. = 0.0075, p = 0.385). Mean gap cover was almost 3-fold higher in March than in August (66.1% vs. 22.7%; One Sample t-test of paired differences: t = 12.12, df = 23, p-value < 0.00001).

(b) Tussock cover (mean %) in *Holcus/Agrostis* grassland in March(t+1) (red symbols) and August(t) (black symbols) as a function of sheep numbers in August(t). In March the negative relationship was significant (effect = -0.012, s.e. = 0.003, p = 0.0005), but not in August (effect = -0.012, s.e. = 0.007, p = 0.094) despite the similar effect size. The seasonal difference in mean tussock cover was 1.9-fold (23.8% in August and 12.3% in March, t = 6.59, df = 23, p-value = < 0.00001).

The seasonal means for gap and tussock cover in the other plant communities are shown in Table S D 2, with significant differences only in *Nardus* grassland, where gaps had greater cover in March than in August. Seasonal differences were not expected in Heather, given the woody skeleton of the canopy.

3.4 Gap and tussock dry mass

In *Holcus/Agrostis* grassland, increasing sheep numbers were associated with reduced total dry mass of individual gaps and tussocks in March, but there was no relationship between sheep numbers and individual gap or tussock mass in August (Fig. S D 6). There was no significant seasonal effect on the mean total mass of either gaps or tussocks. For gaps, this is partly an artifact or our scoring system because in summer, many quadrats that had been gaps in March will have grown to become indeterminate by August, so only ‘permanent gaps’ get measured in August and these are likely to be as closely grazed as typical March gaps. Data on gap and tussock mass for the other plant communities are shown in Table S D 3.

The dry matter compositions (mean g dead organic matter, bryophytes, grasses and forbs) of gaps and tussocks in August and March averaged across the years 1993-2017 are shown in Fig. S B 1. Dead organic matter was more abundant in tussocks than in gaps, and more abundant in March than in August. Bryophytes were more abundant in March than in August. Grasses and forbs were more abundant in August than in March. The differences between gaps and tussocks were often more pronounced in relative abundance of species rather than number of species (see **3.7** below). In *Holcus/Agrostis* grassland, for instance, the biomass of *Trifolium repens* was more than twice as great in gaps (1.13g) as in tussocks (0.54g, $t = 5.92$, variance-adjusted d.f. = 40.21, $p<0.0001$).

3.5 Plant biomass

Biomass depends upon the dry mass of individual gaps and tussocks (**3.4**, above) and on the relative cover of gaps and tussocks (**3.3**, above) as explained in Methods (**2.5)**. Total dry mass (live + dead + bryophytes) across the different plant communities in August and March (with Heather separated into Tall (B6, D5, D6) and Short (B5, C5)) is shown in Fig. 4. The most striking feature is the seasonal difference of total biomass in some plant communities (biomass was significantly higher in August than in March in *Holcus/Agrostis, Nardus* grasslands and in Short Heather), but not in others (Tall Heather, *Plantago* Sward and Wet Heath).

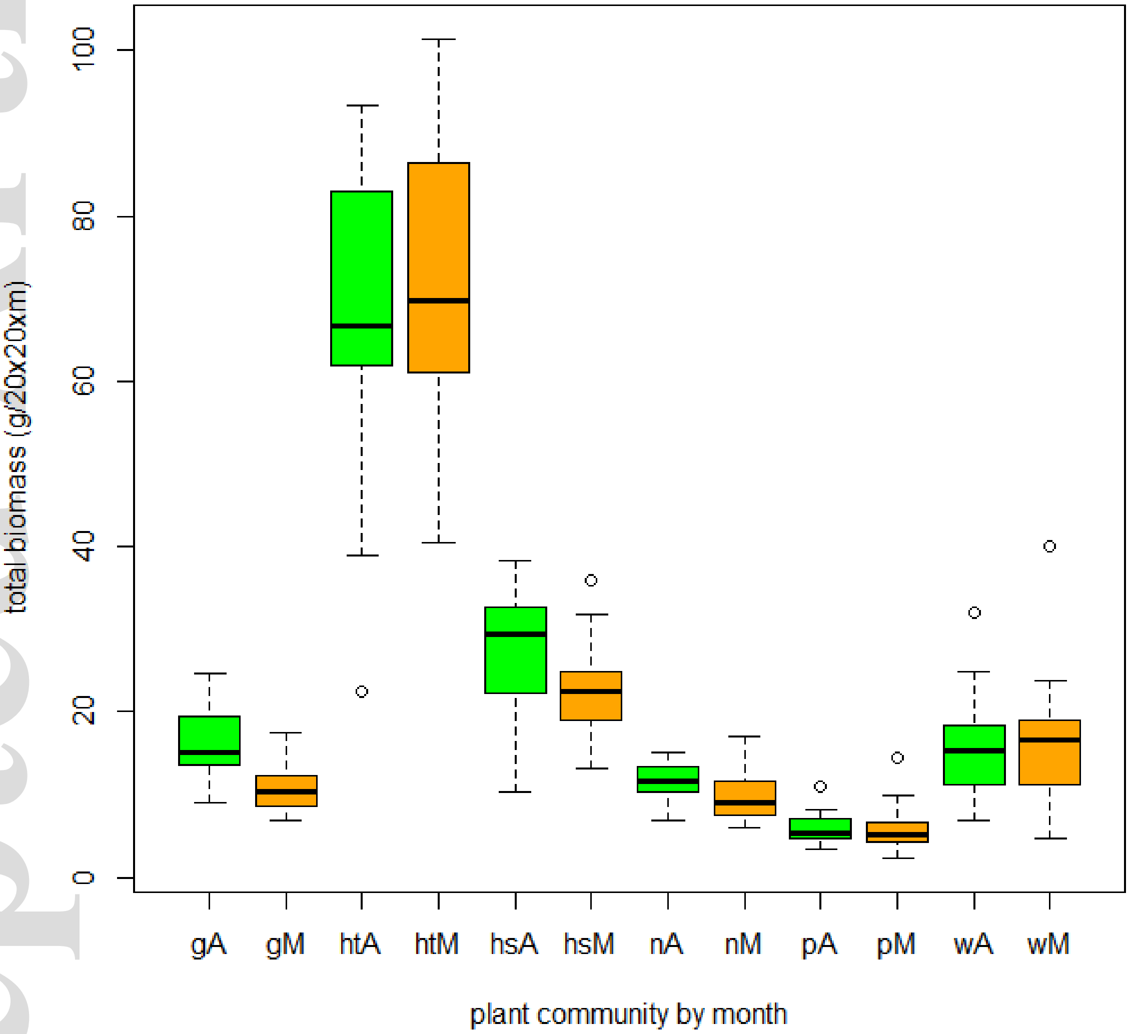

Fig. 4. Total biomass (live + dead + bryophytes; g dry matter / 20 cm x 20 cm) in August (A) and March (M) in plant communities: g = *Holcus/Agrostis* grassland (within-year replication = 14 sampling locations), ht = Tall Heather (3), hs = Short Heather (2) , n = *Nardus* grassland (2), p = *Plantago* Sward (4), w = Wet Heath (4). Boxes and whiskers show the extent of between-year variation in mean dry mass within each plant community. Total biomass was lower in March than

in August in *Holcus/Agrostis* and *Nardus* grasslands and in Short Heather, but not in Tall Heather, *Plantago* Sward or Wet Heath.

