

# Grasslands in a changing climate

Summer drought and winter warming effects on grassland vegetation

Nina Roth





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Academic dissertation for the Degree of Doctor of Philosophy in Physical Geography at Stockholm University to be publicly defended on Thursday 7 December 2023 at 13.00 in De Geersalen, Geovetenskapens hus, Svante Arrhenius väg 14 and online via Zoom: <https://stockholmuniversity.zoom.us/j/68534967825>.

### Abstract

Grasslands harbour a high biodiversity of both plants and animals, and they provide many ecosystem services such as fodder production, pollination, and carbon storage. Climate change is likely to alter grassland ecosystems, with the effects varying according to the exact nature and timing of changes. Hence, understanding of seasonal climate change effects on grasslands and how negative impacts can be reduced is important to maintain biodiversity and to ensure continued delivery of ecosystem services.

In this thesis I explored how seasonally specific aspects of climate change, i.e. summer drought and winter warming, affect aboveground plant biomass, plant community composition, and floral resources for pollinating insects. Moreover, I aimed to outline ways to mitigate potential negative climate change effects by adapting conventional grazing and mowing regimes and/or by applying soil amendments (i.e. compost) as a novel management method. Soil amendments have been suggested as a method to increase carbon sequestration and they might mitigate negative drought effects. However, there is no empirical evidence of how European grassland ecosystems would be affected should such measures be applied.

A literature review of climate change studies revealed that the terms 'wetter' and 'drier' can be defined by a variety of hydroclimatic variables, or are not defined at all, making it difficult to synthesise climate change effects on ecosystems and societies. In two *in-situ* experiments I investigated the effects of summer drought (using rain-out shelters), soil amendments and mowing on four Swedish grasslands, and the effects of winter warming (using open-top chambers) and sheep grazing on three British Upland grasslands. The experimental summer drought caused a non-significant decline in aboveground plant biomass (i.e. fodder production), plant species diversity, and floral resources. Applying soil amendments increased aboveground plant biomass and floral resources (in yearly mown plots), but these positive effects were reduced under drought. There were signs of negative soil amendment effects on legumes. Winter warming led to an increase in graminoid biomass and a decrease in bryophyte biomass. Sheep grazing buffered the growth of a competitive species under winter warming but had only minor effects overall.

My thesis emphasizes that it is important to clearly define terms like 'wetter' and 'drier' when studying effects of climate change on ecosystems, since clarifying the effects of climate across habitats and management interventions will require the synthesis of results across a range of experimental and observational systems. My field experiments indicate that even relatively small climatic changes affect grassland plant biomass and biodiversity, and that these effects depend on the season and grassland site in question. Furthermore, soil amendments have mainly positive effects on the grassland vegetation, indicating that they have potential for broad-scale application as a method to increase carbon sequestration. Given that my experiments were set up *in-situ* in grasslands and the treatments were rather mild and realistic in magnitude according to local climate change predictions, the observed vegetation changes within only three years are quite remarkable. They therefore highlight the need for detailed empirical and mechanistic understanding of how climate change processes are likely to affect grassland ecosystems.

**Keywords:** *biodiversity, climate change, compost, floral resources, grasslands, in-situ experiments, mowing, nectar, open-top chambers, plants, rain-out shelters, sheep grazing, soil amendments, summer drought, winter warming.*

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# Abstract

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My thesis emphasizes that it is important to clearly define terms like ‘wetter’ and ‘drier’ when studying effects of climate change on ecosystems, since clarifying the effects of climate across habitats and management interventions will require the synthesis of results across a range of experimental and observational systems. My field experiments indicate that even relatively small climatic changes affect grassland plant biomass and biodiversity, and that these effects depend on the season and grassland site in question. Furthermore, soil amendments have mainly positive effects on the grassland vegetation, indicating that they have potential for broad-scale application as a method to increase carbon sequestration. Given that my experiments were set up *in-situ* in grasslands and the treatments were rather mild and realistic in magnitude according to local climate change predictions, the observed vegetation changes within only three years are quite remarkable. They therefore highlight the need for detailed empirical and mechanistic understanding of how climate change processes are likely to affect local grassland ecosystems.

