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Pakeman, R.J. orcid.org/0000-0001-6248-4133, Stevenson, I., Pilkington, J. et al. (6 more authors) (2024) Plant community-specific greening patterns predict population size increases in a temperate herbivore. Oikos, 2024 (12). e10551. ISSN 0030-1299

https://doi.org/10.1111/oik.10551

OIKOS

Research article

Plant community-specific greening patterns predict population size increases in a temperate herbivore

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Oikos
2024: e10551
doi: 10.1111/oik.10551
Subject Editor: Bente J. Graae
Editor-in-Chief:
Gerlinde B. De Deyn
Accepted 31 July 2024

Climate change-driven impacts on vegetation productivity have been shown to drive mammalian herbivore population dynamics in Arctic and alpine environments. However, there is less evidence for temperate systems. To address this, we examined the contribution of increasing plant biomass in different vegetation communities (measured by NDVI, normalised difference vegetation index) and winter weather on the observed long-term upward trend in the population of the Soay sheep of Hirta, St Kilda, UK. We found that biomass had increased in all vegetation communities present and increased the fastest in vegetation types preferred by the sheep. Specifically, those communities with high specific leaf area and Ellenberg's N, low leaf dry matter content. Peak summer NDVI and either winter average wind speed or winter North Atlantic Oscillation data added to the variance explained by a simple density dependence model of yearly sheep population growth rates. The highest explanatory power was found for preferred vegetation types including maritime cliff communities dominated by *Plantago* species, but also for both inaccessible (*Rumex acetosa*-dominated) or unpreferred (*Eriophorum vaginatum*- or *Sphagnum*-dominated) communities where seasonal variation more closely reflects productivity due to minimal grazing. Although the climate is getting windier and wetter, it is also getting warmer allowing increased plant productivity and this appears to be behind the long-term increases in the Soay sheep population. Our study indicates that analysing key vegetation communities may reveal these links better than using landscape-level averages, and that oceanic-temperate systems may show similar climate-driven herbivore population trends to those reported in Arctic and alpine systems.

Keywords: normalised difference vegetation index, North Atlantic Oscillation, *Ovis aries,* population dynamics, productivity, vegetation, wind

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Introduction

Increasing vegetation productivity ('greening') has been observed over recent decades at high latitudes (Jia et al. 2003, Bhatt et al. 2010, 2014) and altitudes (Carlson et al. 2017). This is evidenced by increases in normalised difference vegetation index (NDVI), which is correlated to biomass (Jia et al. 2003, Epstein et al. 2012, Raynolds et al. 2012) and is driven by increasing temperatures and longer snow-free periods. Trends are not universal as some areas show browning, reduced biomass, driven by extreme events such as drought and increased winter temperatures (Phoenix and Bjerke 2016) as well as by high levels of herbivory (Zhang et al. 2024). For some areas (e.g. northern Alaska) greening has not been accompanied by plant community change (Arndt et al. 2019), but in others there has been an increase in shrubs and an advance of the treeline (Frost and Epstein 2014).

Greening is likely to impact herbivore population dynamics across latitudes and ecosystems due to the dependence of herbivores on the availability and quality of their forage (Owen-Smith 1990). However, to date most studies linking NDVI and herbivore demography or population size have focussed on Arctic and alpine ecosystems and have produced mixed results. For instance, longer plant growing seasons and increased food availability in autumns have enhanced overwinter survival in reindeer leading to increased population size in Svalbard (Loe et al. 2021), musk oxen have increased in population size as a result of early spring greening, but caribou have declined in the same area of west Greenland (Eikelenboom et al. 2021). A similar declining trend in population size for caribou has been observed in North America, likely driven by a decline in forage quality as shrubs with strong anti-browsing defences have expanded (Fauchald et al. 2017). Annual warming also results in earlier declines in nutritional quality leading to reduced food quality for herbivores in late summer as they build up body mass prior to winter (Doiron et al. 2014).

Greening is expected and in evidence in more temperate regions associated with generally warming temperatures (Currey et al. 2022, Shen et al. 2022). This has the potential to impact the population dynamics of temperate herbivores, for example if changing climate increases plant productivity or shifts community dominance. However, we currently lack detailed studies of the relationship between greening and herbivore population dynamics in temperate habitats outside of mountain areas. Here, we test whether and how greening has shaped the dynamics of a wild Soay sheep *Ovis aries* population over the last four decades.

Studies in the Arctic and alpine systems linking herbivore population trends to changes in vegetation biomass have taken an approach of assessing this at relatively large scales, i.e. regional levels (Epstein et al. 2012) or at the level of the entire population (Fauchald et al. 2017, Van de Kerk 2020). However, where there is heterogeneity in vegetation cover, there will be vegetation types that are preferred by herbivores due to their high digestibility and nutrient contents (Jefferies et al. 1994, Raynor et al. 2016). If this heterogeneity exists, herbivore population dynamics may be linked more closely to patterns of greening in preferred plant communities rather than less preferred/avoided vegetation or changes at the landscape scale. However, greening patterns in preferred communities may be damped compared to non-preferred communities, as they are the focus of grazing, and hence the behaviours of non-preferred communities may more accurately reflect changes in net primary productivity.

The Soay sheep population of Hirta (St Kilda archipelago) has shown an increasing trend in abundance through time (Crawley et al. 2021), and whilst the island's hyper-oceanic climate contrasts with the drier high-latitude areas where greening impacts on herbivore population dynamics have been studied, increasing plant productivity may explain this increase in population size through time. The island vegetation communities have proved remarkably stable over decadal timescales (Crawley et al. 2021), so the impacts on Soay sheep dynamics are most likely to be driven by productivity rather than species turnover. Earlier modelling of the island population demonstrated the importance of density dependence in driving short-term population dynamics (Grenfell et al. 1992). Later models identified the additional role of winter weather impacting annual mortality rates, summarised in terms of the balance of weather system types by the North Atlantic Oscillation (NAO), and its ability to predict population fluctuations alongside population density (Milner et al. 1999, Coulson et al. 2001, Berryman and Lima 2006, Crawley et al. 2021). Poor winter weather also reduces fecundity (Coulson et al. 2000). The importance of weather was underlined by its roles as the external driver of the synchronous population dynamics of separate sheep populations across the St Kilda archipelago (Grenfell et al. 1998). The role of greening in Soay sheep population dynamics was not apparent using a twenty-year run of data (Berryman and Lima 2006; for technical reasons this used NDVI data from the nearby Hebrides chain of islands with quite different vegetation). In contrast, there was a correlation between measured primary production in grassland and positive between-year population changes from 2000 to 2017 (Crawley et al. 2021).

In the present study we took advantage of a longer time series of sheep population data and concurrent availability of 30 m spatial resolution NDVI data. We tested a set of hypotheses: first, that the long-term population trend of increasing sheep abundance is driven 1) by increases in food supply and/or 2) by an ameliorating climate. Second, if the population trend is driven by increased food supply, we test whether this is most closely linked to 1) increased availability of preferred vegetation (high in digestibility and protein), 2) trends in vegetation biomass at the island level, or 3) changes in less preferred vegetation communities as these may better reflect productivity changes (preferred communities are subject to high levels of grazing that could partly obscure productivity increases).