The effects of sheep numbers on live biomass (total – dead organic matter - bryophytes) are shown across plant communities in Table S D 4. All of the 8 grazing effects in non-woody vegetation had negative signs, but only 2 were significant *Holcus/Agrostis* grassland and *Plantago*, both in August. The apparently positive effects of grazing in both tall and short Heather communities are explained below.

Within the *Holcus/Agrostis* grasslands, dead organic matter in March declined significantly with sheep numbers in the previous August (slope = -0.0042, s.e. = 0.0011, $p < 0.001$, $r^2 = 0.3973$) but there was no significant relationship between dead organic matter in August and contemporary sheep numbers (slope = 0.00057, s.e. = 0.0009, p = 0.534, $r^2 = 0.017$). In contrast, there was no significant relationship between bryophyte dry mass and sheep numbers in March (slope = 0.0007, s.e. = 0.0004, s.e. = 1.627, p = 0.118, $r^2 = 0.107$), but there was a significant positive relationship in August (slope = 0.0004, s.e. = 0.00021, p = 0.045, $r^2 = 0.164$). As expected, there was a significant negative relationship between sheep numbers and grass biomass in both March (slope = -0.00178, s.e. = 0.0004, $p < 0.0001$, , $r^2 = 0.523$) and August (slope = -0.0047, s.e. = 0.0016, $p < 0.01$ $r^2 = 0.265$). However, there was no significant relationship between total herb biomass and sheep numbers in either March (slope = 0.000015, s.e. = 0.00007, p = 0.84, $r^2 = 0.002$) or August (slope = -0.00036, s.e. = 0.00019, p = 0.063, $r^2 = 0.14$).

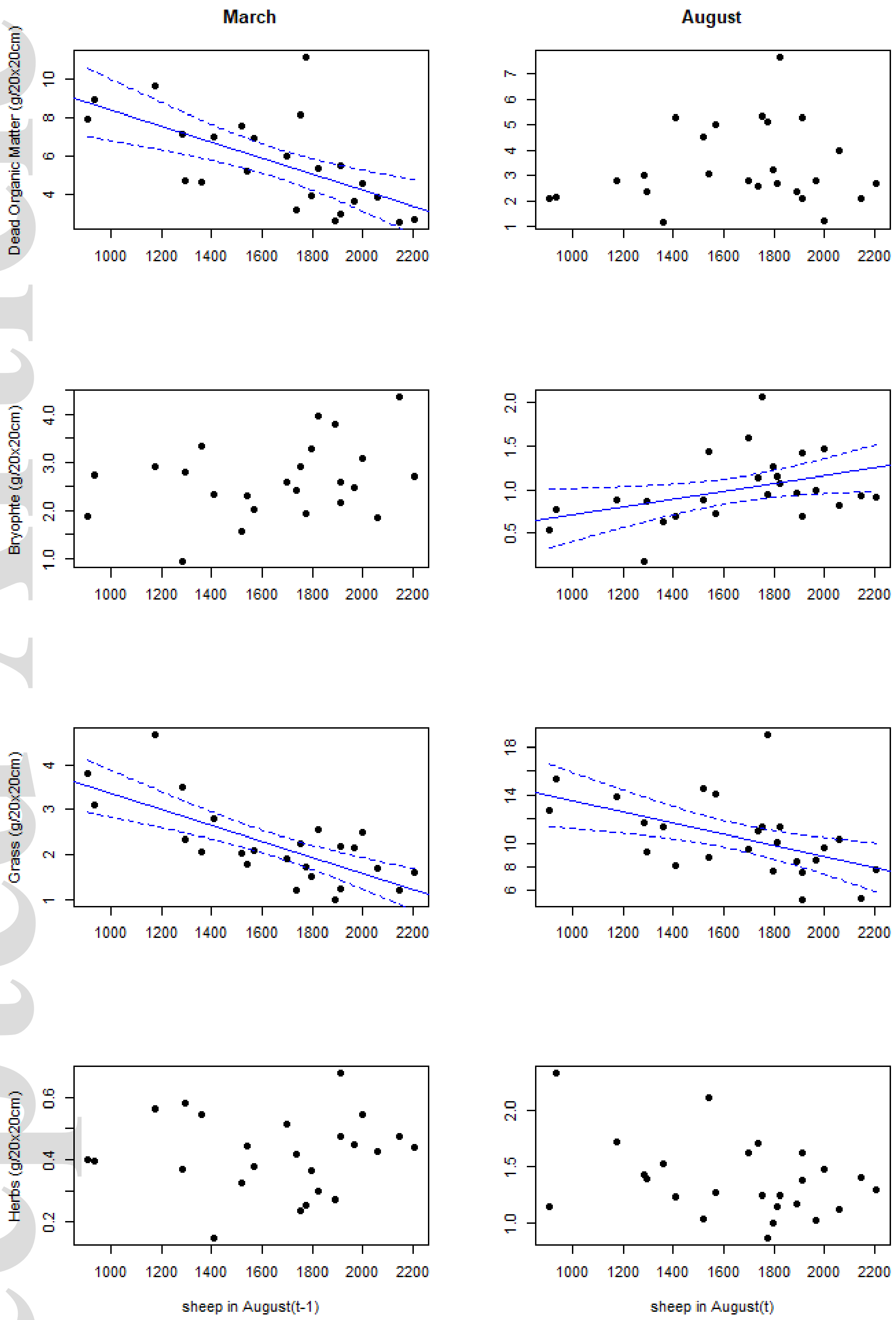

Fig. 5. Biomass components of the *Holcus/Agrostis* sward in March (left column) and August (right column) as a function of sheep population size (on all the x axes). Dead organic matter (DOM) declined significantly with sheep numbers in March, but the relationship was not significant in August. Total bryophyte biomass shows no relationship with sheep numbers in

March, but a marginally significant positive relationship in August. Total live grass biomass declined with increasing sheep numbers in both March and August, but the residual variation was greater in August (note the large change in y axis scales). Total live herb biomass was variable from year to year, but was not significantly related to sheep numbers in either March or August (statistics in the text).

The importance of the effect of grazing on each plant species is described by the ratio of predicted biomass at minimal sheep density to predicted biomass at maximal sheep density (Table S D 5). This measure of importance only works if the species is not so palatable that it is excluded altogether (e.g. *Angelica sylvestris*) or is grazed to an inaccessible stubble even at the lowest sheep densities (e.g. *Trifolium repens*), because in that case the regression has a slope of zero. The palatable species like the grass *Festuca rubra* and the herb *Ranunculus acris* show the expected negative correlations with sheep numbers. For less palatable species like the herb *Cerastium fontanum* there was no significant correlation between biomass and sheep numbers. The case of the abundant grass *Holcus lanatus* is interesting: there was no significant effect of sheep numbers on biomass in August, but there was a highly significant decrease in biomass with increasing sheep numbers in March. The three lowest-growing species (*Viola riviniana, Galium saxatile* and *Sagina procumbens*) all increased with sheep numbers, but not significantly. We did not find any species that exhibited a significant positive correlation between biomass and sheep numbers, as might be shown by a highly unpalatable species benefitting from pronounced competitor-release.