**Keywords:** biodiversity, climate change, compost, floral resources, grasslands, *in-situ* experiments, mowing, nectar, open-top chambers, plants, rain-out shelters, sheep grazing, soil amendments, summer drought, winter warming

## Sammanfattning

Gräsmarker härbärgerar en hög biodiversitet både när det gäller växter och djur och de erbjuder många ekosystemtjänster som till exempel produktion av foder, pollinering och lagring av kol. Klimatförändringarna kommer troligtvis att förändra gräsmarkernas ekosystem där effekterna varierar med förändringens natur och tidpunkt. Det är därför viktigt att förstå vilken effekt säsongsmässiga klimatförändringar har på gräsmarker och hur negativ påverkan kan minskas för att bevara biodiversiteten och säkra oförändrade ekosystemtjänster.

I den här avhandlingen undersökte jag hur specifika säsongseffekter orsakade av klimatförändringar, det vill säga sommartorka och varma vintrar, påverkar vegetationens biomassa ovan jord, växtsamhällets sammansättning och blomresurser för pollinerande insekter. Därutöver hade jag som mål att visa på olika sätt att begränsa potentiellt negativa effekter av klimatförändringar genom att anpassa betning och slättermarker och/eller genom att tillämpa jordförbättring (kompost) som en ny metod. Jordförbättring har föreslagits som en metod för att öka markens förmåga att binda kol och för att mildra negativa effekter av torka. Dock, finns det inga empiriska bevis för hur europeiska gräsmarkers ekosystem skulle påverkas om sådana åtgärder tillämpades.

En litteraturstudie av klimatförändringar visade att termerna ”fuktigare” och ”torrare” kan definieras av en mängd olika hydrologiska variabler, eller att de inte är definierade alls.

Detta gör det svårt att ge en samlad bild av klimatförändringarnas effekter på ekosystem och samhällen. I två olika *in-situ* experiment undersökte jag effekterna av sommartorka och varmare vintrar. I experimenten med sommartorka använde jag ytor som var regnskyddade och undersökte effekten av jordförbättring och gräsklippning på fyra olika lokaler i Sverige. I det andra experimentet undersökte jag effekten av varmare vintrar med hjälp av öppna kammare och betande får på tre gräsmarker på brittiska högländet. Den experimentella sommartorkan orsakade en icke signifikant minskning av biomassa ovan jord (dvs foderproduktion), en mångfald av olika växtarter och växtresurser. Markförbättringar ökade växternas biomassa och blomresurser ovan jord (på årligt klippta ytor), men dessa positiva effekter minskade under torra förhållanden. Det fanns tecken på negativa markförändringseffekter på baljväxter. Varmare vintrar ledde till en ökning av graminoidbiomassa (örtartad växt med en gräslignande morfologi) och en minskning av biomassa hos mossor. Betande får buffrade tillväxten av en konkurrerande art under vinteruppvärmningen men hade bara mindre effekter totalt sett.

Min avhandling betonar att det är viktigt att tydligt definiera termer som ”fuktigare” och ”torrare” när man studerar climateffekter på ekosystem, eftersom tydliggörande av climateffekter på livsmiljöer och vid påverkan av markskötsel kommer att kräva att resultat från en bredd av olika experiment och observationer sammanställs. Mina fältexperiment visar att även små klimatförändringar påverkar gräsmarkernas växtbiomassa och biodiversitet och att de här effekterna beror på årstid och vilka gräsmarker det är frågan om. Att tillsätta kompost har till största delen positiva effekter på gräsmarkernas vegetation, vilket indikerar att det har potential för en storskalig användning som metod för att öka markens förmåga att binda kol. Med tanke på att mina experiment gjordes *in-situ* på gräsmarker och att behandlingarna var ganska milda och att dess omfattning var realistiska enligt lokala förutsägelser av klimatförändringar, är de observerade vegetationsförändringarna inom loppet av bara tre år ganska anmärkningsvärda. Resultaten från experimenten visar på behovet av detaljerad empirisk och mekanistisk förståelse av hur klimatförändringsprocesser sannolikt kommer att påverka lokala gräsmarksekosystem.

