Experimental warming outside the growing season and exclusion of grazing has a mild effect on upland grassland plant communities in the short term

Nina Roth[1,2]*, Robert Baxter[3], Martin Furness[4], Adam Kimberley[1] and Sara A. O. Cousins[1,2]

[1] Department of Physical Geography, Stockholm University, Stockholm, Sweden; [2] Bolin Centre for Climate Research, Stockholm, Sweden; [3] Department of Biosciences, Durham University, Durham, UK; [4] Natural England, North Pennine NNR, Langdon Beck, UK

*Corresponding author. Email: nina.roth@natgeo.su.se

Abstract

Background: Winters are expected to warm more than summers in central and northern Europe, with largely unknown effects on grassland plant communities.

Aims: By studying the interactions between winter warming and summer grazing, we aimed to disentangle their effects and give recommendations for future grassland management.

Methods: Our study area Upper Teesdale, England has winter temperatures close to 0 °C and a well-studied vegetation, known for its arctic-alpine species growing at their climatic warm range limits. We set up a winter warming experiment using open top chambers (*ca*. +0.5 °C) from mid-September until mid-May 2019 to 2022 and excluded sheep grazing during summer in a fully factorial design.

Results: Graminoid biomass increased, and bryophyte biomass decreased with winter warming. There was little to no evidence that winter warming affected any of the other plant response variables we measured, neither did grazing nor the interaction between winter warming and grazing.

Conclusions: Our experiment was relatively short in duration and treatments were realistic in magnitude, therefore the plant communities responded only slightly. Nevertheless, our data suggest a change towards more dominant vascular species and less bryophytes with winter warming, which might lead to lasting changes in the plant communities in the longer-term if not buffered by suitable grazing management.

Keywords

British Uplands, grasslands, grazing, open top chambers, plant biomass, plant communities, *Sesleria caerulea*, winter warming

Introduction

Winter warming

In central and northern Europe, winters are expected to warm more than summers by 2071-2100 (RCP8.5 scenario; EAA 2014). However, the potentially critical ecological effects of winter warming on plant communities remain poorly understood, since most studies to date have only been performed during the growing season (Kreyling 2010; Williams et al. 2015). This is especially true for temperate regions (Kreyling 2010). Winter in temperate ecosystems has long been regarded, erroneously, as the dormant season, yet there are plants that remain photosynthetically active and many important ecological processes take place during winter (e.g., soil microbiological activity, mineralisation, nutrient cycling and physical changes to soil properties) (Edwards et al. 2007; Kreyling et al. 2011). Winter warming can affect herbaceous plant communities directly by a potential combination of a prolonged growing season and reduced snow cover, increasing the risk of frost damage, which can have complex effects on plant phenology, productivity and community composition (Inouye 2008; Bokhorst et al. 2010; Williams et al. 2015; Liu et al. 2018; Kreyling et al. 2019).

It has been suggested that primary productivity in temperate mountain grasslands was governed mainly by the length of the snow-free period, rather than by temperature and precipitation during the growing season (Choler 2015). In areas that are usually covered by snow and have soil temperatures around 0 °C during winter, plants can remain active under the snowpack and rapidly start growing once the snow has melted (Edwards et al. 2007). In line with this, other studies have also found plant biomass to increase with winter warming (Schuerings et al. 2013; Grant et al. 2017; Zeeman et al. 2017; Kreyling et al. 2019). Furthermore, warmer winter temperatures can alter the plant community composition (Grant et al. 2017; Kreyling et al. 2019; Niittynen et al. 2020). For example in temperate grasslands, winter warming favours mainly tall, competitive species, which might eventually outcompete smaller, light-demanding species (Kreyling et al. 2019). Similarly, in the Alps, plant communities with tall, slow-growing plant species were mostly growing in sites with early snow melt (Jonas et al. 2008). In the Arctic, warmer winter conditions have been shown to promote vascular plant communities and to reduce lichen occurrences (probably partially due to competition) (Niittynen et al. 2020).

Winter warming and grazing

To the best of our knowledge the interactive effects of rising winter temperatures and grazing on grassland plant communities have not been studied explicitly, to date. There are, however, studies on summer or all-year experimental warming and grazing. Globally, climate warming increases above- and below-ground net primary productivity, but decreases plant species richness (He et al. 2022). Warming-induced increases of plant biomass and changes in plant communities can often be buffered by grazing (Klein et al. 2004; Post and Pedersen 2008; Wang et al. 2012; Zhang et al. 2015). In a long-term experiment in the US, community composition was resistant to warming for 7 years, whereas yearly clipping affected community composition consistently (promoting species richness, but decreasing evenness) (Shi et al. 2015). However, the combined warming and grazing effects can be non-additive, suggesting that we cannot make realistic predictions from single-factor studies (Klein et al. 2007). Also Li et al. (2018) concluded that multi-factor experiments on the joint effects of climate change and grazing are needed for a comprehensive understanding of future grassland management. We addressed this knowledge gap using a winter warming experiment across different grazing pressures located in the British Uplands. The British Uplands cover 16.7 to 42.1% of the British land surface (depending on the definition), they are important providers of ecosystem services, and many of them include semi-natural habitats and are protected for nature conservation (House et al. 2010).

Winter warming and grazing in the British Uplands

The UK Environmental Change Network analysed climatic data between 1993-2007 from 12 terrestrial sites in the UK and found that the average temperature had increased by 1.2 °C in the British Uplands compared to only 0.7 °C in the Lowlands (Morecroft et al. 2009). Temperature changes were stronger in winter than in summer, with temperature minima increasing more than maxima (Morecroft et al. 2009; Burt and Holden 2010). A further reduction of frost events in upland

Britain can be expected in the future (Pepin et al. 2009). The frequency of air frosts has been found to decrease from 129 to 99 days per year (between the periods 1953-1980 and 1991-2006), which the authors warn ‘may have major implications for the functioning of terrestrial and aquatic systems in the region’ (Holden and Rose 2011). Average yearly snow cover has declined since 1960 in Great Britain, especially in mountain areas in northern England (Brown 2019). At Moor House (close to our study area), the growing season prolonged by *ca.* 1 day per year between 1993-2012, however this trend was not statistically significant (Monteith et al. 2016). Many of the British Uplands have mean winter temperatures close to 0 °C (Burt and Holden 2010). Hence warming winters in particular could have measurable consequences for the local vegetation, e.g., changes in species ranges, species composition, phenology and frost injury (Kreyling 2010). However, vegetation in cold, nutrient-poor environments are known to be quite resistant to environmental change, and potential changes in plant communities usually happen very slowly (Grime et al. 2008; Damgaard et al. 2016; Alday et al. 2021).

Upper Teesdale, our study area, has a unique flora, the so called ‘Teesdale assemblage’, which includes disjunct populations of species that predominantly have both southern and northern distributions (Pigott 1956). The ‘Teesdale rarities’, i.e. pre-alpine, alpine, arctic-alpine and sub-arctic species, have been interesting for scientists and in focus for conservation efforts for more than 50 years (Bellamy et al. 1969; Squires 1971; Turner et al. 1973; Bradshaw and Doody 1978; Cranston and Valentine 1983; Bradshaw 2023). Pollen analyses suggest that many of those rare species, e.g. *Gentiana verna* and *Dryas octopetala*, have been present in the area throughout the post-glacial period and can therefore be considered ‘relict species’ (Turner et al. 1973; Squires 1978). The harsh climate, together with metal-rich soils are thought to hamper biomass production and therefore allow the ‘Teesdale rarities’ to persist (Pigott 1956; Waughman et al. 1983). In addition to the distinctive climatic and edaphic conditions in Upper Teesdale, sheep grazing has shaped the vegetation over the last centuries – creating a short, open sward with a wide range of microhabitats (Gilbert et al. 1978). Grazing also promotes the ‘Teesdale rarities’ since they are sensitive to competition (Squires 1978; Bradshaw 2023). For example, a relatively competitive grass species in the area is *Sesleria caerulea*, which has a wide ecological tolerance and can form dense litter layers supressing other plant species (Lewthwaite 1999). Milder winters and a longer growing season might increase the competitive ability of *S. caerulea* and change plant composition in the long-term. On the other hand, vegetation changes in our study area might happen very slowly due to cold and nutrient-poor conditions (Elkington 1981; Alday et al. 2021). The distinct climatic conditions coupled with a very well-studied vegetation make this area highly suitable for climate change experiments.