During winter when sheep feed more on Heather communities we found a significantly greater biomass of green heather was lost over winter when sheep numbers were higher (Fig.10b; effect = 0.0048, s.e. = 0.0018, p = 0.009). In contrast, green biomass increment between March(t) and August(t) did not decline with sheep numbers measured either in August(t-1) (effect = +0.0036, s.e. = 0.0028, p = 0.203) or in August(t) (effect = +0.0019, s.e. = 0.0029, p = 0.524).

3.6 Flower stem densities

The most highly palatable species (e.g. *Festuca rubra* and *Rumex acetosa*) were never observed to flower at all in the grazed sward in 24 years (1994-2017), despite flowering freely in ungrazed places like cliff ledges, cleit roofs (S E Figs 15, 16)) and on the sheep-free island of Dun in the archipelago (Crawley, 2017). The highest flower stem densities were typically recorded for the less palatable grass species like *Holcus lanatus* and *Anthoxanthum odoratum*.

The effects of sheep numbers on flower stem densities of grass and herb species are shown in S D Table 6. A few plant species show an immediate increase in flowering when sheep numbers are low, most notably *Leontodon autumnalis* and *Ranunculus acris*. Other species show a time lag of one or more years in flowering response to grazing intensity. Of the 14 species that were sufficiently abundant to analyse, 5 showed significant negative correlations between flower stem density and current sheep population, 6 showed non-significant negative correlations, 3 showed a non-significant positive correlation, and none showed a significant positive correlation. Five species showed significant negative correlations after a time-lag of 1 year, and 2 species after a lag of 2 years. The large residual variance in all species indicates that other factors (e.g. weather conditions and/or historical effects) play an important role in determining flower stem densities, except in the extreme cases of *Festuca rubra* and *Rumex acetosa* where grazing completely precluded flower stem survival.

3.7 Plant species richness

Mean vascular plant species richness was greatest (14.3) in gaps in *Nardus* grassland and lowest (6.6) in tussocks in Heather (Table S D 7 - 20 cm x 20 cm; see Table S B 1 for larger spatial scales). Within communities, species richness was higher in gaps than in tussocks in *Holcus/Agrostis* grassland, *Nardus* grassland and Heather, and lower in *Plantago* Sward and Wet Heath but the differences are small in all cases.

Species richness in biomass data (e.g. Fig. S D 13) is higher than in gaps or tussocks because the area sampled is twice as large (it is the weighted average across 2 quadrats, 1 gap and 1 tussock). Highest mean species richness in biomass samples was in *Nardus* grassland (19.58 species per 40 cm x 20 cm), then Wet Heath (18.97), *Plantago* sward (17.03), Heather (13.44) and lowest in *Holcus/Agrostis* grassland (11.03).

We predicted that across sampling locations within plant communities, species richness would decline with increasing mean biomass: this was observed in *Holcus/Agrostis* grassland (Fig. S D 13), but replication was too low for a reliable test in the other plant communities. Across years, there were no significant effects of sheep numbers on mean species richness at the scale of

40 cm x 20 cm in any of the plant communities (Fig. S D 12a). Note, however, that long-term sheep exclusion was associated with a dramatic decline in species richness (see **3.10**, below).

3.8 Above ground net plant production

We measured above ground net primary production (ANPP) in 4 locations from ungrazed quadrats protected beneath temporary exclosures twice per year: in August(t) and in March(t+1). There were 2 replicate pyramids at each site. We have no data on ANPP from Heather or Wet Heath.

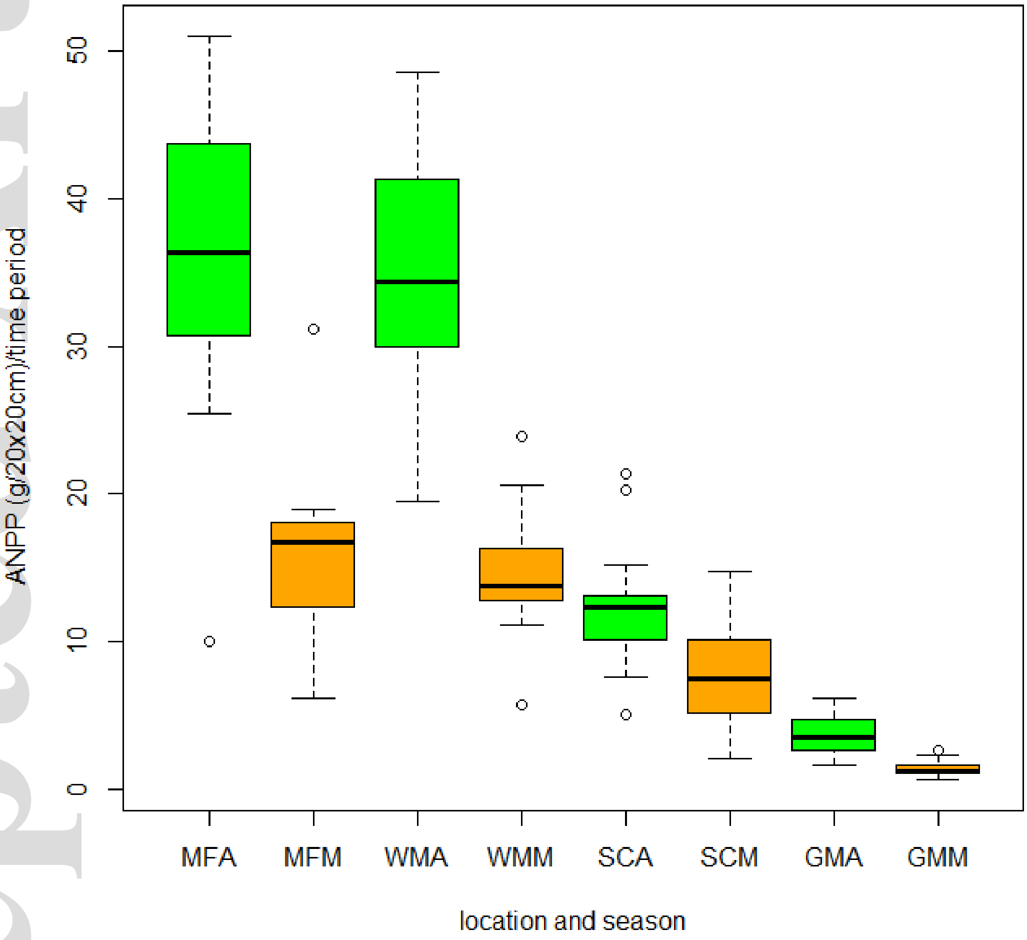

Fig. 6. Above ground net production (ANPP in four locations: MF = Mid Fields, WM = West Meadow (both in *Holcus/Agrostis* grassland), SCA = St Columba (*Nardus* grassland) and Gun Meadow (*Plantago* sward), measured in two seasons (A = August in green; M = March in Orange). Statistical analysis in Table S D 8. Boxes and whiskers indicate the variation in mean ANPP (*n*=2) within each location and season across the years 2000-2017 in West Meadow and Mid Fields and 2003-2017 in Gun Meadow and St Columba.