## Content of this thesis

This thesis consists of this summary and the following four papers, which are referred to by their Roman numerals in the text. The raw data that my analyses are based on is not attached to this thesis, but can be found in the appendices of my published papers.

- I** Roth, N., Jaramillo, F., Wang-Erlandsson, L., Zamora, D., Palomino-Ángel, S. & Cousins, S.A.O. (2021). A call for consistency with the terms ‘wetter’ and ‘drier’ in climate change studies. *Environmental Evidence*, 10, 8. <https://doi.org/10.1186/s13750-021-00224-0>
- II** Roth, N., Kimberley, A., Manzoni, S., Guasconi, D., Hugelius, G. & Cousins, S.A.O.  
Soil amendments promote plant biomass in Swedish grasslands without impairing plant diversity, but they can only partly mitigate negative drought effects. *Manuscript*
- III** Roth, N., Kimberley, A., Guasconi, D., Hugelius, G. & Cousins, S.A.O. (2023).  
Floral resources in Swedish grasslands remain relatively stable under an experimental drought and are enhanced by soil amendments if regularly mown. *Ecological Solutions and Evidence*, 4, e12231.  
<https://doi.org/10.1002/2688-8319.12231>
- IV** Roth, N., Baxter, R., Furness, M., Kimberley, A. & Cousins, S.A.O. Experimental warming outside the growing season and exclusion of grazing has a mild effect on upland grassland plant communities in the short-term. *Under review in Plant Ecology & Diversity*

## Author contributions to each paper

- I** Conceived and designed the study: FJ, SAOC, **NR**, LW-E  
Collected the data (literature review): **NR**, FJ, LW-E, DZ, SP-Á  
Analysed and visualised the data: **NR**  
Wrote the paper: **NR**. All co-authors contributed critically to the manuscript drafts.
- II** Conceived and designed the study: GH, SAOC, SM, **NR**, DG  
Collected the data (field and lab work): **NR**  
Analysed and visualised the data: **NR**, AK  
Wrote the paper: **NR**. All co-authors contributed critically to the manuscript drafts.
- III** Conceived and designed the study: **NR**  
Collected the data (field work and from database): **NR**  
Analysed and visualised the data: **NR**, AK  
Wrote the paper: **NR**. All co-authors contributed critically to the manuscript drafts.
- IV** Conceived and designed the study: RB, SAOC, **NR**, MF  
Collected the data (field work): **NR**, MF, RB, SAOC  
Analysed and visualised the data: **NR**, AK  
Wrote the paper: **NR**. All co-authors contributed critically to the manuscript drafts.



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# **1 Grasslands and climate change**

## **1.1 Northern European grasslands – values, history, threats**

Grasslands are one of the largest terrestrial biomes, covering ca. 40% of the Earth's land surface (O'Mara, 2012). They provide many ecosystem services, such as food for both wild animals and for livestock, pollination, erosion prevention, recreation, and carbon storage (O'Mara, 2012; Tälle et al., 2016; Bengtsson et al., 2019). In addition to these ecosystem services, grasslands can harbour a high biodiversity of both plants and animals (Tälle et al., 2016; Dengler et al., 2020). Some traditionally managed grasslands are extremely species-rich, especially on a small scale (Wilson et al., 2012), providing habitat for many specialized plants that exist only in grasslands with specific environmental conditions and management history (Habel et al., 2013).