Material and methods

Study system and sheep population counts

The Soay sheep population of the island of Hirta (57°48'53''N, 8°34'59''W) in the St Kilda archipelago has been the subject of intensive study since 1985 (Clutton-Brock and Pemberton 2004). Since their introduction to the recently depopulated island in the early 1930s from the neighbouring island of Soay, the population has been unmanaged. On Soay the sheep had been occasionally harvested but otherwise unmanaged since at least the middle of the first millennium AD (Fleming 2021). As part of the long-term study, whole island counts are conducted every year in summer (Clutton-Brock and Pemberton 2004). Three standard routes are walked simultaneously to cover the whole island, in particular accessing vantage points to cover the steep-sided coastal cliffs and slopes. Radio contact is maintained so that groups of sheep in view to two parties are only counted once. All adult males, adult females, and lambs are counted, along with a record of coat colour.

The vegetation is a mosaic of 20 mapped vegetation communities (Gwynne et al. 1974, Jewell et al. 1974). The steep slopes around Village Bay are dominated by the dwarf shrub *Calluna vulgaris* (heather, Supporting information), but elsewhere the vegetation is dominated by herbaceous species. Steep ground around the coast and the former agricultural land in Village Bay are dominated by grassy vegetation with preferred species such as *Agrostis capillaris*, *Festuca rubra*, and *Holcus lanatus* which typically show high NDVI values (Supporting information). Areas with a high salt spray input are dominated by *Plantago* species, particularly *Plantago coronopus* and *P. maritima*, but those inaccessible to sheep are dominated by *Rumex acetosa*. Flatter areas have mire vegetation dominated by *Eriophorum angustifolium* and *Molinia caerulea* with a ground layer of *Sphagnum*. Drier grassland at altitude is dominated by *Nardus stricta*, whilst that on sloping ground is covered by species-poor and relatively unproductive *Agrostis–Festuca* grasslands.

NDVI data

The NDVI is a measure of chlorophyll and is, hence, a proxy for green plant biomass which has been used for a range of purposes to assess productivity (Anderson et al. 1993) and as a method to detect Arctic greening through either earlier increase in NDVI in the growing season or higher peak summer NDVI (Jia et al. 2003). A digitised version of the vegetation map from Jewell et al. (1974) was used to convert shapefiles of the twenty vegetation types to GeoJSON files using the package 'sf' (Pebesma 2018) in R ver. 4.2.2 (www.r-project.org). These GeoJSON files were then used as input spatial data into Google Earth Engine (Gorelick et al. 2017) to obtain a time series of NDVI data for each vegetation type from 1985 to 2020 by combining output from Landsat 4, 5, 7, and 8, specifically the atmospherically corrected surface reflectance data from Level 2, Collection 2, Tier 1 for each satellite (courtesy of the US Geological Survey). NDVI values below 0.15 were removed from the data as they likely occurred when snow was on the ground (Knight et al. 2006). The same process was used to derive an NDVI time series for the whole island.

Vegetation and plant functional trait data

Plant composition data for 17 out of the 20 vegetation types used in the NDVI time series was available from Gwynne et al. (1974, summarised in the Supporting information). Trait data for each species was assembled from the LEDA trait database (Kleyer et al. 2008). Two traits were chosen that have a clear link to diet quality for the sheep (Cingolani et al. 2005, Mládek et al. 2013, Pakeman 2014) and productivity (Garnier et al. 2004): leaf dry matter content (LDMC) and specific leaf area (SLA). In addition, the Ellenberg indicator value for nitrogen (EIV-N, Hill et al. 2004) was chosen as another proxy for diet quality (Mouissie et al. 2005). As studies have indicated that wetter communities have greened faster in the Arctic (Arndt et al. 2019), Ellenberg's indicator for moisture (EIV-F) was also included in the analysis. Community weighted means (CWM) of the traits were calculated for each vegetation type by multiplying the matrix of mean species composition of each vegetation type by the species by trait matrix, as the dominant species have the greatest influence on ecosystem properties (Grime 1998, Garnier et al. 2004). CWMs of the chosen traits were highly correlated, absolute values between 0.73 and 0.91 (Table 1), suggesting redundancy between the traits, but all were used in the analysis as communities had somewhat different rankings for the different traits.

Weather data

Three weather stations were installed on Hirta in 1999 (Signals, SIGM: 57°48'43''N, 8°34'7''W) and 2000 (St Brianans STBR: 57°48'16''N, 8°34'28''W, and Quarry QUAR: 57°48'51''N, 8°34'44''W). To extend the period of overlap between the weather data, the sheep population data, and the NDVI data, statistical models were built to predict monthly weather variables based on the nearest weather station at Stornoway Airport (58°13'0''N, 6°20'0''W) based on the overlap between the Hirta weather data and the Stornoway data (2000–2020). The weather variables chosen were monthly mean daily temperature (°C), daily rainfall (mm), and mean daily wind speed (m s^{-1}). Multivariate linear regression was used to build a model predicting the nine Hirta

Table 1. Correlations between community weighted mean traits for the 17 communities. EIV-F – Ellenberg's indicator value for moisture, EIV-N – Ellenberg's indicator value for nitrogen, LDMC – leaf dry matter content, and SLA – specific leaf area.

	EIV-F	EIV-N	LDMC
EIV-N	−0.87		
LDMC	0.76	−0.87	
SLA	−0.84	0.91	−0.73

Table 2. Explained variances (R^2) in the models linking weather station data on Hirta to Stornoway Airport from 2000 to 2020 (df = 180).

Weather variable	Quarry	Signals	St Brianans
Mean monthly mean daily wind speed ($m\ s^{-1}$)	0.878	0.870	0.869
Mean monthly mean daily temperature (°C)	0.990	0.978	0.972
Monthly total rainfall (mm)	0.739	0.769	0.697

weather variables (three stations × three variables) based on the same three Stornoway variables. To account for the possibility that these relationships may vary depending on the predominance of different weather systems and the time of year, additional terms were added from the Stornoway data, namely mean wind speed in a north–south direction, mean wind speed in an east–west direction, and time since the start of the dataset (years) modelled as a time series with sine and cosine terms to allow for seasonal changes in the regression functions (Stolwijk et al. 1999). The final model was then used to predict the period prior to the weather station installation. Model fits ranged from R^2 values of 0.70–0.99 (Table 2), with temperature modelled best (R^2 of 0.97–0.99), followed by wind (R^2 of 0.87–0.88), and then rainfall (R^2 of 0.70–0.77). Including the seasonal terms increased average R^2 values from 0.84 to 0.86. Modelled relationships were very similar, but as Signals had the longest run of data this station was used for the rest of the analysis.