The box-and-whisker plots in Fig. 6 illustrate the magnitude of year-to-year variation in plant growth within seasons at the 4 locations: 2014 was particularly good for primary production in both seasons, and March 2003 and 2007 were particularly poor across all localities. ANPP for Mid Fields and West Meadow were not significantly different in either season, so were averaged for subsequent analysis to give a single figure for ANPP in *Holcus/Agrostis* grassland for each season in each year.

Plant production was greatest in *Holcus/Agrostis* grasslands in both seasons (means of 35.3g/ 20 cm x 20 cm/time period in August (over 5 spring months) and 15.2g in March (over 7 autumn and winter months), intermediate in *Nardus* grassland (12.5g and 7.7g) and lowest in *Plantago s*ward (3.8g and 1.4g). For comparative purposes, these figures equate to 12.6 t/ha, 5.1 t/ha and 1.3 t/ha dry matter per year (August + March) across the three plant communities. The seasonal differences were significant for all locations (pairwise t-tests; details in Table S D 8). A more detailed analysis of the year-to-year differences in plant production will be presented in a subsequent paper, but there were no significant effects of monthly mean temperatures, or temperatures averaged across groups of months (data not shown). There was no significant correlation (*r*) between primary production and sheep numbers in either time period (March(t) to August(t) , $r = 0.32$, $p = 0.203$ or August(t) to March (t+1) $r = 0.18$, $p = 0.485$) indicating that initial leaf area did not have a lasting impact on dry mass accumulation over a period of 5 months or more.

3.9 Soay sheep population dynamics

The multiple regression models of sheep population growth (*delta*) over the period 2000-2017 when we had estimates of ANPP from the *Holcus/Agrostis* grassland, as well as winter precipitation and population size are shown in Table S D 10. The models differ only in the period over which ANPP was measured (i.e.: p12=p1+p2, p23=p2+p3, p13=p1+p3 and p123= p1+p2+p3). All the models had significant positive effects on *delta*, and the best model (as judged by AIC) included the sum over all three periods, However, winter precipitation was not significant. The model i.e. `lm(delta ~ N + p123)` (Fig 7) accounted for 65% of the variance in *delta*, with the effect of ANPP = 0.00773 (s.e.0.0029, p = 0.02); see Table S D 10). This indicates that production over the entire 17-month period affected sheep population change, but with different intervals being most influential in different years (Fig. 7.b). Although the term for winter precipitation had a negligible influence on the population growth rate, over the longer period since 1985 there was a significant negative effect of both increasing population and increasing winter precipitation. (Fig. S D 16: effect = 0.00104, s.e. = 0.00044, p = 0.024).

It is noteworthy that the maximum value of ANPP measured in 2014 (Fig. 9) was associated with the only example we encountered of a 3rd successive increase in sheep population (2014-2015; Fig 2). All other runs of data had population declines following 1 or 2 years of increase.

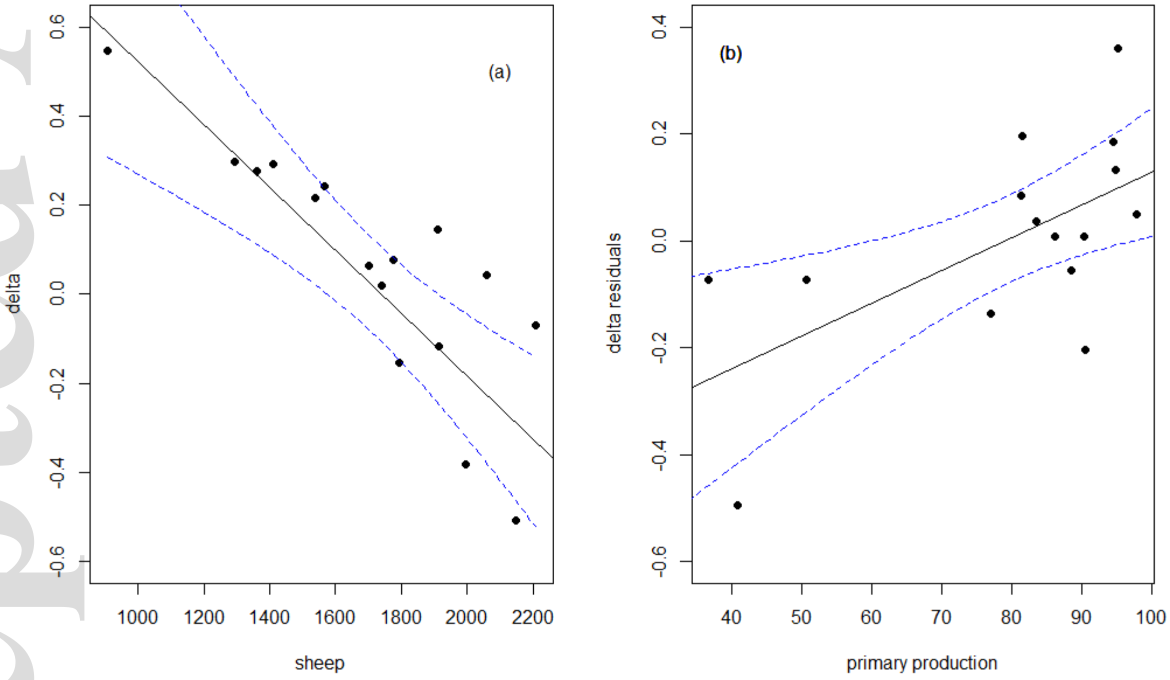

Fig. 7 The relationship between sheep population change *delta* (= ln (N(t+1)/N(t))) and a) the whole island count (sheep = N(t)), b) plant production data in *Holcus/Agrostis* grassland, between 2000-2017. The strength of density dependence (effect = -0.00093, s.e. = 0.000163, p = 0.00016), after controlling for plant production. The effect of plant production (+0.0077 ,s.e. = 0.0029, p = 0.02) after controlling for sheep population size. Blue dashed lines show the 95% confidence envelope for the linear regression (black line).

3.10 Long-term sheep exclusion

Long-term exclusion of Soay sheep led to the replacement of a species-rich sward of grazing-tolerant grasses and forbs by a tall, species-poor sward dominated by a few highly palatable species. Some of these species persist at lower densities in the grazed sward (e.g. *Festuca rubra*) but others are so palatable to the sheep that they are excluded altogether from grazed swards (e.g. *Angelica sylvestris*).

The differences between grazed and long-term ungrazed swards in March and August (Fig. 8) illustrates that dead organic matter (DOM) was 5 times more abundant in ungrazed swards in both March and August. Bryophytes showed the opposite pattern: they were much more abundant in grazed swards than in ungrazed swards. Both DOM and bryophytes were more abundant March than in August. In contrast, all vascular plant species were more abundant in August than in March.

The most extreme response to exclusion of Soay sheep is shown by the highly palatable, winter-green grass, *Festuca rubra* which was 44 times more abundant in the ungrazed sward in March and 12 times more abundant in August. The highly palatable herb *Rumex acetosa* was 27 times more abundant in ungrazed swards in August. In contrast, *Cerastium fontanum* was only 1.2 times more abundant when ungrazed. The major components of the grazed sward, like the less-palatable grasses *Holcus lanatus* and *Anthoxanthum odoratum*, declined dramatically in abundance in the absence of herbivory (33-fold and 4-fold declines respectively in August; see Fig. 8).