Grasslands can be either of natural origin (shaped by natural disturbances or climates not suitable for woody vegetation) or result from human activities (Tälle et al., 2016). In Europe, most grasslands are a consequence of human land use, such as mowing for haymaking or grazing with livestock (Habel et al., 2013). However, these traditional low-intensity management practices became less and less economically viable during the nineteenth century due to the modernisation of agriculture (Poschlod & WallisDeVries, 2002; Bucharová et al., 2012). Changing agricultural practices meant that many grasslands were either subject to intensification (e.g. by draining them or adding synthetic fertilizers), transformed to arable fields or plantation forests, or were simply abandoned and left to natural succession. This caused a steep decline of grasslands in Europe, both in terms of area and biodiversity (Pärtel et al., 2005; Kahmen & Poschlod, 2008; Habel et al., 2013; Cousins et al., 2015; Tälle et al., 2016; Dengler et al., 2020). Some ancient grasslands that had been converted to agricultural fields have later been transformed back into grasslands. However, such former arable fields only have a fraction of the species richness of an ancient grassland.

Alongside other key global change drivers, such as habitat loss, nitrogen deposition and invasive species, climate change is likely to have an important influence on ecological processes in grasslands (Stevens et al., 2004; Habel et al., 2013; Bardgett et al., 2021). Understanding climate change effects on different grassland plant communities is therefore key to ensure continued ecosystem service provision and biodiversity protection in remaining grassland habitats. Furthermore, since many grasslands are subject to regular human management activities, it is important that management practices properly consider ongoing pressures which ecosystems might be under (Cousins & Eriksson, 2001; Kapás et al., 2020). In my thesis, I focus on former arable fields in Sweden, which are now mown and grazed by deer, and on upland grasslands in the UK, which are grazed by sheep and rabbits. These two different types of grasslands represent examples of anthropogenically-shaped habitats which are of conservation interest and are under threat from environmental change.

## **1.2 Complexity of climate change effects**

Anthropogenic climate change includes alterations of mean temperature and precipitation, and an increased frequency and severity of extreme events such as droughts, heavy rainfall, heatwaves or storms (Seneviratne et al., 2012; Cook

et al., 2020; IPCC, 2023). The effects of extreme events on ecosystems are expected to be equally, if not more severe than gradual changes in mean temperature and precipitation (Easterling et al., 2000; Jentsch et al., 2007; Smith, 2011b; Beier et al., 2012; Ummenhofer & Meehl, 2017). Effects of extreme events on plants include for example mechanical damage, physiological stress, reduced fitness and mortality at an individual level, species loss and abundance shifts on a population level, changes in species composition on a community level, and alterations in productivity and nutrient cycling on an ecosystem level (Felton & Smith, 2017). However, plant responses to extreme events are highly variable at the individual and population levels, which hampers the scaling-up of processes to the community and ecosystem levels (Felton & Smith, 2017).

### **Drought events in summer...**

During summer, grasslands may be more sensitive to changes in soil moisture than temperature, since they are strongly water-controlled systems (Byrne, 2012; Moeslund et al., 2013). Summer droughts can affect both aboveground plant biomass as well as plant community composition (Schwalm et al., 2017; Wilcox et al., 2017; Liu et al., 2021). Plant biomass usually decreases during droughts, but can recover relatively quickly within several months to a few years (Tilman & El Haddi, 1992; Jentsch et al., 2011; Mariotte et al., 2013; Hoover et al., 2014; Isbell et al., 2015; Stampfli et al., 2018; Mackie et al., 2019). However, regarding plant community composition, droughts can induce long-lasting changes (Tilman & El Haddi, 1992; Stampfli & Zeiter, 2004; Stampfli et al., 2018; Liu et al., 2021). In response to drought, plant communities can change in terms of their phenology, taxonomic and functional composition (De Boeck et al., 2018). This can have subsequent effects on other taxa, for example changes in the flowering phenology, nectar production or taxonomic composition of plant communities can cause a lack of floral resources for pollinating insects (Brown et al., 2016; Descamps et al., 2021), which is one of the main reasons why insect pollinators are declining (Carvell et al., 2006; Goulson et al., 2015; Dicks et al., 2021).