As previous analyses used the NAO as a proxy for weather, this weather variable was also tested in the analysis. NAO is a measure of pressure differences between the Azores and Iceland, with positive vales equating to stronger westerly winds and stronger, more frequent storms. NAO data were downloaded from https://www.ncei.noaa.gov/access/monitoring/nao/ and the sum of values for December to March used in the analysis (Milner et al. 1999, Coulson et al. 2001).

Statistical analysis

Long-term trends in NDVI values for each vegetation type were assessed using linear mixed models, with fixed terms fitted to account for the yearly variation between winter and summer (sine and cosine terms) and a linear term for time (Crawley 2012). Models were initially fitted with maximum likelihood to allow comparison of models with and without the linear term, and then fitted with residual maximum likelihood for unbiased parameter estimation. Models were fitted with the *lmer* function in 'lme4' (Bates et al. 2015) in R with year as a random term.

Relationships between estimated rate of change in NDVI through time for the different vegetation types and the CWM of the chosen plant traits were assessed using linear models (function *lm* in R). As summer maximum NDVI values were predicted from different numbers of observations, the regression models were weighted by the number of NDVI values recorded each year.

For use in modelling the relationships between NDVI values and sheep population counts, maximum yearly values of NDVI were estimated by fitting hierarchical generalized additive models (Pedersen et al. 2019) with a smooth term for time and a combined smooth term for time and individual year, with curves kept simple by specifying the penalised regression smoother k to 3 and by keeping the smooth parameters the same across years (bs = 'fs'). The maximum NDVI value was used as an estimate of food availability as it represents a high point after which consumption exceeds production and is therefore a good estimate of winter food availability. Models were fitted using mgcv with residual maximum likelihood (Wood 2011). Yearly minimum values could not be fitted due to an absence of satellite images over winter (between 11 November and 1 February) as the satellite passes over in darkness.

Relationships between the three weather variables and NAO with time were fitted with linear models separately for summer (May–October) and winter (November–April). They were also fitted separately for the whole period, so including both predicted and locally measured data (1984–2020), and for just the local weather station data (1999 onwards).

For modelling changes in sheep population growth rate, the log of the ratio of two successive counts $\delta_t = \ln\left(\frac{N_{t+1}}{N_t}\right)$ (Crawley et al. 2021) was used as the dependent variable. It is known that there is strong density dependence (Grenfell et al. 1992), so N_t was included in an initial model with the three winter weather variables (mean winter wind speed and temperature, total winter rainfall) and the maximum summer NDVI value for each vegetation type. As an alternative to using specific weather variables, we also fitted NAO, which has been used successfully as a predictor in previous studies (Milner et al. 1999, Coulson et al. 2001). It could not be used in the same model as the weather variables as it captures the same information in a single variable. We employed a strategy of model simplification used to identify strong drivers of δ_t by removing terms that had low support for inclusion ($p > 0.05$). We did not assess how climate mediated the strength of the density dependence as the focus was on the additive effects of weather and vegetation growth. A separate model was built for each vegetation type to identify which ones might be important in driving the population dynamics. Again, as summer maximum NDVI values were predicted from different numbers of observations, the regression models were weighted by the number of NDVI values recorded each year. Models were compared using the Akaike information criterion (AIC) and the utility of individual terms shown by their associated t- and p-values.

Results

Population counts

Sheep numbers have, on average, increased over the period of the study, though with considerable inter-annual variation

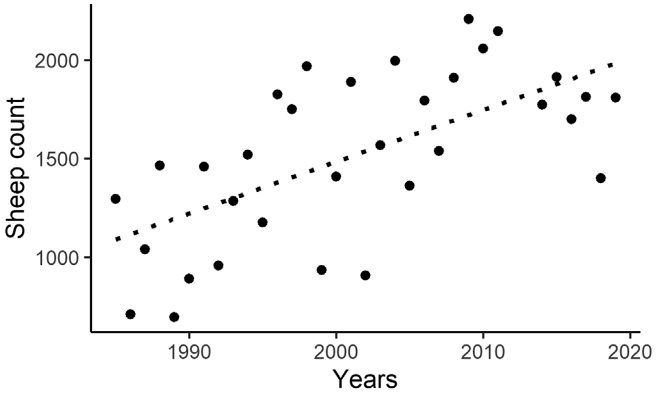

Figure 1. Island sheep population counts for Hirta, St Kilda.

(Fig. 1). A linear model suggests an increase of 24.8 sheep per year between 1985 and 2019 ($t=4.25$, $p < 0.001$, $R^2=0.361$, Fig. 1).

NDVI

Estimated rates of change from the whole NDVI data for all twenty vegetation types were positive with slopes ranging from 0.0025 in Dry heath to 0.0059 in *Rumex* vegetation (Supporting information). The positive effect of time in the model was always supported, with p-values of < 0.001 for all vegetation types except for Dry heath ($p=0.003$). For NDVI across the whole island p was also < 0.001. The sine and cosine parts of the fitted models were always highly significant, indicating repeated seasonal variation in NDVI.

Vegetation types with higher community weighted means for Ellenberg's nitrogen indicator (EIV-N) and specific leaf area (SLA) showed faster rates of increase in NDVI through time than those with lower values (Fig. 2, Table 3). Vegetation types with higher leaf dry matter contents (LDMC) showed lower rates of increase in NDVI. The steepest increases in NDVI were shown by communities with high EIV-N, low LDMC, and high SLA including *Holcus–Poa* grassland and *Rumex* communities. Relationships with EIV-N, LDMC, and SLA all explained a moderate amount of variation, ca 30%. There was no relationship between community wetness (EIV-F) and the rate of increase in NDVI (Table 3).

Increases in estimated yearly maximum NDVI were also positive for all vegetation types (Supporting information) and the whole island, with the shallowest slope for Dry heath and the steepest for *Rumex*. All slopes had low p-values (< 0.001). Similar relationships and explanatory power (ca 30%) were found for associations between the three traits and the slopes of NDVI maxima, positive for EIV-N and SLA, negative for LDMC (Table 3). There was a weak relationship between the slopes of NDVI maxima and EIV-F but it was negative, indicating drier communities had shown faster increases in NDVI maxima than wetter ones.