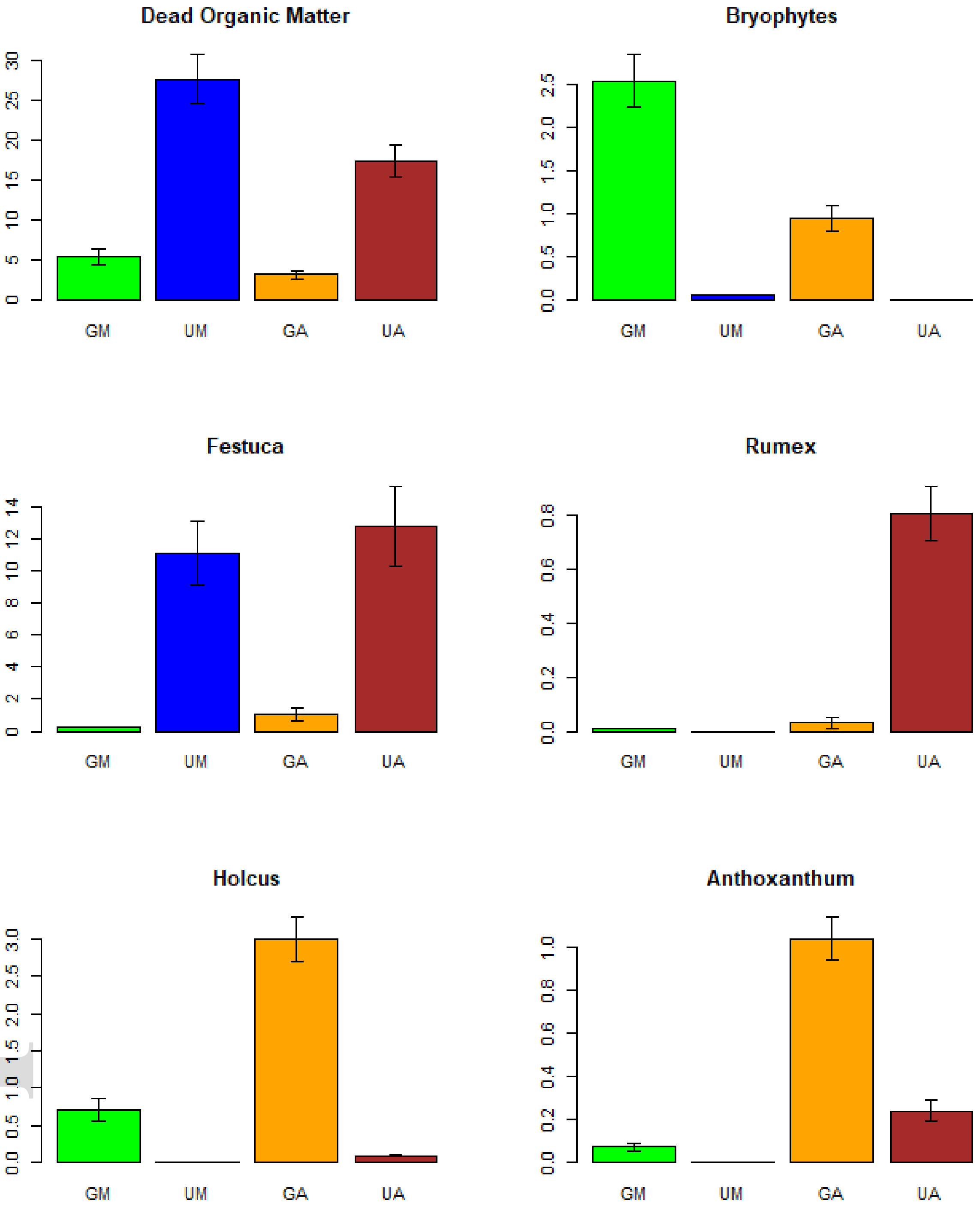

Fig. 8. Long-term ungrazed plant communities (U) on inaccessible cleit roofs compared with nearby open swards grazed by Soay sheep (G) in March (M) and August (A). See text for details. The response variables are mean dry weights (g) from 20 cm x 20 cm sample quadrats (note the large scale changes between species). Error bars show +/- 1 s.e. mean (*n* = 4).

3.11 Temporal Trends

The botanical composition of the *Holcus/Agrostis* grassland has changed remarkably little since the Soay sheep were introduced from Soay to Hirta in 1932 (Table S D 11). The grassland was surveyed in 1931 after the domestic Blackface sheep had been removed but before the Soay were introduced (Petch, 1933). All the important grasses and herbs had the same abundance rating in 2017 as in 1931. Differences in the less abundant species are noted in Table S D 11, and it is particularly interesting that *Jacobaea vulgaris* appears to have declined: it may have been less palatable to the domestic Blackface sheep prior to 1930 than to the Soay sheep after 1932.

The study period 1985-2017 has seen significant upward trends in average temperatures: winter (December(t-1)-March(t)) increased by 0.0288 °C/yr (s.e. = 0.013, p = 0.038); the rapid growth phase (April-July) increased by 0.037 °C/yr (s.e. = 0.012, p = 0.004) and autumn (August-November) increased by 0.0368 °C/yr (s.e. = 0.0104, p = 0.0013). There were no significant seasonal trends in rainfall, most importantly winter rain (January – March) which has a significant negative impact on sheep population change over the same period (Fig. S D 17).

Given that sheep numbers have increased over the study period (Fig. 2) we predicted that botanical composition would change, with palatable species declining in biomass and unpalatable species increasing. The observed patterns (Table S D 12) show trend lines whose signs are broadly consistent with declines in palatable species biomass and increases in unpalatable species, but only 3 out of 13 were significant. In short, sward height explains none of the variation in delta trends.

Temporal trends in plant productivity over the period 2000-2017 varied across plant communities (Fig. 9): in the most productive *Agrostis/Holcus* grasslands there was a significant upward trend (p = 0.0026), while on both the *Nardus* grasslands and *Plantago* swards there was a close-to-significant upward trend (p = 0.061 and p = 0.051, respectively),