In my study area in Sweden, an increase in both temperature (more in winter than in summer) and precipitation (in every season) is predicted (Swedish Meteorological and Hydrological Institute, 2023). Even though precipitation is expected to increase in Scandinavia in general, due to a poleward shift of circulation patterns, droughts are likely to become more frequent and severe, especially in eastern Svealand (and Götaland) where my study area is located (Swedish Meteorological and Hydrological Institute, 2019). Subject to uncertainties in the trend (IPCC, 2023), northern Europe seems to be in the process of changing from ca. 60 years of drought decrease towards a drought increase in the future, particularly in Scandinavia (Spinoni et al., 2018). For example in summer 2018, a long period of warm temperatures and little precipitation led to a prolonged drought over large parts of northern Europe, which had severe consequences for people (e.g. health problems, excessive mortality rate) and the environment (e.g. forest fires, water shortages in arable land and pastures, lack of animal fodder) (Wilcke et al., 2020). The probability of such a summer occurring in Sweden has strongly increased in the recent past (comparing 1861-1890 with 1989-2018) (Wilcke et al., 2020). To summarize, droughts have not been a prominent problem in Sweden in the past, but they are likely to become so in the near future.

### **...warmer temperatures in winter...**

The rate of warming is greater in winter than in summer in central and northern Europe (European Environment Agency, 2014; Xia et al., 2014). Higher temperatures in winter can prolong the growing season and reduce snow cover, thereby increasing the risk of frost damage, which has direct effects on grassland plant communities (Inouye, 2008;



Bokhorst et al., 2009; Williams et al., 2015; Fridley et al., 2016; Liu et al., 2018; Kreyling et al., 2019). Furthermore, physical soil properties and ecological processes such as microbiological activity or nutrient cycling can change with winter warming, which can indirectly affect grassland vegetation (Edwards et al., 2007; Kreyling et al., 2011). For example species- or growth form-specific differences in nutrient uptake and productivity can lead to changes in plant community composition (Kreyling et al., 2011). Overall, warming during winter stimulates grassland ecosystem processes more than during summer (which is often water-limited rather than temperature-limited) (Schuerings et al., 2013). Yet, ecological effects of winter warming are not well understood, since most studies have been performed during the growing season (Kreyling, 2010; Williams et al., 2015).

The average temperature in the British Uplands, of which my study area is a part, has increased by 1.2 °C compared to only 0.7 °C in the lowlands between 1993-2007 (Morecroft et al., 2009). During this time the total annual precipitation has also increased (no differences between uplands and lowlands) (Morecroft et al., 2009). The temperature increase in the British Uplands was stronger in winter than in summer (Burt & Holden, 2010). In line with that, air frosts have been found to decrease (Pepin et al., 2009; Holden & Rose, 2011) and the yearly snow cover has declined in Great Britain since 1960, especially in mountain areas in northern England (Brown, 2019). Also in my study area, on Widdybank Fell, the minimum temperatures have increased by 0.38 °C per decade between 1968 and 2006 (Pepin et al., 2009). Since many of the British Uplands have mean winter temperatures close to 0 °C (Burt & Holden, 2010), even a slight increase in temperature could have pronounced consequences on the local ecosystems (Henry, 2008; Holden & Rose, 2011).

#### **...and inconsistent definitions all contribute to the complexity of climate change effects**

Adding to the complexity of understanding climate change effects on ecosystems are the inconsistent definitions of relevant terms. For example ‘wetter’ and ‘drier’ can describe a broad range of hydroclimatic variables such as precipitation, soil moisture or run-off (Trenberth, 2011; Dirmeyer et al., 2016). Also the word ‘drought’ has different meanings in meteorology, hydrology and agriculture (Dracup et al., 1980; Wilhite & Glantz, 1985; Hisdal & Tallaksen, 2000). Even within the same research field, in this case ecology, ‘droughts’ can be characterized in many different ways by different researchers (Slette et al., 2019). Similar to those hydroclimatic terms, the manifold meanings of ‘temperature’ (e.g. maximum, minimum, mean, length of growing season) can explain diverse effects on plants, such as freezing can impact plants within minutes (extreme temperatures), while gradual changes of temperature over months may alter plant metabolism (Graae et al., 2018; Körner & Hiltbrunner, 2018). An important step for being able to compare and generalize climate change effects on ecosystems is to clearly define relevant terms. In my experiments as part of this thesis, I defined ‘summer drought’ as a precipitation reduction between early April until late October and ‘winter warming’ as a surface temperature increase between mid-September until mid-May (both treatments are described in more detail in chapter 4.2).