Weather

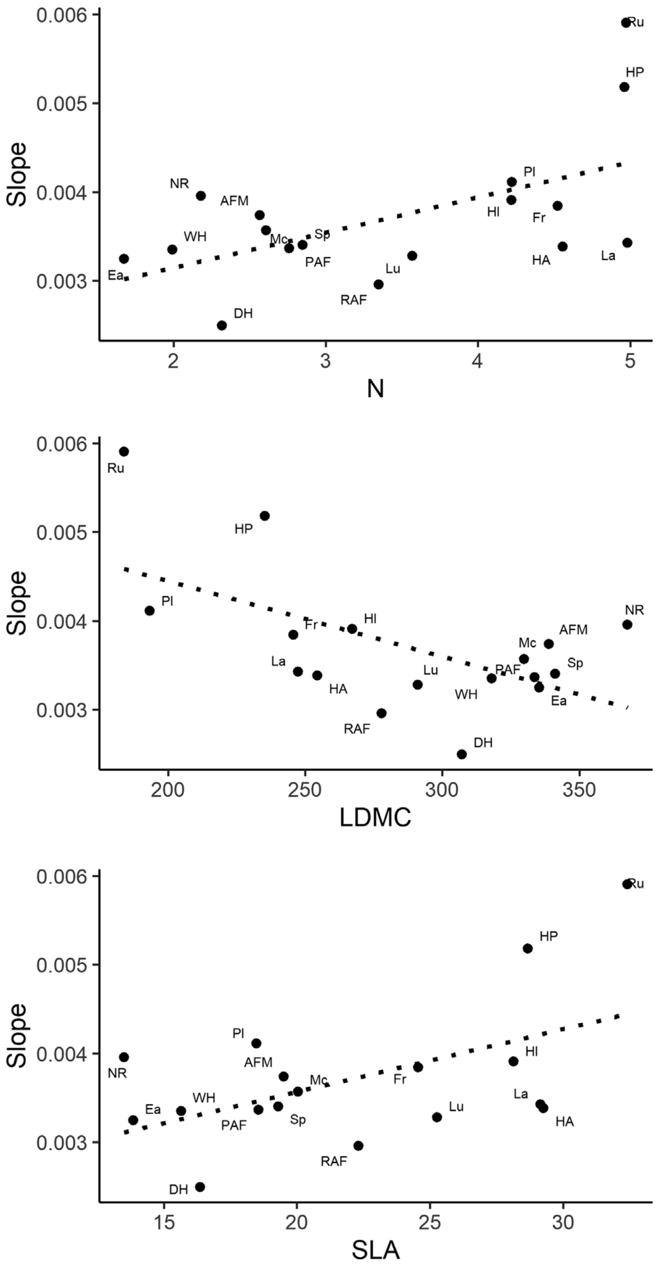

Figure 2. Relationships between community weighted mean values for N – Ellenberg's nitrogen indicator, LDMC – leaf dry matter content (mg g^{-1}), and SLA – specific leaf area (mm^2 mg^{-1}) and the linear regression slopes from the time series analysis of NDVI changes through time. Vegetation type abbreviations: AFM *Agrostis–Festuca–Molinia*, Cl Cliff, DH Dry heath, Ea *Eriophorum*, Fr *Festuca rubra*, Hl *Holcus*, HA *Holcus–Agrostis*, HAS *Holcus–Agrostis–Sphagnum*, HP *Holcus–Poa*, La Lair, Lu *Luzula*, Mc *Molinia*, NJ *Nardus–Juncus*, NR *Nardus–Racomitrium*, Pl *Plantago*, PAF species-poor *Agrostis–Festuca*, RAF species-rich *Agrostis–Festuca*, Ru *Rumex*, Sp *Sphagnum*, WH Wet heath.

Mean wind speed, mean temperature, and total rainfall have increased over the period of the study for both the winter and the summer periods (Fig. 3, Table 4). When the analysis was restricted to the short-term weather station data (2000–2020) the trends either weakened, winter mean wind speed ($p=0.072$) or disappeared (all other variables). NAO values have increased since 1950 ($p < 0.001$ for a linear trend),

Table 3. Regression models and statistics from analysing the relationship between slopes of increases in NDVI and the community weighted mean traits for 17 vegetation types (df = 15). EIV-N Ellenberg nitrogen indicator, LDMC leaf dry matter content, SLA specific leaf area, EIV-F Ellenberg moisture indicator.

Trait	Slope	t	p	R^2
All data				
EIV-N	3.96×10^{-4}	2.667	0.018	0.322
LDMC	-8.51×10^{-6}	2.717	0.016	0.330
SLA	7.06×10^{-5}	2.379	0.031	0.274
EIV-F	-4.55×10^{-4}	1.476	0.161	0.068
Maxima				
EIV-N	4.46×10^{-4}	2.533	0.023	0.300
LDMC	-9.65×10^{-6}	2.602	0.020	0.311
SLA	8.46×10^{-5}	2.468	0.026	0.289
EIV-F	-6.19×10^{-4}	1.765	0.098	0.172

but no trend is apparent from 1984 ($p = 0.523$ for a linear trend, Fig. 3).

Population dependence on productivity and climate

Model simplification identified that neither winter mean temperature nor winter total rainfall had any influence on the change in sheep numbers between years (δ_t), with p-values between 0.25 and 0.42 (not shown). In the three-term models (population size, weather, NDVI), sheep population size in year t was always highly supported ($p < 0.001$), but the support for the other terms varied between vegetation types (Table 5). For three vegetation types, *Plantago*, *Rumex*, and *Sphagnum*, the relationship between the change in sheep numbers between years and both the maximum NDVI value and mean wind speed had p-values less than 0.05, with adjusted R^2 values between 0.527 and 0.540. For one vegetation type, Lair (nutrient-rich grassland with moderate sea spray input), the NDVI term had a p-value less than 0.05 but that for the mean wind speed term was between 0.1 and 0.05 ($R^2 = 0.514$). For a further four vegetation types, Cliff, *Holcus–Poa*, *Molinia* and species-poor *Agrostis–Festuca*, the p-value associated with the NDVI term was between 0.1 and 0.05, whilst that for the mean wind speed was lower than 0.05 (R^2 between 0.507 and 0.520). Population size in year t was significant on its own as a predictor of δ_t, but the R^2 value was only 0.345, and adding only the wind variable did not improve the model fit. Mean wind speed as a single predictor explained only a relatively small proportion of the variation ($R^2 = 0.113$, $p = 0.052$). Comparing AIC values suggested a wider set of vegetation types were supported as useful predictors, but the strongest evidence was for *Eriophorum*, *Rumex*, and *Sphagnum*. Using data from the whole island provided a good model but one that ranked poorer than eight vegetation types using AIC as a measure, by more than 2 AIC units from the model with *Sphagnum*, and four types if using adjusted R^2 as the measure. All fitted terms for NDVI were positive, whilst mean wind speed and population in year t terms (N_t) were always negative.