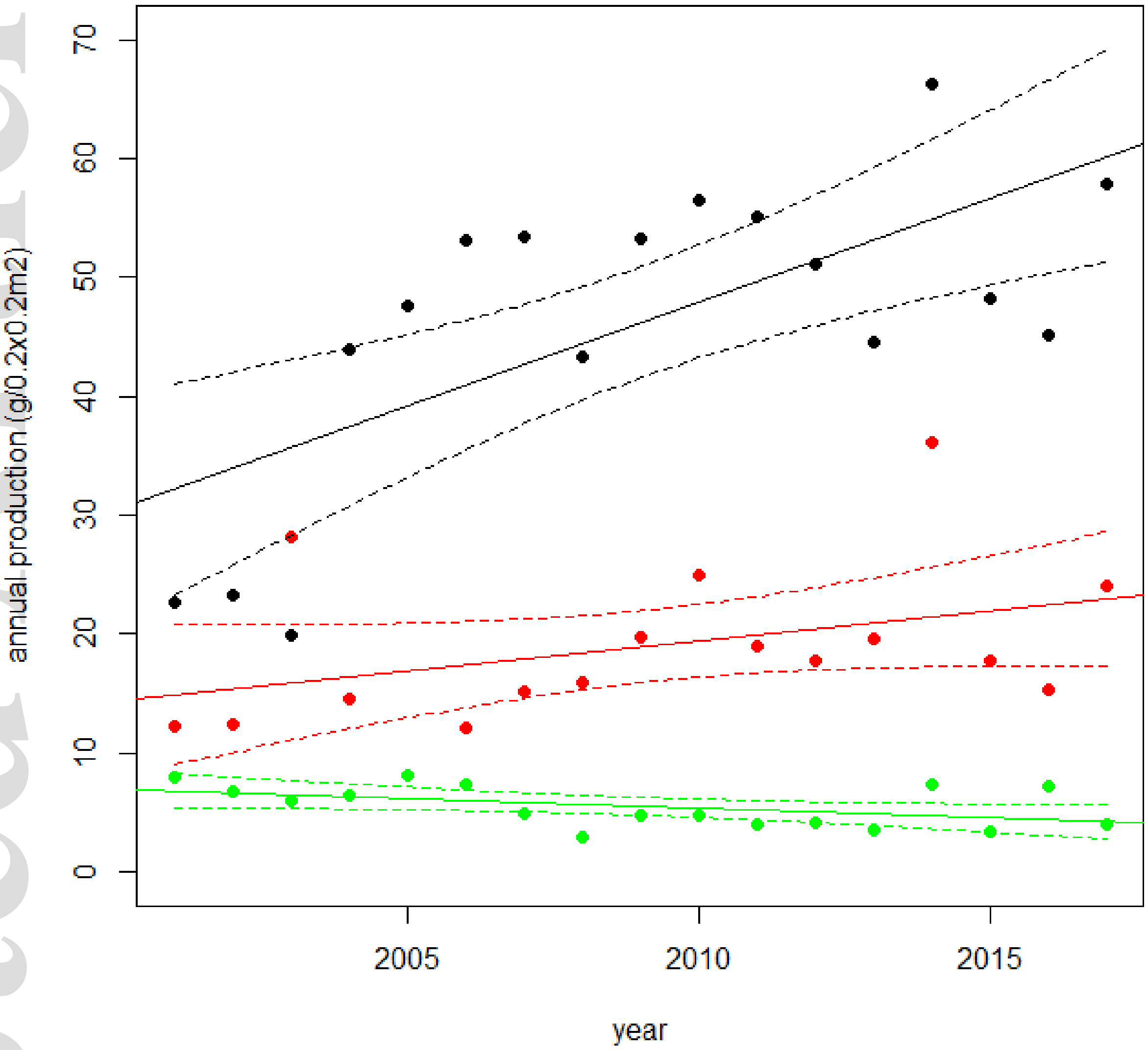

Fig. 9. Time-series of primary production inside temporary grazing exclosures (‘pluck down’ = estimated offtake measured as total dry weight of pluck-down in a 20 cm x 20 cm quadrat) summed across March and August of each year. For the *Holcus/Agrostis* grasslands (black), the data were averaged across the 4 pyramids in West Meadow and Mid Fields (slope = 1.749, s.e. = 0.485, r^2 = 0.465, p = 0.0026). For St Columba *Nardus* grassland (red;) the data are averaged across two pyramids (slope = 0.561, s.e. = 0.277, r^2 = 0.215, p = 0.061) and Gun Meadow *Plantago* Sward (green) the data are averaged across two pyramids (slope = -0.165, s.e. = 0.078 0.230, p = 0.051)

One of the most pronounced patterns in the entire study has been the steady increase in *Calluna vulgaris* in the Tall Heather community (Fig. 10a). At B6, D5 and D6 (blue symbols) mean Tall Heather biomass increased at 2.55 g/yr (s.e.= 0.279, $p < 0.00001$). The closely-grazed Short Heather (at B5 and C5, green symbols) did not increase significantly (Fig. 10a). This pattern suggests that Tall Heather is recovering from a major but undocumented setback, pre-1993 (e.g.: salt spray during severe winter storms like 13 February 1989) and it is likely that biomass will asymptote in future, once the rate of plant senescence increases (Gimingham 1988). It is clear, however, that grazing by Soay sheep is not causing deterioration of the heather stands on Hirta. Associated with this increase in biomass has been a substantial reduction in associated small-scale vascular plant species richness (from c. 14 species / 40 cm x 20 cm to c. 9 species; S D Fig. 11). There was no significant change in biomass or species richness in the Short Heather community.

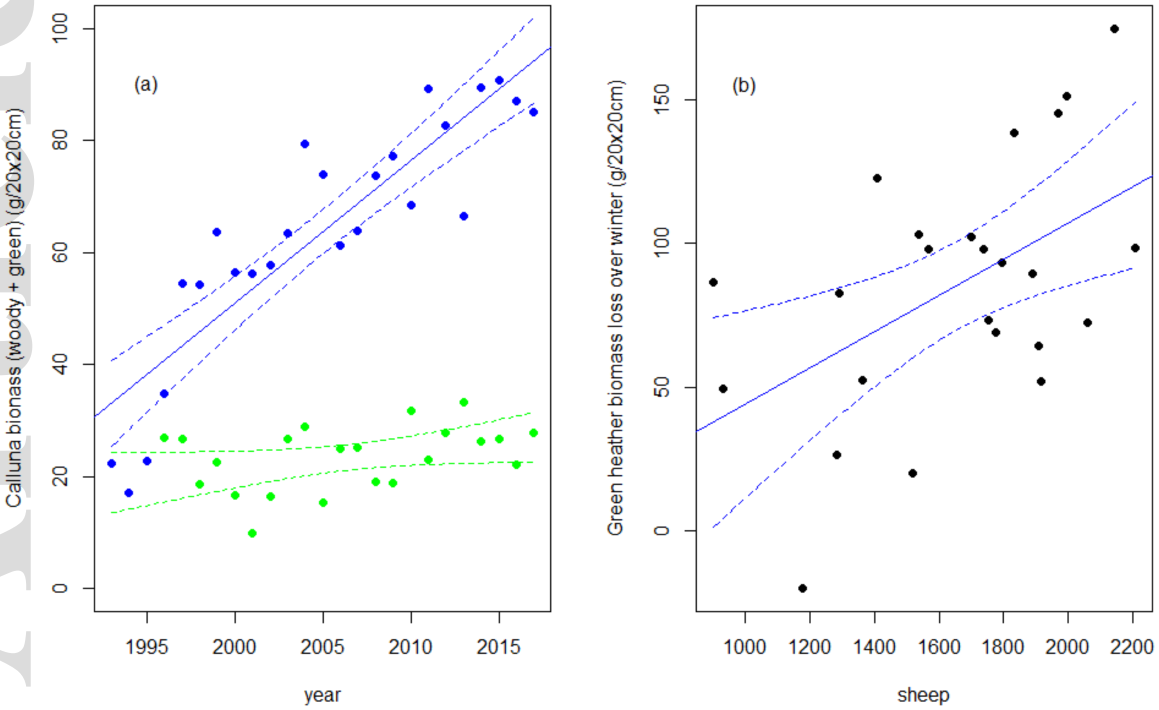

Fig. 10 (a) The dry mass of *Calluna vulgaris* (woody plus green; g/ 20 cm x 20 cm) in August in tall Heather communities (blue symbols; B6, D5, D6) and short Heather communities (green symbols; B5, C5) over the period 1993-2017. The increase in tall heather is highly significant (effect = 2.5501 g/yr, s.e. = 0.2789, p = 4.02e-09), but not significant in closely grazed short heather (effect = 0.3364, s.e. = 0.1845, p = 0.0832).