To the best of our knowledge, there are no published studies addressing the interactive effects of winter warming and grazing management on grassland plant communities. By studying the interactions between winter warming and grazing, we aimed to better determine appropriate management regimes that can help maintain the current plant communities, even under future climate warming.

Taking the main factors above into consideration, we hypothesised that:

H1: Winter warming would increase plant biomass, favouring mainly competitive species.

H2: Grazing could buffer winter warming effects on plant biomass and community composition.

Materials and methods

Experimental setup and treatments

Our experiment was located in the Moor House – Upper Teesdale National Nature Reserve in northern England (Figure 1). The Nature Reserve is grazed by Swaledale sheep (*ca.* 100 sheep per km^2 from 15 May to 1 November and less than 25 sheep per km^2 from 2 November to 14 May) and by wild rabbits. The grasslands of our study area are situated on so-called ‘sugar limestone’, i.e. metamorphosed limestone that after weathering resembles granulated sugar (Pigott 1956; Johnson et al. 1971). In September 2019, we established 60 plots (25 cm diameter, distance between plots *ca.* 1.5 m) in a full factorial design with the two treatments ‘winter warming’ and ‘grazing exclosure’. The plots were arranged in a 5 x 4 grid in three sites: (1) Widdybank Fell (N 54°39’22’’, W 2°16’48’’, 503 m a.s.l.), (2) Thistle Green (N 54°39’02’’, W 2°14’36’’, 542 m a.s.l.) and (3) Cronkley Fell (N 54°39’04’’, W 2°14’17’’, 528 m a.s.l.). The sites were chosen to cover the whole spectrum of grazing intensities present in the area. Widdybank Fell has the lowest grazing pressure, Cronkley Fell the highest, and Thistle Green falls in-between. On Thistle Green, sheep and rabbits are excluded by a fence that is opened only for a few weeks in late summer (usually opened up from August/September to end of October/early November, depending upon sward conditions). All three sites are on flat terrain and 0.3 to 2.7 km away from each other. Characteristics on how the three sites differ regarding their vegetation and microclimate can be found in Table 1.

The plots measure 25 cm in diameter (491 cm^2), which is quite a small plot size but comparable to several other vegetation studies in British upland grasslands (Waughman et al. 1983; Bates et al. 2005). For the winter warming treatment, we built 30 open-top-chambers (OTCs) (Figure 1). The design of the OTCs was inspired by the International Tundra Experiment (Marion et al. 1997): they were cone-shaped with a 60° angle, measured 84.6 cm diameter on ground level, 50.0 cm at the top and were 30.0 cm tall. They were made of 3 mm thick plastic sheets (polyethylene terephthalate glycol) and were attached to the ground with tent pegs and wooden sticks. The OTCs were placed on every second of the plots in each site. They were in place from mid-September until mid-May 2019 to 2022, apart from the first winter when a storm destroyed 17 OTCs in January 2020, which we replaced in March 2020. We chose this timeframe for our winter warming treatment to capture the entire period outside of the growing season, which used to be between mid-May and mid-September (Manley 1942) and is still considered ‘very short’ (Bradshaw 2023) in our study area.

To experimentally manipulate the grazing pressure, we set up a fence on each site that excluded sheep (but not rabbits) from half of each site between mid-May and mid-September each year. For the rest of the year, we re-arranged the fences so that they encompassed the entire sites in order to protect the OTCs from animal destruction during winter.

Measurements

At the beginning of the experiment, we installed two TOMST temperature and soil moisture sensors at Cronkley Fell, in September 2021 we added another 14 to be able to measure the effects of the OTCs on soil and near-surface temperature and soil moisture. We paired the loggers, one inside the OTC and one outside the OTC next to the adjacent control plot. Loggers were placed at the edge of each plot so as not to disturb the vegetation. Two pairs of TOMST were located on Widdybank Fell, two pairs on Thistle Green and three pairs on Cronkley Fell. The loggers capture the climatic conditions experienced by the plants, i.e. air temperature at the height of the canopy (at +15 cm), surface temperature at the position of their overwintering buds (at 0 cm) and soil temperature (at -8 cm) as well as soil moisture (between 0 and -15 cm) in the rooting zone (Wild et al. 2019). Measurements were logged every 15 min. One of the loggers was malfunctioning and therefore data were discarded in the analysis.

Regarding the vegetation, we took three types of measurement. First, we weighed biomass. For that, we cut the above-ground parts of plants in all plots at ground level and collected litter and bryophytes at the end of our experiment in May 2022. The biomass was sorted into the following five categories: forbs (incl. legumes and low-growing shrubs), graminoids (excl. *Sesleria caerulea*), *S. caerulea*, litter and bryophytes. Lichens were also collected, but only found in eight plots and therefore not included in our analyses. The biomass was dried to constant weight at 60 °C for 48 h and cooled before weighing of dry mass. Total graminoid biomass was calculated by adding *S. caerulea* biomass to the other graminoids. Second, we recorded the plant community composition of each plot at the beginning of the experiment in September 2019, and again in May 2022. We visually estimated the cover of each vascular plant species to the nearest 1%. Species that could not be clearly identified because they were grazed or in an early development stage were grouped to genus level. Third, we measured the 10 longest (only healthy and fully developed) leaves of *S. caerulea* from base to tip. These measurements were taken in each plot in September 2019 and May 2022. *S. caerulea* is known as a particularly competitive species in our study area (Lewthwaite 1999) and one indicator trait for its competitiveness is leaf length, since plants with longer leaves can benefit directly from increased photosynthetic rates and indirectly by reducing the growth of neighbouring, shorter plants via shade (Craine and Dybzinski 2013). Because of the restrictions during the pandemic we were not able to take measurements every year as initially planned. All vegetation data can be found in the Online Supplementary Material Table S1.

x

Data analysis

To analyse treatment effects on above-ground plant biomass, we fitted linear mixed effect models (LMMs) using the function 'lmer' from the R package 'lme4' (Bates et al. 2015). Diagnostic plots were checked to ensure that the assumptions of heteroscedasticity and normality of residuals were fulfilled. A separate LMM was fitted for each plant group (i.e. 'forbs', 'graminoids', 'S. caerulea', 'litter' and 'bryophytes') using the square root of the 'dry biomass weight in g' (n=60) as response variable. Each LMM contained as fixed effects 'winter warming' (2 levels: warming, no warming) and 'grazing' (2 levels: grazing, no grazing) including their interaction, and as random effect 'site' (3 levels: Cronkley Fell, Thistle Green, Widdybank Fell). We fitted the LMMs using the restricted maximum likelihood (REML) method. P-values for the fixed effects were obtained from a Chi-square test using the function 'Anova' from the R package 'car' (Fox and Weisberg 2019). An adjusted pseudo R-squared was derived through the R function 'rsq' from the R package 'rsq' (Zhang 2021).

For each plot and year (2019 and 2022), the Shannon diversity index was calculated, based on the plant community data. The Shannon diversity index reflects both species richness (number of species) and evenness (relative abundances of species) present in a plot. In a second step, we subtracted the 2019 index values from the 2022 values to see how the diversity had changed in each plot. We then performed the same LMM as described above, using 'change in Shannon diversity index 2019-2022' (n=60) as response variable. Treatment effects on plant communities were further analysed with a permutational multivariate analysis of variance (PERMANOVA) with 999 permutations, based on a Bray-Curtis dissimilarity matrix of the plant community data from 2022, using the function 'adonis2' from the R package 'vegan' (Oksanen et al. 2023). PERMANOVA is a useful statistical tool for the analysis of multivariate data on the basis of dissimilarity measures (Anderson 2017). Since it is not possible to include random effects in PERMANOVAs, we accounted for ‘site’ by including it as the first term in our model and using sequential sums of squares, so that the variation among sites is accounted for before testing the effects of ‘winter warming’ and ‘grazing’.