The model combining sheep numbers in year t and NAO explained more variance than the model using wind and sheep

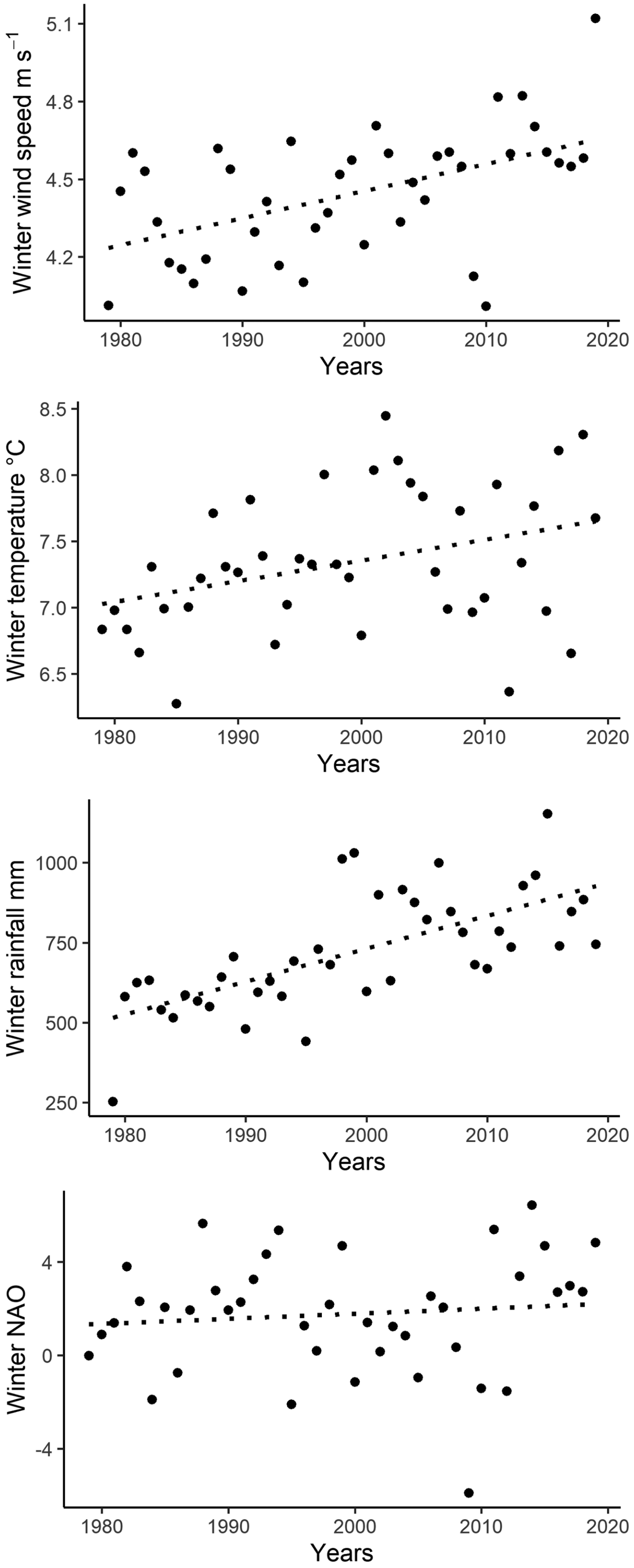

Figure 3. Mean winter weather variables with fitted regression lines (Table 3).

Table 4. Regression relationships between winter and summer weather and time for the whole dataset (predicted 1984–1999 and measured 1999–2020) and just for the Signals Meadow weather station data (1999–2020).

	All data (df = 39)					Weather station data (df = 18)				
	Slope	SE	t	p	R^2	Slope	SE	t	p	R^2
Winter										
Mean wind speed m s^{-1}	0.010	0.003	3.658	< 0.001	0.255	0.017	0.009	1.908	0.072	0.168
Mean temperature °C	0.016	0.007	2.338	0.025	0.123	−0.013	0.024	0.558	0.583	0.017
Total rainfall mm	10.29	1.802	5.710	< 0.001	0.455	5.065	5.255	0.964	0.348	0.049
Summer										
Mean wind speed m s^{-1}	0.008	0.003	2.941	0.006	0.186	0.005	0.005	1.097	0.287	0.063
Mean temperature °C	0.019	0.005	3.520	0.001	0.246	−0.002	0.018	0.105	0.917	0.001
Total rainfall mm	8.588	1.346	6.382	< 0.001	0.517	−0.246	3.219	0.076	0.940	0.001

numbers (R^2 of 0.480 versus 0.356, Table 6). Also, more vegetation types had NDVI maxima that were included in model selection than for the previous analysis with wind speed. Terms for *Eriophorum*, *Festuca rubra*, Lair, *Plantago*, species-poor *Agrostis–Festuca*, *Rumex*, and *Sphagnum* all had p-values less than 0.05, whilst terms for *Holcus*, *Holcus–Agrostis–Sphagnum*, *Holcus–Poa*, and *Molinia* had p-values between 0.05 and 0.1. AIC values also suggested that the majority of vegetation types improved the quality of the model, with the most evidence for *Sphagnum*, *Rumex*, and *Plantago*. The whole island model had terms for both NDVI and wind with p-values less than 0.05, but 12 vegetation types had higher adjusted R^2 and nine lower AIC values and five vegetation types (*Eriophorum*, Lair, *Plantago*, *Rumex*, *Sphagnum*) had AIC values more than two units lower. The average R^2 value across vegetation types for models incorporating NAO was 0.524 compared to 0.507 for models incorporating wind (mean AIC values were 1.27 lower for NAO models). This, alongside the improvement of model fit compared to the model with sheep N_t alone, suggests some enhanced power for this proxy for weather system dominance compared to a direct measure of weather. When used in models together NAO was always maintained at the expense of wind speed.

Discussion

Weather

The climate of Hirta has got warmer between 1979 and 2019 (summer 0.016, winter 0.019°C $year^{-1}$), wetter (8.59 and 10.3 mm $year^{-1}$), and windier (0.008 and 0.010 m s^{-1} $year^{-1}$) in line with general Scottish trends (Sniffer 2021). The same trends are seen for the training data set from Stornoway: here temperature increases of 0.030 and winter of 0.028°C $year^{-1}$, rainfall increases of 23.8 and 20.9 mm $year^{-1}$ and wind speed increases of 0.045 and 0.039 m s^{-1} $year^{-1}$ occurred. Over the period of recording of the Soay sheep population sizes, there has been no long-term trend in NAO.

NDVI

There was a clear indication of greening across all the vegetation communities present on Hirta and for the island as a whole (Fig. 2, Supporting information). The relationship between rates of NDVI increase or rates of maximum NDVI increase and time suggest that it is communities dominated by plants with faster growth rates and lower investment in leaf longevity (high EIV-N and SLA) and communities most preferred by sheep (with higher digestibility, low LDMC) that are increasing fastest. Greening, which indicates an increase in live biomass, suggests that the production in these communities is outstripping consumption during the summer period; unfortunately, the lack of winter NDVI data hinders understanding of changes in vegetation biomass across the full year. The faster increase in the more preferred communities may also be driven by increased inputs nutrients from urine and faeces (Koltz et al. 2022).

The increase in green biomass of the dry and wet heath agrees with field sampling of the heather-dominated communities on Hirta (Crawley et al. 2021) which showed increasing biomass through time. Similarly, the productivity of the *Holcus–Agrostis* grassland increased through time and there was an indication of an increase in productivity of the species-rich *Agrostis–Festuca* community in the same data (labelled *Nardus* in Crawley et al. 2021).

Unlike Arctic studies (Arndt et al. 2019, Campbell et al. 2021) there was an indication that it was the drier communities (lower EIV-F) that showed the highest rates of biomass increase. As Hirta has a hyperoceanic climate and frequent precipitation, water limitation is unlikely to be a strong control on photosynthesis and, hence, productivity. However, the faster NDVI increase in graminoid communities rather than those dominated by dwarf shrubs agrees with data from the Arctic (Raynolds et al. 2008).