(b). Sheep numbers and green biomass loss in *Calluna vulgaris* over winter (August(t) to March(t+1). The variance is inflated by spatial heterogeneity in heather biomass, so that some ‘negative losses’ are recorded in a period when heather growth would not be expected to occur. A significantly greater biomass of green heather was lost over winter when sheep numbers were higher (effect = 0.00484, s.e. = 0.00177, p = 0.0091).

4 DISCUSSION

As anticipated our decadal study adds to current understanding of the long-term consequences of changes in herbivore numbers on the biomass of coexisting plant species, and the numerical responses of herbivore populations to changes in plant productivity brought about by year-to-year variation in growing conditions, which previously have been poorly documented.

Grazing impact and plant production

As predicted (Hypothesis H1), grazing impact differed between plant communities, with bigger impacts associated with higher productivity. *Holcus/Agrostis* grassland had the highest productivity (Fig. 6) and showed the greatest impact of grazing on plant biomass, both seasonally and with changes in sheep numbers (Fig. 5). Wet Heath was little grazed even when sheep numbers were at their highest. Nardus grassland, dominated as it is by one of the least palatable of grasses (Chadwick, 1960), showed intermediate levels of primary production (Fig. 6). However, the *Plantago* sward is puzzling. It is grazed close to ground level in both winter and summer, even in years when sheep numbers are at their lowest (Regan et al., 2017). The sward is so short (Fig. S D 4) that bite-size must be extremely small, and primary production is much lower than in the other two grassland types (Fig. 6). The most likely explanation of its attraction to the sheep is that *Plantago* sward provides an essential nutrient, and the most plausible candidate is sodium from salt spray (Malloch 1972). We return to this when discussing the influence of nutrient and microclimate later. Heather was the only community dominated by woody plants and proved to be recalcitrant to our attempts at measure grazing offtake using temporary sheep exclosures.

Grazing and flowering of palatable and unpalatable species

There was enormous variation from year to year in which species flowered prolifically, and contrary to our expectations (Hypothesis 2) only a handful of species showed a significant relationship between sheep numbers and flower stem density (Table S D 6). The two most palatable species, *Festuca rubra* and *Rumex acetosa*, although they flowered abundantly every year on ungrazed cleit roofs, were never once observed to flower in grazed grassland in 24 years: grazing by even the lowest densities of sheep prevented flowering altogether. A similar pattern was observed in the high nutrient quality short-grass plains in Serengeti, where the wildebeest migrate to have their calves (Belsky, 1992). It was noteworthy that there was no evidence of any unpalatable species where flowering was positively correlated with current or previous sheep numbers, as one might expect if there was significant competitor-release, as a result of selective defoliation of more palatable species (Crawley 1983). This may be because Soay sheep grazing is less selective than we hypothesized, or because the plant species capable of benefitting from competitor release, either never arrived on the island, or were excluded by centuries of heavy grazing by domestic livestock.

With just a single visit each year it is tricky to obtain a detailed understanding of flowering behaviour. For example, where flowering declines with increasing sheep numbers, we don't know whether this is due directly to sheep feeding on the flowers, or indirectly to a reduction in the rate of floral initiation, as a result of defoliation leading to resource-limitation within the plants. Furthermore, there is huge year-to-year variation in flowering of less palatable plant species like *Holcus lanatus, Anthoxanthum odoratum* and *Cerastium fontanum* that exhibits no apparent dependence on grazing pressure. Finally, we do not know whether variation is plant recruitment is related to variation in seed-set (i.e.: which species, if any, have seed-limited recruitment; Crawley 1983), because seedling establishment is observed so seldom in these dense, perennial-dominated communities.

Plant species richness and plant biomass

We hypothesized (Hypothesis 3) that plant species richness would decline with increasing biomass (exemplified by the Park Grass Experiment at Rothamsted; Crawley et al., 2005), and that by reducing biomass, grazing would enhance species richness. The relationship between production, biomass and species richness on Hirta is complicated by the fact that grazing offtake varies so much across plant communities (Fig. 6), but nevertheless, it is clear that the net effect of grazing on small-scale species richness is positive. Evidence from several aspects of this study support this: ungrazed cleit roofs had more than 5 times the live biomass and roughly half the species richness (c. 4 spp.) of adjacent grazed *Holcus/Agrostis* grassland (c. 9 spp). While across the 14 different spatially separated sampling locations within *Holcus/Agrostis* grassland there was a significant negative relationship between species richness and biomass (Fig. S D 12). Also, species richness beneath the canopy of Tall Heather declined as the biomass of *Calluna* increased (Fig. 9). However, across years, within plant communities, there is no evidence of a relationship between average small-scale species richness and sheep numbers (Fig. S D 12a).

Plant production in relation to nutrients and microclimate

As predicted (Hypothesis 4) biomass accumulation within temporary grazing exclosures varied in relation to soil nutrients and microclimate. Above ground plant production was greatest in the *Holcus/Agrostis* grasslands on what was previously cultivated ground, fertilized by centuries of human and livestock dung and urine, supplemented by peat ash and the carcasses of huge numbers of seabirds (Meharg et al., 2006). This high soil-nutrient status underpinned annual dry matter production of 12.6 t/ha/yr. Plant production was intermediate in unfertilized Nardus grasslands (5.1 t/ha/yr) and lowest in *Plantago* sward (1.3 t/ha/yr), which, as noted above, is found in locations susceptible to salt spray. We know that sodium is important in sheep nutrition (Underwood 1966) and we know that the plants in salt-sprayed *Plantago* communities have relatively high sodium concentrations (Malloch, 1972). An alternative hypothesis is that halophytes like *Plantago coronopus* accumulate compatible solutes in the cytoplasm to counteract the osmotic stress of accumulating sodium in the vacuoles. One of these is proline, which is a nitrogen containing compound. Levels of these compatible solutes can get so high that they make up a considerable proportion of plant nitrogen. So potentially the sheep are targeting high nitrogen (Sleimi et al., 2015; Hanley et al., 2020). This remains to be investigated.

Long term herbivore exclusion impacts palatable/unpalatable species

As expected (Hypothesis 5), long-term exclusion of sheep led to increased growth of the most palatable species leading to the competitive exclusion of less palatable species. The flora of Hirta includes a small group of plant species that are so palatable to Soay sheep that they are completely excluded from all the habitats to which the sheep have access (e.g. *Angelica sylvestris, Tripleurospermum maritimum* and *Jacobaea vulgaris*). These plants persist only on ungrazed islands like Dun, and on cliffs and inaccessible cleit roofs (3.7) where there is no grazing (Fig 8). There is a huge build-up of dead organic matter, virtual disappearance of bryophytes and the development dominance by a few highly palatable species like *Festuca rubra* and *Rumex acetosa*. It is noteworthy that Ragwort (*Jacobaea vulgaris*), normally such a pernicious increaser under grazing in most of Britain, was a dramatic decreaser on Hirta, completely absent from the grazed sward (Table S B 1) and found only on ungrazed cleit roofs (Crawley, 2017) and on the green roof of the new accommodation block (in August 2021). This suggests that there could be a role for using Soay sheep on farms in mainland Britain to help manage Ragwort infestations.