To analyse *S. caerulea* leaf length, the change in mean leaf length per plot between September 2019 (before treatment) and May 2022 was calculated. The same LMM was then performed as described before, but using as response variable the ‘change in mean *S. caerulea* leaf length 2019-2022 in mm’ (n=60).

Figures were created with the R package ‘ggplot2’ (Hadley 2016). All analyses and figures were performed in R v.4.1.3 (R Core Team 2022).

Results

Effects of open top chambers on microclimate

The open top chambers (OTCs) increased the air temperature by 0.35 °C (mean 5.12 °C vs. 4.77 °C in controls), the surface temperature by 0.48 °C (mean 5.49 °C vs. 5.01 °C in controls) and the soil temperature by 0.37 °C (mean 5.85 °C vs. 5.48 °C in controls). Most of that warming happened in autumn and spring, whereas the chambers had almost no warming effect during November, December and January (Figure 2 (A)). The mean growing degree days (GDD) with a base temperature of 2 °C and a maximum temperature of 30 °C (measured at 0 cm) were 1001 GDD inside the OTCs and 803 GDD in the control plots. The OTCs also increased the minimum temperatures by 1.25 °C in the air (minimum -11.0 °C vs. -12.25 °C in controls) as well as on the surface (minimum -8.0 °C vs. -9.25 °C in controls) and by 0.38 °C in the soil (minimum 0.75 °C vs. 0.37 °C in controls). None of our plots experienced soil frost during the winter we measured. Regarding air frost however, the surface temperature dropped below 0 °C on average on 85 days in the control plots and on 81 days inside the OTCs. In late spring (2022-03-01 until 2022-04-27), when frosts can be particularly detrimental to plant development, the surface temperature dropped below 0 °C on average on 27 days in the control plots and on 25 days inside the OTCs. The mean volumetric soil water content was 0.59 in the control plots and 0.58 inside the OTCs. It increased from *ca.* 0.45 in early September to *ca.* 0.60 in mid-October and remained more or less stable until May (Figure 2 (B)).

Winter warming and grazing effects on vegetation

The data revealed strong evidence that bryophyte biomass had decreased with winter warming (LMM: chi-square = 7.249; P = 0.007) and moderate evidence that graminoid biomass had increased with winter warming (LMM: chi-square = 4.086; P = 0.043) (Figure 3). We found little to no evidence that winter warming affected any of the other plant response variables we measured, neither did the presence or absence of sheep grazing nor the interaction between winter warming and grazing. Tables with the results of all analyses can be found in the Online Supplementary Material 2.

Concerning plant community composition, we found 36 vascular plant taxa in total (31 identified to species level and 5 to genus level) (Figure 4). At the start of the experiment, there were on average (±SD) 10.5 ±2.0 taxa in each plot (25 cm diam., n=60). Overall, changes were small and primary attention should be given to the relative differences between treatments, not to the absolute values. This is because in 2019, data were collected in September and in 2022 in May, which caused natural differences in plant cover. Taxa that increased with the warming treatment were for example *Thymus polytrichus*, *Viola* spp., *Helianthemum nummularium* and *Sesleria caerulea*, the latter two even more so with no grazing. Taxa that decreased with warming included *Carex* spp. and *Festuca ovina*. There was little to no evidence that plant diversity, as reflected in the Shannon diversity index, was affected by our treatments, however it decreased slightly without grazing, and increased in variability with winter warming (i.e. some plots becoming more diverse, others less diverse) (Figure 5 (A)). Likewise, the PERMANOVA results showed little to no evidence for a treatment effect on plant community composition (Online Supplementary Material 2).

The leaves of *Sesleria caerulea* tended to become longer in the non-grazed plots, and this trend was increased by warming (Figure 5 (B)), however these trends were not statistically significant. Leaves were shorter in 2022 than in 2019, because the earlier measurements were taken in September and the later ones in May, i.e. just at the beginning of the growing season when all leaves were still relatively short. Therefore, main focus should be given to differences between treatments rather than changes in absolute values.

Discussion

H1: Winter warming would increase plant biomass, favouring mainly competitive species

The increase of graminoid biomass and decrease of bryophyte biomass in response to winter warming could indicate that taller graminoids are outcompeting bryophytes. This is in accordance with other studies that found warmer winter temperatures favour mainly tall, productive species at the cost of smaller species (Kreyling et al. 2019; Niittynen et al. 2020). On the other hand, Grant et al. (2017) have found no significant increase of graminoid biomass in a mesic temperate grassland, rather increases in other plant groups. A winter warming experiment in another upland limestone grassland in the UK, where soil surface temperature was increased by +3 °C relative to control using electrical soil heating cables, found that total bryophyte cover decreased slightly (non-significantly) with winter warming, with two bryophyte species significantly decreasing and one species increasing (Bates et al. 2005). This indicates that results might depend on the bryophyte species in question, which was also found in summer and all-year warming studies (Lett et al. 2022; van Zuijlen et al. 2022; Hollister et al. 2023). Another explanation for the bryophyte decrease in our experiment could be an increase in air vapour pressure deficit caused by the OTCs (Hollister et al. 2023), however we cannot confirm this as we did not measure air humidity. Since bryophytes can impede the germination and establishment of vascular plants by altering light and moisture conditions (Bates et al. 2005), a decrease in bryophyte biomass could have subsequent effects on the vascular plant community composition.

Regarding species diversity, as reflected in the Shannon diversity index, the plots that were exposed to winter warming increased in variance compared to control plots, indicating that community shifts were happening but with no clear direction. This could be natural variation or the beginning of a shift in species diversity.

The biomass of *Sesleria caerulea*, known as a particularly dominant grass species in our study area that can form dense litter layers (Lewthwaite 1999) with negative effects on other plants, did not change markedly with winter warming, neither did litter mass. Yet, regarding the leaf length of *S. caerulea* as well as the abundance of the species, we observed a slight increase relative to control plots in the treatment with winter warming without grazing. These could be early warning signs that *S. caerulea* might increase in size if not grazed regularly (Reisch and Poschlod 2003), even more so under future climate scenarios.

The fact that we observed overall modest changes with our winter warming treatment could have two main reasons. Firstly, our warming effect was relatively low (*ca.* +0.5 °C) compared to other studies (Grime et al. 2008; Grant et al. 2017; Suonan et al. 2017; Birgander et al. 2018). However, a similar study that increased winter air temperatures by +0.6 °C over 4 years in a semi-natural grassland in Germany, observed an increase in above-ground plant biomass by 18%, with increasing effect sizes over time (Kreyling et al. 2019). Secondly, the time-span of our study is rather short (three winter seasons), considering that plant communities can remain resistant to warming for many years (Grime et al. 2008; Shi et al. 2015). Upper Teesdale is known for changes in plant communities to happen very slowly due to the harsh climate and nutrient-poor soils (Elkington 1981). This is in line with other studies from cold, nutrient-poor environments that showed a high resistance and very slow response of the vegetation to environmental change (Grime et al. 2008; Damgaard et al. 2016; Alday et al. 2021), although some alpine plant communities have been found to change in relatively short periods of time (Hamid et al. 2020; Nicklas et al. 2021; Lamprecht et al. 2021). Løkken et al. (2019) have previously warned about the dangers of using short-term experiments for predictions of long-term consequences of environmental change. Manley (1942) has mentioned the ‘marginal’ character of the climate in Upper Teesdale and warned that only a small increase in temperature might alter the vegetation fundamentally. Therefore, the tendencies we notice should be continued to be monitored, in order to distinguish fluctuations from directional change and to observe if effect sizes will increase over time or if the grasslands will remain resistant to changes in composition.

Our results are based on three grassland sites which might not be representative for other grasslands with different plant communities, as results are known to be often site-specific (Rustad et al. 2001; Bates et al. 2005). Regarding the biomass measurements, the natural variation of species composition among plots might also obscure treatment effects, since these data were collected only once in 2022, i.e., there is no baseline data (before treatment). Moreover, different populations of the same species might react differently in other winter warming studies. For example, Grime et al. (2008) have found in a comparable study in a limestone grassland in the UK that *Helianthemum nummularium* declined consistently in response to winter warming, whereas we observed a slight increase in its abundance, especially if coupled with no grazing. In addition, the timespan when plants are truly inactive during winter depends on the species and year in question. Therefore, generalising/upscaling such local/species-specific results is difficult, as other authors have pointed out too (Rumpf et al. 2014; Schuerings et al. 2014; Krab et al. 2018; Niittynen et al. 2020). Still, as there are so few winter warming experiments even information from few sites can contribute to our knowledge of the effects of winter warming on grassland plant communities in the future.