## 1.3 Climate-smart grassland management

### **We can adapt conventional grassland management...**

In order to ensure that ecosystem services and biodiversity are maintained it may be necessary to modify conventional practices, such as mowing and grazing, in terms of intensity, timing and duration. For example warming-induced increases of plant biomass and shifts in plant community composition can be buffered by higher grazing pressure (Klein et al., 2004; Post & Pedersen, 2008; Wang et al., 2012; Y. Zhang et al., 2015). Positively phrased, a higher productivity in European grasslands under climate warming can lead to a higher grazing capacity and longer grazing seasons (Chang et al., 2017). In the event of drought on the other hand, management intensity and duration might need to be reduced to avoid overgrazing of land which has become less productive (Loeser et al., 2007; Deléglise et al., 2015). Loeser et al. (2007) suggest that an intermediate level of grazing intensity during drought may maintain native plant diversity better than short-term high-intensity grazing or no grazing at all. Comparing mowing with grazing, Deléglise et al. (2015) observed that productivity loss under drought was twofold higher in grazed grasslands than in mown grasslands, which could be explained by the more frequent defoliation under grazing compared to mowing. Furthermore, management history can determine grassland responses to climate change, such that intensively used grasslands might be more vulnerable to climate change. Vogel et al. (2012) found that frequent mowing reduced the resistance of grassland biomass against droughts, and Grime et al. (2000) found that a fertile grassland was more responsive than an infertile grassland to simulated climate change (winter warming and summer drought and additional summer rainfall) in terms of plant biomass and composition. Even in cases where the productivity response to climate change is not altered by land-use intensity, the community composition can be. For example Stampfli et al. (2018) found that drought-induced declines of forbs were exacerbated by increasing land-use intensity. In conclusion, climate-change induced effects on grasslands can determine the way grassland management should be adapted, and previous grassland management can influence the way climate change affects the vegetation.

### **...and try new methods**

In addition to adapting existing grassland management practices, there are novel approaches which aim to increase carbon sequestration in grasslands. Globally, grasslands store ca. 30% of the terrestrial soil organic carbon (Harden et al., 2018) and this carbon storage could be further increased by a variety of methods such as fertilization, improved grazing management, conversion from arable fields or leys to permanent grasslands, or sowing of legumes (Conant et al., 2001; Jones & Donnelly, 2004; O'Mara, 2012; Harden et al., 2018). Therefore, grasslands could play a key role in climate change mitigation (O'Mara, 2012). Grasslands that have been depleted of soil organic carbon, for example because of poor management practices, have the greatest potential for carbon sequestration (Smith, 2014; Harden et al., 2018). One way to add more carbon into grassland ecosystems is to apply soil amendments, such as compost or biochar (Ryals & Silver, 2013; Paustian et al., 2016). This has been tested in two Californian grasslands (see Box 1) but is novel to European grasslands. Besides mitigating climate change through carbon sequestration, soil amendments furthermore increase the soil organic matter content, which can help to retain and supply plant nutrients, decrease bulk density, improve soil aggregation, reduce erosion and enhance the water holding capacity of soils (Henderson et al., 2015). These long-lasting positive effects of soil amendments might serve to buffer negative effects of drought on grasslands (Ryals & Silver, 2013; Henderson et al., 2015). However, soil amendments might have negative side effects, such as nitrogen altering plant communities and biodiversity.