Population dependence on productivity and climate

The analysis confirms earlier work that sheep population growth rates are higher at low values of winter NAO (dry and cold, Milner et al. 1999, Coulson et al. 2001), but also highlights that this might be driven by periods of storminess (high average winds and rain) rather than by wet weather directly (Table 5–6, Hindle et al. 2019). The dependence of population dynamics on NAO is shared with that of other herbivores including hare *Lepus europaeus* in the Czech Republic (Tkadlec et al. 2006) and muskox in the Arctic (Forchhammer et al. 2002). However, NAO may also be capturing the effect of high rainfall as increased

Table 5. Regression relationships and statistics for models predicting population change parameter δ_t ($\ln(N_{t+1}/N_t)$). The models containing maximum NDVI also contained mean wind speed and summer sheep population N_t. Adjusted R^2 are given for the models and p-values less than 0.05 are shown in bold and those between 0.05 and 0.1 in italics. AIC values for models more than 2 less than the AIC value of the sheep N_t model are shown in bold. Degrees of freedom for single factor models 31, two factor 30, three factor 29.

	NDVI				Mean wind speed				Sheep population N_t					
Vegetation type	Slope	SE	t	P	Slope	SE	t	P	Slope	SE	t	P	R^2adj	AIC
Null model														39.22
Sheep numbers only									-5.40×10^{-4}	1.23×10^{-4}	4.284	**< 0.001**	0.345	19.75
Sheep + Wind only					−0.277	0.222	1.247	0.222	-4.94×10^{-4}	1.30×10^{-4}	3.798	**< 0.001**	0.356	19.34
Wind only					−0.514	0.254	2.021	*0.052*					0.113	35.12
Agrostis–Festuca–Molinia	1.617	0.978	1.653	0.109	−0.402	0.208	1.931	*0.063*	-5.40×10^{-4}	1.23×10^{-4}	4.384	**< 0.001**	0.490	**16.66**
Cliff	2.375	1.338	1.775	*0.086*	−0.490	0.212	2.302	**0.029**	-5.93×10^{-4}	1.19×10^{-4}	5.002	**< 0.001**	0.507	17.37
Dry heath	1.598	1.462	1.093	0.283	−0.352	0.206	1.711	*0.097*	-6.01×10^{-4}	1.25×10^{-4}	4.803	**< 0.001**	0.478	19.15
Eriophorum	2.291	1.128	2.032	*0.051*	−0.341	0.185	1.846	*0.075*	-5.91×10^{-4}	1.17×10^{-4}	5.063	**< 0.001**	0.542	**15.56**
Festuca rubra	1.978	1.219	1.624	0.072	−0.379	0.204	1.863	*0.072*	-6.08×10^{-4}	1.22×10^{-4}	4.985	**< 0.001**	0.500	18.21
Holcus	1.482	0.960	1.544	0.133	−0.424	0.213	1.991	*0.056*	-6.16×10^{-4}	1.25×10^{-4}	4.913	**< 0.001**	0.493	19.16
Holcus–Agrostis	2.583	1.554	1.661	0.107	−0.402	0.210	1.917	*0.065*	-6.13×10^{-4}	1.20×10^{-4}	5.093	**< 0.001**	0.519	17.92
Holcus–Agrostis–Sphagnum	2.073	1.271	1.631	0.113	−0.364	0.195	1.861	*0.073*	-5.94×10^{-4}	1.17×10^{-4}	5.067	**< 0.001**	0.514	**16.29**
Holcus–Poa	1.379	0.767	1.798	*0.082*	−0.447	0.204	2.191	**0.036**	-6.11×10^{-4}	1.19×10^{-4}	5.145	**< 0.001**	0.515	**16.55**
Lair	2.611	1.203	2.170	**0.038**	−0.387	0.195	1.988	*0.056*	-5.79×10^{-4}	1.18×10^{-4}	4.921	**< 0.001**	0.514	**16.64**
Luzula	1.602	1.217	1.317	0.198	−0.346	0.203	1.698	0.100	-6.17×10^{-4}	1.24×10^{-4}	4.970	**< 0.001**	0.497	18.94
Molinia	2.997	1.533	1.954	*0.060*	−0.426	0.199	2.146	**0.040**	-6.16×10^{-4}	1.20×10^{-4}	5.141	**< 0.001**	0.520	**16.78**
Nardus–Juncus	2.205	1.265	1.743	*0.092*	−0.370	0.208	1.776	*0.086*	-6.62×10^{-4}	1.34×10^{-4}	4.960	**< 0.001**	0.506	20.96
Nardus–Racomitrium	1.541	1.237	1.246	0.222	−0.381	0.207	1.835	*0.077*	-6.08×10^{-4}	1.27×10^{-4}	4.787	**< 0.001**	0.484	19.63
Plantago	2.593	1.212	2.139	**0.041**	−0.393	0.191	2.053	**0.049**	-5.90×10^{-4}	1.16×10^{-4}	5.088	**< 0.001**	0.527	**16.41**
Poor *Agrostis–Festuca*	2.115	1.139	1.858	0.073	−0.413	0.197	2.096	**0.045**	-5.82×10^{-4}	1.11×10^{-4}	4.976	**< 0.001**	0.520	**16.46**
Rich *Agrostis–Festuca*	1.160	1.652	0.702	0.104	−0.368	0.220	1.675	0.104	-5.91×10^{-4}	1.25×10^{-4}	4.715	**< 0.001**	0.465	19.79
Rumex	1.649	0.752	2.192	**0.036**	−0.491	0.199	2.462	**0.020**	-6.18×10^{-4}	1.17×10^{-4}	5.306	**< 0.001**	0.532	**15.46**
Sphagnum	2.888	1.407	2.053	**0.049**	−0.391	0.188	2.080	**0.046**	-5.96×10^{-4}	1.14×10^{-4}	5.245	**< 0.001**	0.540	**14.19**
Wet heath	1.533	1.349	1.136	0.265	−0.415	0.224	1.855	*0.074*	-5.94×10^{-4}	$1.27 \times 10{-}^{4}$	4.683	**< 0.001**	0.472	20.29
Whole island	2.333	1.028	2.269	**0.031**	−0.491	0.206	2.386	**0.024**	-5.83×10^{-4}	1.16×10^{-4}	5.002	**< 0.001**	0.521	**16.63**

Table 6. Regression relationships and statistics for models predicting population change parameter δ_t ($\ln(N_{t+1}/N_t)$). The models containing maximum NDVI also contained mean winter NAO and summer sheep population N_t. Adjusted R^2 are given for the models and p-values less than 0.05 are shown in bold and those between 0.05 and 0.1 in italics. AIC values for models more than 2 less than the AIC value of the sheep N_t model are shown in bold. Degrees of freedom for single factor models 31, two factor 30, three factor 29.