H2: Grazing could buffer winter warming effects on plant biomass and community composition

The absence of sheep grazing caused no significant effects on any of the vegetation parameters we measured. This is in line with the observations of Alday et al. (2021), who found that >40 years of sheep grazing exclosure in Moor House (close to our study area) caused relatively little change in dominant plant species. Plant community change in the British Uplands in response to lack of grazing may take a very long time (Alday et al. 2021). Additionally, the continued grazing pressure exerted by rabbits in our study area is probably masking the effect of excluding sheep grazing. The increase in graminoid and decrease in bryophyte biomass we observed with winter warming did not differ much between the two grazing treatments, indicating that sheep grazing could not buffer this warming induced change.

Without sheep grazing, plant diversity showed a tendency to decrease both in the warmed and un-warmed plots, indicating that grazing should be continued in our study area where the goal is to maintain current levels of plant diversity, irrespective of the winter temperatures. Changes in the abundance of species were overall small in our experiment. Typical grassland species such as *Briza media*, *Campanula rotundifolia* and *Prunella vulgaris* decreased slightly without grazing. The strongest effects we observed in *Festuca ovina* (which increased without grazing, but decreased if coupled with warming), *S. caerulea* (which increased without grazing, even more if coupled with warming) and *Thymus polytrichus* (which increased without grazing, similar with or without warming).

To some degree, *S. caerulea* leaf length appeared to increase without grazing, especially if coupled with winter warming, indicating that grazing is particularly important under future climate scenarios to regulate this competitive species. Sheep grazing has been a main factor in our study area for centuries, promoting plant diversity by creating a short, open sward with a variety of microhabitats, and in particular the diminutive 'Teesdale rarities', which are light-demanding and sensitive to competition (Gilbert et al. 1978; Squires 1978; Bradshaw 2023).

Despite our results only showing tendencies, it points towards grazing being able to buffer winter warming effects, which is in line with other studies that focused on the interactions of all-year warming and grazing/mowing (Klein et al. 2004; Post and Pedersen 2008; Wang et al. 2012). For example in a review by Li et al. (2018), the authors have concluded that grazing intensity has greater effects on grassland plant biomass and communities than warming, and the review by He et al. (2022) has suggested that global change might be more important for below-ground biodiversity and ecosystem functioning, and grazing for above-ground organs in grasslands.

In order to maintain the current levels of plant diversity in the British Uplands and to protect the 'Teesdale rarities' in our study area, grazing might have to be adjusted towards higher intensity and duration, if the winter warming trends that we observed in this experiment become apparent in the vegetation. This is supported by a modelling study that found higher productivity under climate warming leads to a higher grazing capacity in European grasslands, particularly in the autumn in the case of Northern UK, and to a seasonal shift in grazing, thus allowing an increase of management intensity (Chang et al. 2017).

Using open top chambers for winter warming experiments

As far as we are aware, OTCs have only been used to simulate summer or all-year warming, but not solely winter warming. More commonly used methods to simulate winter warming *in situ* are e.g. electrical heating cables in the ground, overhead infrared lamps, greenhouses or snow removal (Rustad et al. 2001; Kreyling 2010; White Shannon R. et al. 2012). The fact that these methods are expensive and difficult to install is considered to be a main reason for the lack of such winter warming experiments (Kreyling and Beier 2013). Therefore, we wanted to test if OTCs could be potentially used for winter warming experiments in remote areas, where power supply or regular maintenance are not feasible.

Compared to the warming effects that OTCs cause in all-year warming setups (on average nearly 2 °C (Hollister et al. 2023)), the effects in our winter warming setup were minor (*ca.* +0.5 °C). This is not surprising, since day length and solar angle are major factors controlling the temperature enhancement in OTCs (Marion et al. 1997; Bokhorst et al. 2013). This is also reflected in our study in the stronger warming effects in autumn and spring compared to the darker winter months. Therefore, in areas with no or minimal solar irradiance during winter, OTCs might not be suitable to simulate desired winter warming scenarios.

Two unwanted side-effects are worth mentioning. First, OTCs are known to reduce wind speed (Marion et al. 1997; Hollister et al. 2023), which we can confirm by sporadic measurements. In our case, this is in line with the trends for British Uplands (reductions in wind speed, mostly during winter and spring (Monteith et al. 2016)), but in general, it means that aspects such as the reduction of physical stress (e.g., tearing leaves, causing abrasion) and evapotranspiration should be considered (Marion et al. 1997; Kreyling 2010; Momberg et al. 2021). Second, OTCs can alter snow depth and duration, even though the results from existing studies are not uniform (Marion et al. 1997; Wipf and Rixen 2010; Bokhorst et al. 2013; Hollister et al. 2023). In our case, we found no pronounced differences between OTCs and control plots (based on visual impressions, surface temperature and soil moisture data), however the slightly fewer frost days at surface level inside the OTCs might indicate insulation by snow. Since snow cover can have strong effects on plant communities (e.g. protection from frost), it would be advisable to monitor snow effects with temperature and soil moisture sensors or with a stationary camera. In conclusion, OTCs can be a practical option for winter warming experiments in remote areas if the above-mentioned caveats are fully accounted for.

Conclusions

Our data suggest that changes towards more dominant graminoids and less bryophytes with winter warming may occur, which might lead to lasting changes in the plant communities in the future. Our experiment shows that even a small increase in temperature outside of the growing season can affect the vegetation. Adapting the grazing regime might mitigate some of those effects, if adjusted towards higher intensity and longer duration. The slight vegetation changes that we recorded should be monitored in future years to observe whether these tendencies become more pronounced with time or the grasslands remain resistant to winter warming and lack of grazing.

Acknowledgements

We thank Dr. Margaret Bradshaw for her unbelievable knowledge of the local flora and great enthusiasm for our project, Natural England for their practical and logistical help, and Raby and Strathmore Estates for giving us access to their land. This project formed part of SAOC’s fellowship at the Institute for Advance Studies at Durham University. Funding was provided by the Bolin Centre for Climate Research and the Stiftelsen Carl Mannerfelts fond.

Notes on contributors

Nina Roth is Ph.D. student. Her main research interest are global change effects on plant communities and how to improve management regimes.

Robert Baxter is Professor. His research interests include arctic plant ecology, plant ecophysiology and snow-vegetation-atmosphere interactions.

Martin Furness is Reserve Manager. His aim is to maintain biodiversity within the different habitats of the NRR, e.g. by adapting grazing management.

Adam Kimberley is researcher. His studies focus mainly on landscape ecology, functional connectivity and identifying drivers of plant community change.

Sara A. O. Cousins is Professor. She combines plant community ecology and landscape history to explore effects of fragmentation and land use change on plant dispersal, community composition and diversity.

References

Bates JW, Thompson K, Grime JP. 2005. Effects of simulated long-term climatic change on the bryophytes of a limestone grassland community. Glob Change Biol. 11(5):757–769. https://doi.org/10.1111/j.1365-2486.2005.00953.x

Bellamy DJ, Bridgewater P, Marshall C, Tickle WM. 1969. Status of the Teesdale Rarities. Nature. 222(5190):238–243. https://doi.org/10.1038/222238a0

Birgander J, Olsson PA, Rousk J. 2018. The responses of microbial temperature relationships to seasonal change and winter warming in a temperate grassland. Glob Change Biol. 24(8):3357–3367. https://doi.org/10.1111/gcb.14060

Bjorkman AD, Gallois EC. 2020. Winter in a warming Arctic. Nat Clim Change. 10(12):1071–1073. https://doi.org/10.1038/s41558-020-0900-3

Bokhorst SF, Bjerke JW, Tømmervik H, Callaghan TV, Phoenix GK. 2010. Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event. J Ecol.:1408–1415. https://doi.org/10.1111/j.1365-2745.2009.01554.x@10.1111/(ISSN)1365-2745.GLOBWA

Bradshaw ME. 2023. Teesdale's Special Flora - Places, plants and people. 1st ed. Princeton: Princeton University Press.