#### Box 1: Marin Carbon Project in California

In the Marin Carbon Project (<https://marincarbonproject.org/>), soil amendments in the form of compost (ca. 7 kg dry compost per m<sup>2</sup>) were added to two Californian grasslands in 2008 with the aim to increase net primary productivity (i.e. aboveground plant biomass) and carbon storage, and decrease greenhouse gas emissions from organic waste management (Ryals & Silver, 2013). Even just this single application of compost increased the net ecosystem carbon storage by 25-70% after three years (Ryals & Silver, 2013). The compost induced a long-term increase in plant productivity (Ryals & Silver, 2013), without greatly changing plant communities (Ryals et al., 2016). Compost with organic nitrogen might therefore not alter plant communities as much as synthetic nitrogen fertilizers are known to do, thus avoiding negative effects on plant diversity (Ryals et al., 2016). However, the grasslands in this experiment differ from European grasslands in terms of plant communities, land use, and climate. It is therefore unclear if applying compost to Swedish grasslands would yield the same results as in California.

## 2 Knowledge gaps and study aims

### Summary

To address the need to understand the consequences of key seasonal climate change effects on grassland plant communities, I studied how summer drought and winter warming affect grassland plants, and how we can adapt grassland management (including a novel method) to mitigate potential negative climate change effects on plant biomass and biodiversity (Fig. 1).

### In more detail

Inconsistent definitions add to the complexity of climate change effects and can lead to low confidence in predictions (because the inferred trends depend on the choice of definition) (IPCC, 2014). My first study aim was therefore to get an overview of how the terms ‘wetter’ and ‘drier’ are defined in climate change studies in different environmental research fields, in order to contextualise my later experiments and help evaluate results across previous studies. My second aim was to study seasonal distinct climate change effects on grasslands plant biomass and biodiversity. I chose two study areas that differ in their ecologically most relevant climatic changes. On the one hand, I aimed to investigate summer drought effects in Swedish grasslands (former arable fields), where water stress has not been a severe problem in the past, but droughts are predicted to become more frequent and severe in the near future (Spinoni et al., 2018). It is therefore important to better understand drought effects on local grassland ecosystems. On the other hand, I also studied winter warming effects in grasslands in the UK (upland sheep-grazed grasslands), where winter temperatures are close to 0 °C (Burt & Holden, 2010), which means that only a slight increase in temperature will have strong effects on the vegetation. Hence, it is urgent to understand potential effects on grassland plant biomass and diversity. In general, most climate change studies in grasslands have been performed during the growing season (Kreyling, 2010), which is why I wanted to contribute to filling the knowledge gap about climate change effects during winter. My third study aim was to find appropriate management methods. Since the optimal management practice from the past might not be the best choice in the future in the face of climate change (Bucharová et al., 2012), I tested different grazing

and mowing levels in combination with winter warming and summer drought. The management practices I studied also included one that is novel to European grasslands, namely soil amendments. As climate and management effects can be non-additive (Klein et al., 2007), multi-factor experiments on the combined effects of climate change and grassland management like mine have been suggested to provide useful insights (Li et al., 2018).

My overarching research questions for each paper were:

- ‘Drier’ and ‘wetter’ – how are these terms defined in climate change studies? I
- How will plant biomass and plant communities change with summer drought, soil amendments and both treatments combined? II
- How will the quantity and continuity of floral resources change with summer drought, soil amendments and both treatments combined, depending on the grassland mowing regime? III
- Does winter warming increase plant biomass, favouring mainly competitive species, and can sheep grazing buffer negative winter warming effects on plant communities? IV