	NDVI				Mean winter NAO				Sheep population N_t					
Vegetation type	Slope	SE	T	p	Slope	SE	t	P	Slope	SE	t	p	R^2adj	AIC
Null model														39.22
Sheep N_t only									-5.40×10^{-4}	1.23×10^{-4}	4.284	**< 0.001**	0.345	19.75
Sheep N_t + winter NAO					−0.029	0.018	1.611	0.117	-6.28×10^{-4}	1.20×10^{-4}	5.251	**< 0.001**	0.480	19.02
Winter NAO only					−0.039	0.025	1.632	0.112					0.048	38.65
Agrostis–Festuca–Molinia	1.885	0.983	1.918	*0.065*	−0.041	0.018	2.268	**0.031**	-6.00×10^{-4}	1.14×10^{-4}	5.261	**< 0.001**	0.511	**15.26**
Cliff	2.602	1.315	1.978	*0.057*	−0.048	0.018	2.652	**0.013**	-6.69×10^{-4}	1.13×10^{-4}	5.899	**< 0.001**	0.530	**15.74**
Dry heath	1.554	1.449	1.073	0.292	−0.032	0.182	1.775	*0.086*	-6.47×10^{-4}	1.20×10^{-4}	5.384	**< 0.001**	0.481	18.92
Eriophorum	2.487	1.115	2.320	**0.033**	−0.036	0.016	2.188	**0.037**	-6.33×10^{-4}	1.09×10^{-4}	5.813	**< 0.001**	0.560	**14.18**
Festuca rubra	2.509	1.214	2.067	**0.047**	−0.044	0.018	2.500	**0.018**	-6.64×10^{-4}	1.13×10^{-4}	5.888	**< 0.001**	0.538	**15.50**
Holcus	2.007	0.991	2.026	*0.052*	−0.048	0.019	2.504	**0.018**	-6.91×10^{-4}	1.18×10^{-4}	5.860	**< 0.001**	0.525	**16.93**
Holcus–Agrostis	2.493	1.512	1.642	0.111	−0.038	0.018	2.062	**0.048**	-6.61×10^{-4}	1.14×10^{-4}	5.765	**< 0.001**	0.527	**17.34**
Holcus–Agrostis–Sphagnum	2.107	1.231	1.711	*0.097*	−0.038	0.017	2.264	**0.031**	-6.64×10^{-4}	1.10×10^{-4}	5.771	**< 0.001**	0.537	**14.65**
Holcus–Poa	1.493	0.760	1.881	*0.070*	−0.042	0.018	2.362	**0.025**	-6.73×10^{-4}	1.79×10^{-4}	5.852	**< 0.001**	0.526	**15.80**
Lair	2.917	1.184	2.464	**0.020**	−0.042	0.017	2.494	**0.018**	-6.31×10^{-4}	1.10×10^{-4}	5.760	**< 0.001**	0.545	**14.44**
Luzula	1.408	1.186	1.187	0.245	−0.032	0.018	1.847	*0.075*	-6.60×10^{-4}	1.18×10^{-4}	5.573	**< 0.001**	0.505	18.40
Molinia	2.810	1.515	1.855	*0.073*	−0.037	0.017	2.113	**0.043**	-6.73×10^{-4}	1.16×10^{-4}	5.783	**< 0.001**	0.519	**16.92**
Nardus–Juncus	2.011	1.235	1.628	0.114	−0.037	0.019	2.012	*0.054*	-7.01×10^{-4}	1.27×10^{-4}	5.515	**< 0.001**	0.519	20.05
Nardus–Racomitrium	1.298	1.204	1.077	0.290	−0.033	0.018	1.808	*0.081*	-6.59×10^{-4}	1.23×10^{-4}	5.370	**< 0.001**	0.483	19.72
Plantago	3.117	1.205	2.586	**0.015**	−0.043	0.017	2.619	**0.014**	-6.49×10^{-4}	1.11×10^{-4}	6.030	**< 0.001**	0.561	**13.87**
Poor *Agrostis–Festuca*	2.333	1.141	2.045	**0.050**	−0.039	0.017	2.328	**0.027**	-6.46×10^{-4}	1.11×10^{-4}	5.833	**< 0.001**	0.534	**15.47**
Rich *Agrostis–Festuca*	1.031	1.593	0.647	0.522	−0.034	0.019	1.835	*0.077*	-6.38×10^{-4}	1.22×10^{-4}	5.228	**< 0.001**	0.474	19.21
Rumex	1.975	0.743	2.659	**0.012**	−0.054	0.017	3.097	**0.004**	-6.18×10^{-4}	1.17×10^{-4}	6.408	**< 0.001**	0.574	**12.28**
Sphagnum	3.238	1.379	2.347	**0.026**	−0.043	0.016	2.606	**0.014**	-6.52×10^{-4}	1.05×10^{-4}	6.189	**< 0.001**	0.571	**11.83**
Wet heath	1.187	1.291	0.919	0.365	−0.034	0.019	1.797	*0.082*	-7.04×10^{-4}	1.10×10^{-4}	4.683	**< 0.001**	0.469	20.50
Whole island	2.289	1.017	2.249	**0.032**	−0.044	0.018	2.421	**0.022**	-6.59×10^{-4}	1.13×10^{-4}	5.8.7	**< 0.001**	0.524	**16.47**

precipitation has been shown to reduce survival in the same system (Hindle et al. 2019). The synthetic nature of NAO as a measure appears to give it an advantage over individual weather indices as a predictor of population dynamics (Hallett et al. 2004).

This analysis shows the importance of increasing plant green biomass in driving the higher values of population growth (δ_t) and hence long-term increases seen in sheep population size. The increase in sheep numbers occurs despite an increase in average wind speeds across the study period (Fig. 3) and is independent of the fluctuation in NAO which shows no trend over the same period (Fig. 3).

The expectation was that the plant communities preferred by sheep would drive any population increases. Community trait information suggest this would be *Festuca rubra*, *Holcus*, *Holcus–Agrostis*, *Holcus–Poa*, Lair, *Plantago*, and *Rumex* (Fig. 2), which are the vegetation types with high community weighted EIV-N and SLA and low LDMC. This appears to be the case for *Festuca rubra* (from analysis including NAO, weaker evidence for analysis including wind), Lair, *Plantago,* and *Rumex*, with weaker evidence for *Holcus* (NAO only) and *Holcus–Poa*. This suggests that the increase in biomass in these preferred vegetation types, which was faster than for the less preferred vegetation types, has driven the increase in sheep numbers. *Festuca rubra* and *Rumex* communities only occur where sheep are unable to access the vegetation (Gwynne et al. 1974, Crawley et al. 2021), which suggests that their increased growth as a result of climate change is acting as a proxy for overall increased productivity in the models. This may also underlie the good explanatory power of models involving the NDVI of *Eriophorum* and *Sphagnum*: these unpreferred but accessible species are unlikely to be grazed much and again may be acting as indicators of overall increased productivity. The Lair and *Plantago* vegetation types are relatively restricted in area (2.1 and 3.7% of the area of the island, respectively, Supporting information), so they represent a small proportion of the available forage. However, they are heavily grazed with the *Plantago* swards, especially, the focus of high densities of sheep resulting in very short swards (Crawley et al. 2021). These swards develop where there is considerable salt spray, and the sheep may be focussing on the high levels of sodium accumulated in the cell vacuoles to maintain turgor or on the high levels of nitrogen used in the construction of the compatible solute proline (Sleimi et al. 2015).