Bradshaw ME, Doody JP. 1978. Plant population studies and their relevance to nature conservation. Biol Conserv. 14(3):223–242. https://doi.org/10.1016/0006-3207(78)90012-5

Burt T, Holden J. 2010. Changing temperature and rainfall gradients in the British Uplands. Clim Res. 45:57–70. https://doi.org/10.3354/cr00910

Chang J, Ciais P, Viovy N, Soussana J-F, Klumpp K, Sultan B. 2017. Future productivity and phenology changes in European grasslands for different warming levels: implications for grassland management and carbon balance. Carbon Balance Manag. 12(1):11. https://doi.org/10.1186/s13021-017-0079-8

Choler P. 2015. Growth response of temperate mountain grasslands to inter-annual variations in snow cover duration. Biogeosciences. 12(12):3885–3897. https://doi.org/10.5194/bg-12-3885-2015

Cranston DM, Valentine DH. 1983. Transplant experiments on rare plant species from Upper Teesdale. Biol Conserv. 26(2):175–191. https://doi.org/10.1016/0006-3207(83)90065-4

Dirnböck T, Essl F, Rabitsch W. 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. Glob Change Biol. 17(2):990–996. https://doi.org/10.1111/j.1365-2486.2010.02266.x

EAA. 2014. Projected changes in annual, summer and winter temperature — European Environment Agency [Internet]. [accessed 2022 Nov 28]. https://www.eea.europa.eu/data-and-maps/figures/projected-changes-in-annual-summer-1

Edwards AC, Scalenghe R, Freppaz M. 2007. Changes in the seasonal snow cover of alpine regions and its effect on soil processes: A review. Quat Int. 162–163:172–181. https://doi.org/10.1016/j.quaint.2006.10.027

Elkington TT. 1981. Effects of excluding grazing animals from grassland on sugar limestone in Teesdale, England. Biol Conserv. 20(1):25–35. https://doi.org/10.1016/0006-3207(81)90058-6

Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, GIS User Community. 2021. Basemap of Upper Teesdale [Internet]. [accessed 2023 May 26]. https://www.arcgis.com/apps/mapviewer/index.html?webmap=52bdc7ab7fb044d98add148764eaa30a

Gilbert OL, Earland-Bennett P, Coppins BJ. 1978. Lichens of the Sugar Limestone Refugium in Upper Teesdale. New Phytol. 80(2):403–408. https://doi.org/10.1111/j.1469-8137.1978.tb01574.x

Grant K, Kreyling J, Beierkuhnlein C, Jentsch A. 2017. Importance of Seasonality for the Response of a Mesic Temperate Grassland to Increased Precipitation Variability and Warming. Ecosystems. 20(8):1454–1467. https://doi.org/10.1007/s10021-017-0122-3

Grime JP, Fridley JD, Askew AP, Thompson K, Hodgson JG, Bennett CR. 2008. Long-term resistance to simulated climate change in an infertile grassland. Proc Natl Acad Sci. 105(29):10028–10032. https://doi.org/10.1073/pnas.0711567105

Hamid M, Khuroo AA, Malik AH, Ahmad R, Singh CP, Dolezal J, Haq SM. 2020. Early Evidence of Shifts in Alpine Summit Vegetation: A Case Study From Kashmir Himalaya. Front Plant Sci. 11. https://doi.org/10.3389/fpls.2020.00421

He M, Pan Y, Zhou G, Barry KE, Fu Y, Zhou X. 2022. Grazing and global change factors differentially affect biodiversity-ecosystem functioning relationships in grassland ecosystems. Glob Change Biol. 28(18):5492–5504. https://doi.org/10.1111/gcb.16305

Henry HAL. 2008. Climate change and soil freezing dynamics: historical trends and projected changes. Clim Change. 87(3):421–434. https://doi.org/10.1007/s10584-007-9322-8

Holden J, Rose R. 2011. Temperature and surface lapse rate change: a study of the UK's longest upland instrumental record. Int J Climatol. 31(6):907–919. https://doi.org/10.1002/joc.2136

House JI, Orr HG, Clark JM, Gallego-Sala AV, Freeman C, Prentice IC, Smith P. 2010. Climate change and the British Uplands: evidence for decision-making. Clim Res. 45:3–12. https://doi.org/10.3354/cr00982

Inouye DW. 2008. Effects of Climate Change on Phenology, Frost Damage, and Floral Abundance of Montane Wildflowers. Ecology. 89(2):353–362. https://doi.org/10.1890/06-2128.1

Johnson G a. L, Robinson D, Hornung M. 1971. Unique Bedrock and Soils associated with the Teesdale Flora. Nature. 232(5311):453–456. https://doi.org/10.1038/232453a0

Jonas T, Rixen C, Sturm M, Stoeckli V. 2008. How alpine plant growth is linked to snow cover and climate variability. J Geophys Res Biogeosciences [Internet]. [accessed 2022 Sep 25] 113(G3). https://doi.org/10.1029/2007JG000680

Klein JA, Harte J, Zhao X-Q. 2004. Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. Ecol Lett. 7(12):1170–1179. https://doi.org/10.1111/j.1461-0248.2004.00677.x

Klein JA, Harte J, Zhao X-Q. 2007. Experimental Warming, Not Grazing, Decreases Rangeland Quality on the Tibetan Plateau. Ecol Appl. 17(2):541–557. https://doi.org/10.1890/05-0685

Krab EJ, Roennefarth J, Becher M, Blume-Werry G, Keuper F, Klaminder J, Kreyling J, Makoto K, Milbau A, Dorrepaal E. 2018. Winter warming effects on tundra shrub performance are species-specific and dependent on spring conditions. J Ecol. 106(2):599–612. https://doi.org/10.1111/1365-2745.12872

Kreyling J. 2010. Winter climate change: a critical factor for temperate vegetation performance. Ecology. 91(7):1939–1948. https://doi.org/10.1890/09-1160.1

Kreyling J, Grant K, Hammerl V, Arfin-Khan MAS, Malyshev AV, Peñuelas J, Pritsch K, Sardans J, Schloter M, Schuerings J, et al. 2019. Winter warming is ecologically more relevant than summer warming in a cool-temperate grassland. Sci Rep. 9(1):14632. https://doi.org/10.1038/s41598-019-51221-w

Kreyling J, Jurasinski G, Grant K, Retzer V, Jentsch A, Beierkuhnlein C. 2011. Winter warming pulses affect the development of planted temperate grassland and dwarf-shrub heath communities. Plant Ecol Divers. 4(1):13–21. https://doi.org/10.1080/17550874.2011.558125

Lamprecht A, Pauli H, Fernández Calzado MR, Lorite J, Molero Mesa J, Steinbauer K, Winkler M. 2021. Changes in plant diversity in a water-limited and isolated high-mountain range (Sierra Nevada, Spain). Alp Bot. 131(1):27–39. https://doi.org/10.1007/s00035-021-00246-x

Lewthwaite KJ. 1999. An investigation into the impact of environmental change upon the vegetation of Widdybank Fell, Upper Teesdale. :261.