Seasonal changes in herbivore impacts

As we predicted (Hypothesis 6) plants experience relatively low grazing impact during the growing season (measured in August) and high grazing impact over winter (measured in March) when biomass is low. The fact so few measurements of grazing impact were significant in August, while almost all such measurements were significant in March, is strong evidence that food-limitation during the unfavourable season allows plant species to recover during the rapid growth phase when grazing pressure is relatively low (Sinclair 1975, Crawley 1983, Lezama et al., 2014).

Illius & O'Connor (2000) predicted that herbivores regulated at relatively high population density by the existence of an extensive 'key resource area' will spill over into other habitats, where they impose higher levels of defoliation than would be experienced in a spatially uniform environment that lacked the key resource area. On Hirta, the presence of a substantial area of *Holcus/Agrostis* grassland meant that defoliation suffered over winter by *Calluna* (Fig. 10b) was greater than it would be in a spatially uniform system consisting solely of dry heath.

Sheep population dynamics

As hypothesized (Hypothesis 7) we documented a significant impact of plant production on sheep population dynamics (Fig. 7b). The precise timing of enhanced ANPP varied from year to year, but the influential period seems to span at least 17 months. There is an effect of increased production during the growing season before the year in question (i.e. March(t) to August(t)), presumably through improved body condition going into winter (see also for reindeer: Albon et al., 2017). The biggest effect was measured over autumn and winter (i.e. August(t) to March (t+1)), presumably reducing the intensity of competition for food. There was a smaller effect of enhanced production during spring (i.e. March(t+1) to August(t+1)), improving post-partum availability of high-quality food. We had a reasonably clear understanding of the causes of steep declines in sheep population, from the interaction between high population density, poor body condition and wet winters (Coulson et al. 2001).

We now have the first evidence that above-average annual primary production is an important driver of positive change in sheep numbers (Fig. 7b). Equally, it is now clear that changes in plant biomass, particularly in March, do little more than reflect changes in sheep numbers (Fig. 5).

Sheep population dynamics appear to have changed over the course of the study (Fig. 2). From 1985 to 2011 the population fluctuated widely but showed a sustained increase in mean number of almost 40 extra animals per year. Since 2011 the population has fluctuated less and showed no significant change in mean number (Fig. S D 1). The most striking feature of the time series is that we have never observed two consecutive years of population decline. This indicates that the strength of density dependent mortality is always sufficient to ensure that population density is low enough in the following year that reproduction will exceed mortality (delta > 0) whatever the weather. Likewise, we have never observed more than three successive years of population increase. Of the three distinct patterns of population change described by the series of ups (U) and downs (D) in Fig. 2, the most frequent were UUD and UD (each observed 6 times) with UUUD observed only once (see 3.9). It is noteworthy that 5 of the 6 UUD occurred in the first half of the time series, and that the last 6 years have all been UD, suggesting that there may have been a fundamental change in the pattern of population dynamics after 2011. We plan to address this hypothesis in a subsequent paper).

Other temporal trends

Over the period 1985 to 2020 there were several significant temporal tends. Mean winter minimum temperature (December to March), earliness-of-spring temperature (mean daily maxima in February and March), and average temperatures during the rapid growth phase (April, May and June) all showed significant upward trends. There was no trend, however, in winter wetness, the most important negative correlate of sheep population change (see 3.11 above). Primary productivity increased over the study period, significantly in the most productive plant communities (*Holcus/Agrostis* grasslands, Fig. S E 16). Because we don't have plant production data before 2000, it is not clear what drove the protracted increase in mean population between 1985 and 2000, but it is plausible that, post-2000, increasing food supply led to improved reproductive success and reduced over-winter starvation. We have found out how little we learn about sheep dynamics by measuring plant biomass and how vitally important it is to quantify plant production and grazing offtake. But there is still much to be learned about the causes of seasonal and annual changes in plant productivity, and about the long-term consequences of grazing on botanical composition and relative abundance of plant species (e.g.: the role of plant compensation, as highlighted by McNaughton, 1979 and Anderson et al., 2013).

Some measurement challenges

The demonstration of the importance of plant production draws attention to the need to find effective ways of estimating plant production in the two plant communities where we have so far tried and failed, largely because of small-scale spatial heterogeneity in biomass, which meant that more than half of our measurements of net production returned spurious negative vales. This is most important for the Heather community, because there is a strong indication that sheep are taking substantial amounts of green Heather between August and March (Fig. 10b). Failure to measure primary production in Wet Heath may be less serious, if sheep feed from this community as little as data from other parts of Scotland suggest (Virtanen et al., 2002; Milner et al., 2002).

Wider significance of grazing impacts and the controversy of overgrazing

Much has been written about the potential of unmanaged herbivores to cause severe habitat degradation through overgrazing (Mysterud, 2006). By overgrazing, we mean the process whereby grazing causes a long-term reduction in animal productivity as a result of changes in the botanical composition of the vegetation, with a decline in palatable species and an increase in unpalatable plant species (*sensu* Crawley 1983). Overgrazing is a process associated with mismanagement of herbivore populations by humans, and as such it would not be expected to be a feature of an unmanaged population like Soay sheep on St Kilda. Overgrazing typically occurs when herbivore numbers are held at artificially high numbers through the unfavourable season (e.g. supplying supplementary food in winter, or importing animals for the summer; Mysterud, 2006), with the consequence that grazing impacts during the plant growing season are unnaturally high and damaging to the principal forage plants. If there was overgrazing by Soay sheep on St Kilda we would have seen a downward trend in sheep numbers associated with an upward trend in the biomass of unpalatable plant species. We saw neither of these: on the contrary, sheep numbers increased and there was no significant increase in the biomass of unpalatable plants. The botanical composition of the various plant communities remains much as it was 85 years ago (Petch 1935), with no significant increases in unpalatable species, indicative of a highly resilient plant-herbivore interaction (Table S D 11). There is no evidence from this system to support the hypothesis that a food-limited population necessarily causes overgrazing.

Data Archiving statement

Supporting data can be found in dryad, at https://doi.org/10.5061/dryad.x69p8czjt (Crawley 2021)

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Authors' Contributions

M.J. Crawley collected data, analysed data, and wrote the first draft. R.J. Pakeman collected data and contributed to manuscript drafting. S.D. Albon and I.R. Stevenson were involved from the start of the study in data collection, analysis and much else. J.G. Pilkington ran the field operations, logistics and collected prodigious amounts of data. M.B. Morrissey contributed to analysis of data and manuscript drafting. O.R. Jones, E. Allan, A. Bento, H. Hipperson and G. Asefa sorted biomass samples and collected other data. J.M. Pemberton was the Principal Investigator.

Conflict of Interest

M.J. Crawley and E. Allan are Associate Editors for Journal of Ecology. They were not involved in the peer review of this article. The authors declare no other conflicts of interest.

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