Three other patterns stand out in the models. First, the identification of species-poor *Agrostis–Festuca* as having a significant link between its NDVI values and the increasing sheep population. This ranks poorly (low SLA, low EIV-N, high LDMC) in terms of the likely selection of the vegetation type for foraging, though it does contain a range of moderately preferred grass species such as *Agrostis canina*, *Danthonia decumbens*, and *Festuca vivipara*. However, it is the vegetation type with the largest extent (15.5% of the island), and so its response to the changing climate is likely to feed through into the population dynamics of the sheep. The availability of lower quality vegetation late in the year can function as a buffer against starvation during winter (Owen-Smith 2004) and increased forage availability would only enhance this effect. Second, the lack of even weak support for *Holcus–Agrostis* ($p = 0.107$ for the model containing wind, $p = 0.111$ for NAO), which is heavily selected in Village Bay, the main study area on the island. Previous work has shown its use is correlated to lifetime reproductive performance (Regan et al. 2016) and its productivity is positively correlated to sheep population growth (Crawley et al. 2021). It is possible that it is heavily targeted by foraging sheep and so never achieves high summer NDVI values so that the important measure is productivity rather than biomass. Alternatively, its importance in the diet of sheep in Village Bay may be due to a restricted choice of alternative forage in that part of the island. Finally, whilst the overall island NDVI also predicted population dynamics in the sheep, it was outperformed by information from specific vegetation types that captured either the response of the most preferred types or those that likely captured productivity changes. This study suggests that taking community heterogeneity into account will produce a better understanding of the links between vegetation and herbivore dynamics.

Caveats

Hirta is a part of oceanic north-west Europe which is characterised by frequent cloudy weather; it can develop clouds even on days when the surrounding ocean has none. As a result, there are relatively few clear Landsat images and consequently estimates of yearly NDVI maxima are sometimes based on few data. This was accounted for in the analysis by weighting the maxima according to the number of data points used in its estimation, but it does preclude more detailed analysis such as looking for changes in the timing of green up (Pettorelli et al. 2007). The absence of winter images also restricted the range of the analysis.

As in all studies involving NDVI, it should be remembered that there is a non-linear relationship between NDVI and green biomass; increases in NDVI underestimate increases in biomass (Myers-Smith et al. 2020). Also, NDVI values of different communities may not be directly comparable. Forage availability from *Plantago* species growing as rosettes will be lower than for a grass-dominated community where growth is more vertical. It is possible that the vegetation types that provide the highest explanatory power are those where NDVI values are a more reliable proxy for biomass than the others.

Conclusions

It appears that the upward population trend in Soay sheep on Hirta is driven by increases in food supply and not by the direct impacts of ameliorating climate on the sheep; it occurs despite an increase in mean winter wind speeds. Assessing productivity changes in preferred vegetation is difficult using remote sensing data due its ongoing consumption, but support for the conclusion that food supply is the driving force behind population growth is provided by the increases in productivity seen in unpreferred or inaccessible vegetation types. The model containing whole island trends in NDVI performed well, though not as well as the best models with individual vegetation type NDVI.

Soay sheep join the growing list of studies where global change appears to be driving population dynamics. In moose *Alces alces* population dynamics have been linked to habitat quality with warmer springs reducing density dependence effects on recruitment (Priadka et al. 2022). Increased summer biomass (measured as NDVI) leads to enhanced survival of Dall's sheep *Ovis dalli dalli* (Van de Kerk et al. 2020) and warmer summers lead to an increase in population size in Tatra chamois *Rupicapra rupicapra tatrica* (Ciach and Pęksa 2018). However, other studies have shown that in seasonal environments climate change can lead to a reduction in food availability, for example for Apennine chamois *Rupicapra pyrenaica ornata* (Lovari et al. 2020), or a shortened period for the availability of high-quality forage for juvenile bighorn sheep *Ovis canadensis*, Alpine ibex *Capra ibex*, and mountain goats *Oreamnos americanus* (Pettorelli et al. 2007), which reduces population size.

What is different for this study is the absence of marked seasonal differences in climate for Hirta. The island is hyper-oceanic, with a mean temperature difference between winter and summer of 4.13°C for the 1980–2019 data used in this analysis. This suggests that climate-driven changes in herbivore population dynamics could occur in parts of the world where there are no large seasonal changes in weather; whether these are positive or negative changes in abundance would depend on other controls on population size and their interaction with temperature changes. Alternatively, with winter, and even summer, temperatures close to the typical base temperature used in models of plant growth (whether 0 or 5°C, Arora and Boer 2005, King et al. 2018), then a small increase in the temperature sum (GDD_5 increased at 4.98 per year from 1980 to 2019 for Hirta, $R^2 = 0.16$, $p = 0.010$) could lead to substantial increase in production over time. However, this type of response may only be seen in a cool temperate system where water limitation is rare (Ren et al. 2022). The study also showed that splitting up the area using information on the extent of different vegetation types could provide more insight than treating the island as a single area to calculate NDVI. The analysis showed both the importance of highly preferred vegetation such as *Plantago*-dominated swards and, also, communities likely to be reflecting changes in productivity due to their inaccessibility or their lower preference.

Acknowledgements – The study would not be possible without the permission and collaboration of the National Trust for Scotland and the support from QinetiQ, Eurest, and Kilda Cruises. We are immensely grateful to the many fieldworkers who have collected data and samples on St Kilda over the years and to Luigi Spezia for advice in analysing the meteorological data.

Funding – The long-term study was funded largely by consecutive responsive mode grants from NERC, as well as grants from BBSRC, Wellcome Trust, the Leverhulme Trust, and ERC. This particular paper was enabled by a large NERC grant (NE/R016801/1).

Author contributions

Robin J. Pakeman: Conceptualization (lead); Formal analysis (lead); Writing – original draft (lead). **Ian Stevenson**: Data curation (lead); Investigation (equal); Writing – review and editing (equal). **Jill Pilkington**: Investigation (equal). **Xavier Bal**: Investigation (equal). **Josephine Pemberton**: Funding acquisition (equal); Writing – review and editing (equal). **Andy Fenton**: Writing – review and editing (equal). **Dylan Childs**: Writing – review and editing (equal). **Mick Crawley**: Investigation (equal); Writing – review and editing (equal). **Dan Nussey**: Funding acquisition (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.ttdz08m72 (Pakeman et al. 2024), and https://soaysheep.bio.ed.ac.uk/, https://github.com/RobinPakeman/NDVIpaper.git.

Supporting information

The Supporting information associated with this article is available with the online version.

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