Li W, Li X, Zhao Y, Zheng S, Bai Y. 2018. Ecosystem structure, functioning and stability under climate change and grazing in grasslands: current status and future prospects. Curr Opin Environ Sustain. 33:124–135. https://doi.org/10.1016/j.cosust.2018.05.008

Liu Q, Piao S, Janssens IA, Fu Y, Peng S, Lian X, Ciais P, Myneni RB, Peñuelas J, Wang T. 2018. Extension of the growing season increases vegetation exposure to frost. Nat Commun. 9(1):426. https://doi.org/10.1038/s41467-017-02690-y

Løkken JO, Hofgaard A, Dalen L, Hytteborn H. 2019. Grazing and warming effects on shrub growth and plant species composition in subalpine dry tundra: An experimental approach. J Veg Sci. 30(4):698–708. https://doi.org/10.1111/jvs.12752

Manley G. 1942. Meteorological observations on Dun Fell, a mountain station in Northern England. Q J R Meteorol Soc. 68(295):151–166. https://doi.org/10.1002/qj.49706829502

Marion GM, Henry GHR, Freckman DW, Johnstone J, Jones G, Jones MH, Lévesque E, Molau U, Mølgaard P, Parsons AN, et al. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. Glob Change Biol. 3(S1):20–32. https://doi.org/10.1111/j.1365-2486.1997.gcb136.x

Momberg M, Hedding DW, Luoto M, le Roux PC. 2021. Exposing wind stress as a driver of fine-scale variation in plant communities. J Ecol. 109(5):2121–2136. https://doi.org/10.1111/1365-2745.13625

Morecroft MD, Bealey CE, Beaumont DA, Benham S, Brooks DR, Burt TP, Critchley CNR, Dick J, Littlewood NA, Monteith DT, et al. 2009. The UK Environmental Change Network: Emerging trends in the composition of plant and animal communities and the physical environment. Biol Conserv. 142(12):2814–2832. https://doi.org/10.1016/j.biocon.2009.07.004

Nicklas L, Walde J, Wipf S, Lamprecht A, Mallaun M, Rixen C, Steinbauer K, Theurillat J-P, Unterluggauer P, Vittoz P, et al. 2021. Climate Change Affects Vegetation Differently on Siliceous and Calcareous Summits of the European Alps. Front Ecol Evol. 9. https://doi.org/10.3389/fevo.2021.642309

Niittynen P, Heikkinen RK, Aalto J, Guisan A, Kemppinen J, Luoto M. 2020. Fine-scale tundra vegetation patterns are strongly related to winter thermal conditions. Nat Clim Change. 10(12):1143–1148. https://doi.org/10.1038/s41558-020-00916-4

Niskanen AKJ, Niittynen P, Aalto J, Väre H, Luoto M. 2019. Lost at high latitudes: Arctic and endemic plants under threat as climate warms. Divers Distrib. 25(5):809–821. https://doi.org/10.1111/ddi.12889

Pepin NC, Adamson JK, Benham D. 2009. Creation of a homogenous climate record for Widdybank Fell in the Upper Teesdale National Nature Reserve, northern England: 1968-2006. Theor Appl Climatol. 98(1):47–56. https://doi.org/10.1007/s00704-008-0090-9

Pigott CD. 1956. The Vegetation of Upper Teesdale in the North Pennines. J Ecol. 44(2):545–586. https://doi.org/10.2307/2256835

Post E, Pedersen C. 2008. Opposing plant community responses to warming with and without herbivores. Proc Natl Acad Sci. 105(34):12353–12358. https://doi.org/10.1073/pnas.0802421105

R Core Team. 2022. R: A language and environment for statistical computing [Internet]. https://www.R-project.org/

Reisch C, Poschlod P. 2003. Intraspecific variation, land use and habitat quality – a phenologic and morphometric analysis of *Sesleria albicans* (Poaceae). Flora - Morphol Distrib Funct Ecol Plants. 198(4):321–328. https://doi.org/10.1078/0367-2530-00103

Rumpf SB, Semenchuk PR, Dullinger S, Cooper EJ. 2014. Idiosyncratic Responses of High Arctic Plants to Changing Snow Regimes. PLOS ONE. 9(2):e86281. https://doi.org/10.1371/journal.pone.0086281

Rustad L, Campbell J, Marion G, Norby R, Mitchell M, Hartley A, Cornelissen J, Gurevitch J, GCTE-NEWS. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia. 126(4):543–562. https://doi.org/10.1007/s004420000544

Schuerings J, Beierkuhnlein C, Grant K, Jentsch A, Malyshev A, Peñuelas J, Sardans J, Kreyling J. 2013. Absence of soil frost affects plant-soil interactions in temperate grasslands. Plant Soil. 371(1):559–572. https://doi.org/10.1007/s11104-013-1724-y

Schuerings J, Jentsch A, Walter J, Kreyling J. 2014. Winter warming pulses differently affect plant performance in temperate heathland and grassland communities. Ecol Res. 29(4):561–570. https://doi.org/10.1007/s11284-014-1174-x

Shi Z, Sherry R, Xu X, Hararuk O, Souza L, Jiang L, Xia J, Liang J, Luo Y. 2015. Evidence for long-term shift in plant community composition under decadal experimental warming. J Ecol. 103(5):1131–1140. https://doi.org/10.1111/1365-2745.12449

Squires R. 1978. Conservation in Upper Teesdale: Contributions from the Palaeoecological Record. Trans Inst Br Geogr. 3(2):129–150. https://doi.org/10.2307/622198

Squires RH. 1971. Flandrian History of the Teesdale Rarities. Nature. 229(5279):43–44. https://doi.org/10.1038/229043a0

Suonan J, Classen AT, Zhang Z, He J-S. 2017. Asymmetric winter warming advanced plant phenology to a greater extent than symmetric warming in an alpine meadow. Funct Ecol. 31(11):2147–2156. https://doi.org/10.1111/1365-2435.12909

Turner J, Hewetson P, Hibbert FA, Lowry H, Chambers C, West RG. 1973. The history of the vegetation and flora of Widdybank Fell and the Cow Green reservior basin, Upper Teesdale. Philos Trans R Soc Lond B Biol Sci. 265(870):327–408. https://doi.org/10.1098/rstb.1973.0031

V. Lenth R. 2016. Least-Squares Means: The R Package lsmeans. J Stat Softw. 69(1):1–33. https://doi.org/doi:10.18637/jss.v069.i01

Wang S, Duan J, Xu G, Wang Y, Zhang Z, Rui Y, Luo C, Xu B, Zhu X, Chang X, et al. 2012. Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow. Ecology. 93(11):2365–2376. https://doi.org/10.1890/11-1408.1

Waughman GJ, Kookorinis E, Bellamy DJ. 1983. Influences of Climate and Heavy Metal Concentrations in the Soil on Plants of Grassland and Flush Vegetation in Upper Teesdale. J Ecol. 71(1):177–187. https://doi.org/10.2307/2259970

Wild J, Kopecký M, Macek M, Šanda M, Jankovec J, Haase T. 2019. Climate at ecologically relevant scales: A new temperature and soil moisture logger for long-term microclimate measurement. Agric For Meteorol. 268:40–47. https://doi.org/10.1016/j.agrformet.2018.12.018

Williams CM, Henry HAL, Sinclair BJ. 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. Biol Rev. 90(1):214–235. https://doi.org/10.1111/brv.12105

Zeeman MJ, Mauder M, Steinbrecher R, Heidbach K, Eckart E, Schmid HP. 2017. Reduced snow cover affects productivity of upland temperate grasslands. Agric For Meteorol. 232:514–526. https://doi.org/10.1016/j.agrformet.2016.09.002

Zhang Y, Gao Q, Dong S, Liu S, Wang X, Su X, Li Y, Tang L, Wu X, Zhao H, et al. 2015. Effects of grazing and climate warming on plant diversity, productivity and living state in the alpine rangelands and cultivated grasslands of the Qinghai-Tibetan Plateau. Rangel J. 37(1):57–65. https://doi.org/10.1071/RJ14080

Table captions

Table 1: Characteristics of the three grassland sites of a winter warming and grazing experiment, Upper Teesdale, Co. Durham, England. Values regarding vegetation represent means (± standard errors) of 20 plots (25 cm in diameter) per site, measured in September 2019 before start of the experiment. Values regarding microclimate represent means (± standard errors) of two (on Cronkley Fell three) TOMST TMS-4 loggers, located in control plots, which took measurements every 15 min between 2021-09-06 and 2022-04-27.

Figure legends

Figure 1. Satellite image of Upper Teesdale, Co. Durham, England, showing the location of the three grassland sites of a winter warming and grazing experiment. The map was created using ArcGIS® software by Esri (Esri et al. 2021). The photos on the right side show the vegetation of each site as well as the open-top-chambers used to simulate winter warming (Photographic credit: N. Roth).

Figure 2. Microclimatic data measured with 13 TOMST TMS-4 loggers every 15 min between 2021-09-06 and 2022-04-27 (6 loggers were placed inside OTCs and 7 in control plots) across three study sites, Upper Teesdale, Co. Durham, England. The left panel (A) shows the surface temperature that was measured at ground level (0 cm) and the right panel (B) the volumetric soil water content that was measured in the rooting zone (between 0 and -15 cm). The coloured trend lines are smoothed with generalised additive models and the grey points are showing the measured values. Soil temperature, air temperature and growing degree days (GDD) show similar patterns to surface temperature and are therefore not shown.

Figure 3. Results from a three-year long experiment, studying the effects of winter warming and grazing on grassland plant communities, Upper Teesdale, Co. Durham, England. Box and whisker plots are showing the dry biomass weight per plot (25 cm in diameter) in May 2022, differentiated by

plant group and treatment. Each box represents 15 experimental plots. The horizontal lines inside the boxes indicate medians and the triangles are showing means.

Figure 4. Results from a three-year long experiment, studying the effects of winter warming and grazing on grassland plant communities, Upper Teesdale, Co. Durham, England. The plot shows 36 vascular plant taxa (31 identified to species level and 5 to genus level) and how their cover has changed by 2022 per treatment, relative to 2019. Each point represents the mean of 15 experimental plots (25 cm in diameter).

Figure 5. Results from a three-year long experiment, studying the effects of winter warming and grazing on grassland plant communities, Upper Teesdale, Co. Durham, England. Box and whisker plots are showing changes between 2019 and 2022 in (A) the Shannon diversity index and (B) *Sesleria caerulea* leaf length per plot (25 cm in diameter) per treatment. Each box represents 15 experimental plots. The horizontal lines inside the boxes indicate medians and the triangles are showing means.

Figure 1.

Figure 2.

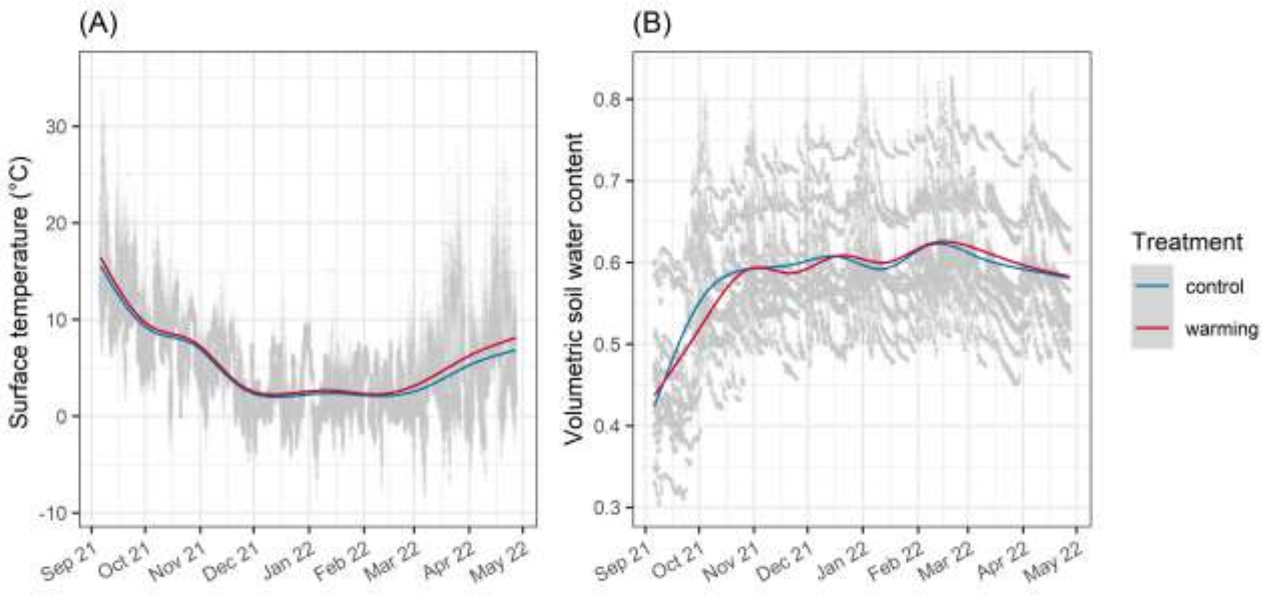


Figure 3.

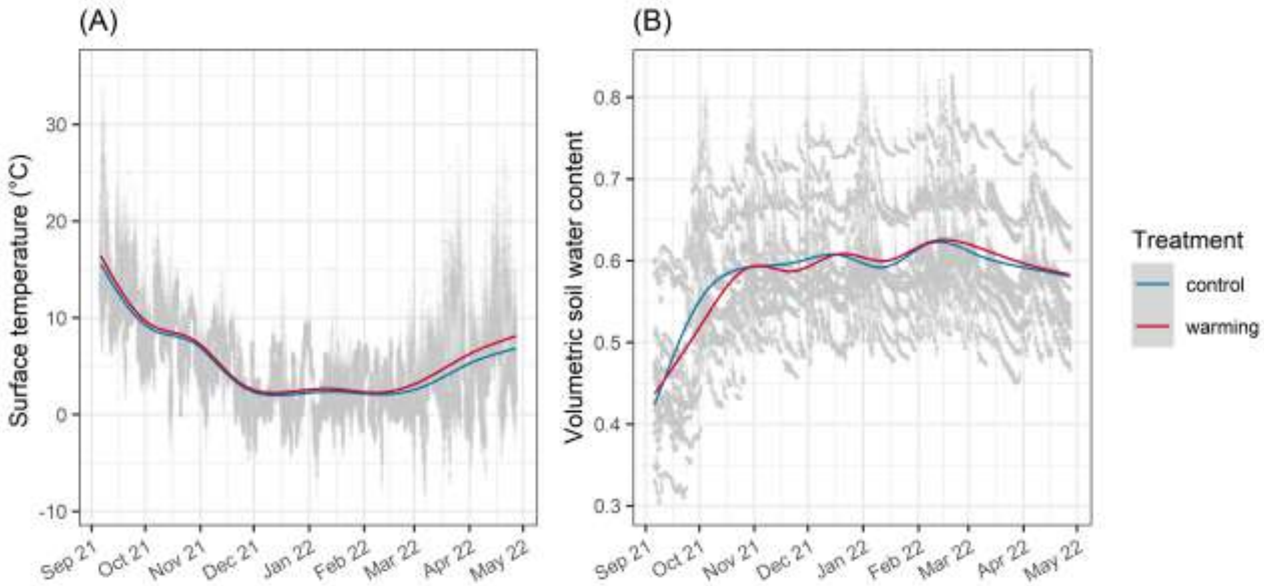


Figure 4.

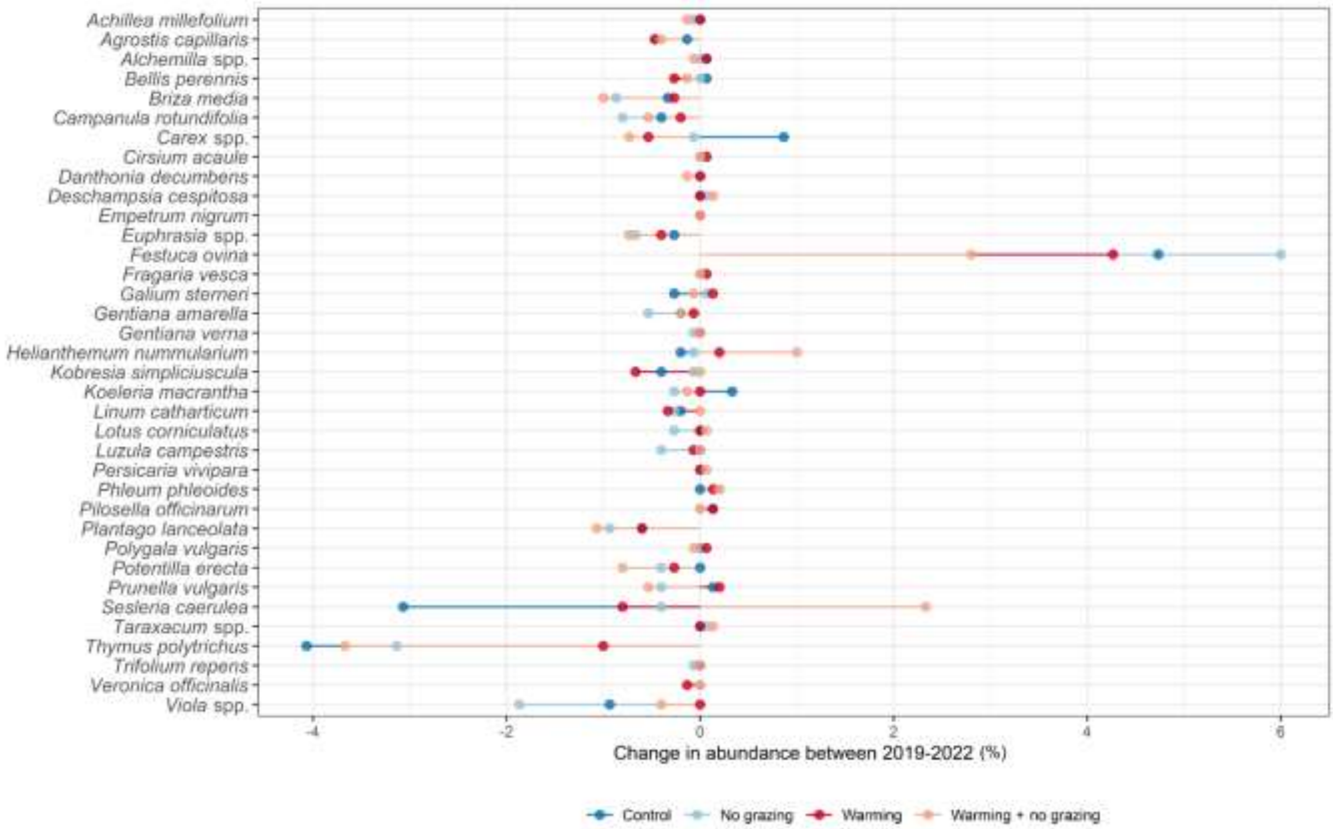
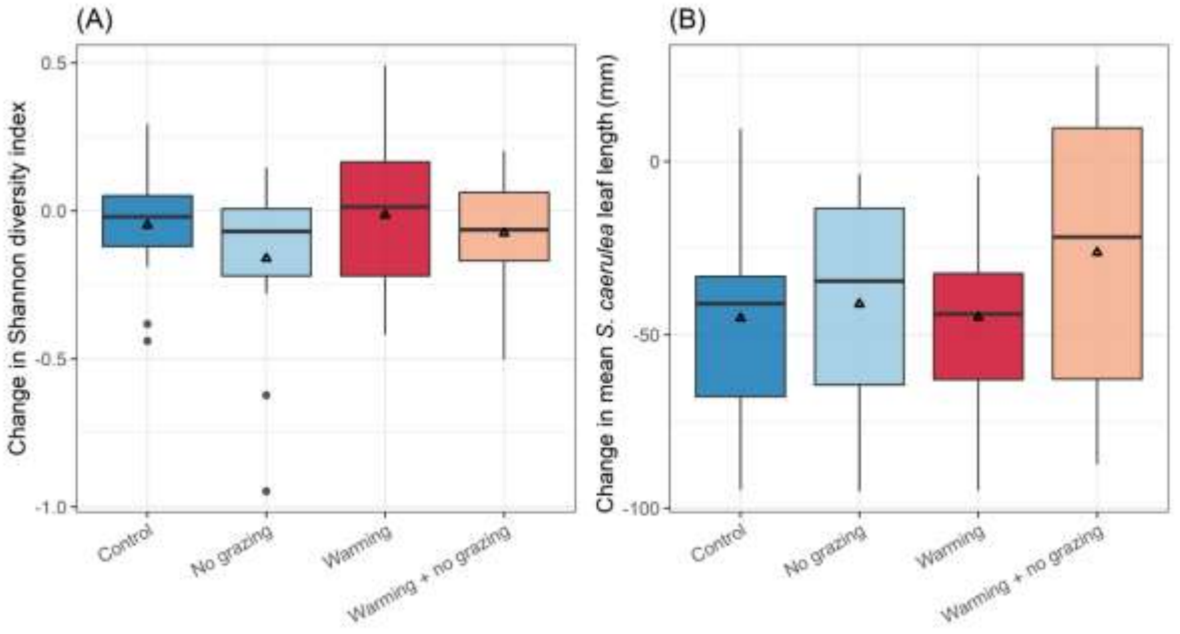


Figure 5.



Online Supplementary Material 2

Levels of significance are indicated by the following symbols: * p < 0.05, ** p < 0.01, *** p < 0.001

A) Linear mixed effect models (LMMs)

1.) Biomass forbs

↓↓↓↓

```
LMM: √Dry forb biomass weight ~ Warming * Grazing + (1|Site)
        n=60           2 levels   2 levels   3 levels

ANOVA:
                   Chisq Df Pr(>Chisq)
Grazing           0.4901  1     0.4839
Warming           0.4300  1     0.5120
Grazing:Warming   0.2273  1     0.6335

Adjusted R-squared: 0.42
```

2.) Biomass graminoids

↓↓↓↓

```
LMM: √Dry graminoid biomass weight ~ Warming * Grazing + (1|Site)
        n=59                2 levels   2 levels   3 levels

ANOVA:
                   Chisq Df Pr(>Chisq)
Grazing           0.1368  1    0.71152
Warming           4.0860  1    0.04324 *
Grazing:Warming   0.0375  1    0.84653

Adjusted R-squared: 0.27
```

3.) Biomass *Sesleria caerulea*

↓↓↓↓

```
LMM: √Dry S. caerulea biomass weight ~ Warming * Grazing + (1|Site)
        n=60                  2 levels   2 levels   3 levels

ANOVA:
```

```
                  Chisq Df Pr(>Chisq)
Grazing          0.1490  1     0.6995
Warming          0.5205  1     0.4706
Grazing:Warming 0.3899  1     0.5323

Adjusted R-squared: 0.45
```

4.) Biomass litter

```
      LMM: √Dry litter biomass weight ~ Warming * Grazing + (1|Site)
                n=60              2 levels   2 levels   3 levels

ANOVA:
                  Chisq Df Pr(>Chisq)
Grazing          1.9573  1     0.1618
Warming          0.6116  1     0.4342
Grazing:Warming 0.4766  1     0.4900

Adjusted R-squared: 0.81
```

5.) Biomass bryophytes

```
      LMM: √Dry bryophyte biomass weight ~ Warming * Grazing + (1|Site)
                n=60                 2 levels   2 levels   3 levels

ANOVA:
                  Chisq Df Pr(>Chisq)
Grazing          0.2044  1   0.651203
Warming          7.2492  1   0.007093 **
Grazing:Warming 0.0116  1   0.914269

Adjusted R-squared: 0.63
```

6.) Shannon diversity index

```
      LMM: Change in Shannon diversity index ~ Warming * Grazing + (1|Site)
                    n=60              2 levels   2 levels   3 levels

ANOVA:
Grazing          2.1084  1     0.1465
Warming          1.0065  1     0.3157
Grazing:Warming 0.1939  1     0.6597

Adjusted R-squared: 0.01
```

7.) *Sesleria caerulea* leaf length

```
      LMM: Change in mean S. caerulea leaf length ~ Warming * Grazing + (1|Site)
                n=45                          2 levels   2 levels   3 levels

ANOVA:
Grazing          0.1492  1     0.6993
Warming          1.5496  1     0.2132
Grazing:Warming 0.2931  1     0.5883

Adjusted R-squared: 0.41
```

B) Permutational multivariate analysis of variance (PERMANOVA)

```
PERMANOVA: Bray-Curtis dissimilarity matrix ~ Site + Warming * Grazing

            60x60 cells                 3 levels   2 levels   2 levels

                 Df SumOfSqs      R2       F Pr(>F)
Site              2   5.3047 0.57354 38.4447  0.001 ***
Warming           1   0.0975 0.01055  1.4138  0.217
Grazing           1   0.1086 0.01174  1.5738  0.184
Warming:Grazing   1   0.0127 0.00137  0.1836  0.975
Residual         54   3.7255 0.40280
Total            59   9.2489 1.00000
```