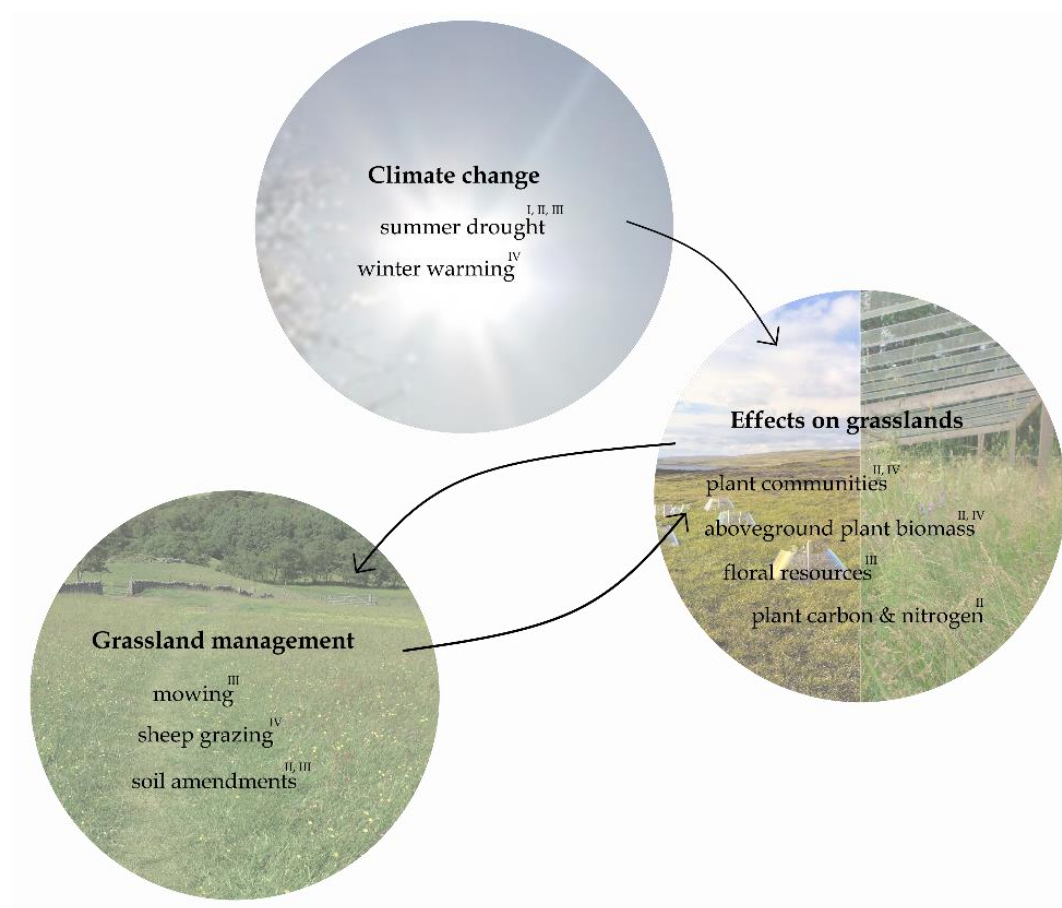


Figure 1: Graphical summary of my thesis. Roman numerals indicate my papers which are listed in the beginning of this thesis.

### 3 Study areas

I set up two *in-situ* experiments: one for studying effects of summer drought, soil amendments and mowing on plant communities in four Swedish grasslands (Tovetorp), and the other one for investigating effects of winter warming and sheep grazing in three British Upland grasslands (Teesdale).

#### 3.1 Tovetorp, Sweden

Tovetorp is located in the county of Södermanland in southern Sweden (Fig. 2). The mean annual precipitation in Södermanland was ca. 500 mm and the mean annual temperature ca. 6.5 °C between 1991 and 2020 (Swedish Meteorological and Hydrological Institute, 2022). The grasslands of this experiment are former arable fields on silty clay that have been converted into grasslands in the early 1990's and since then have been extensively managed for hay and grazing. They represent typical Swedish grasslands regarding their current and historic land use and their vegetation characteristics. The four grassland sites of this study (Fig. 2) are situated in two areas, Tovetorp and Ämtvik, and there are slight differences among the four sites. The sites in Ämtvik are surrounded by trees, whereas the sites in Tovetorp are not shaded. Moreover, the sites in Ämtvik have a higher proportion of forbs and have been mainly grazed by cows, compared to the sites in Tovetorp that have been mainly mown. In each area, the sites are paired into a higher elevation and lower elevation site to capture different ground water levels.

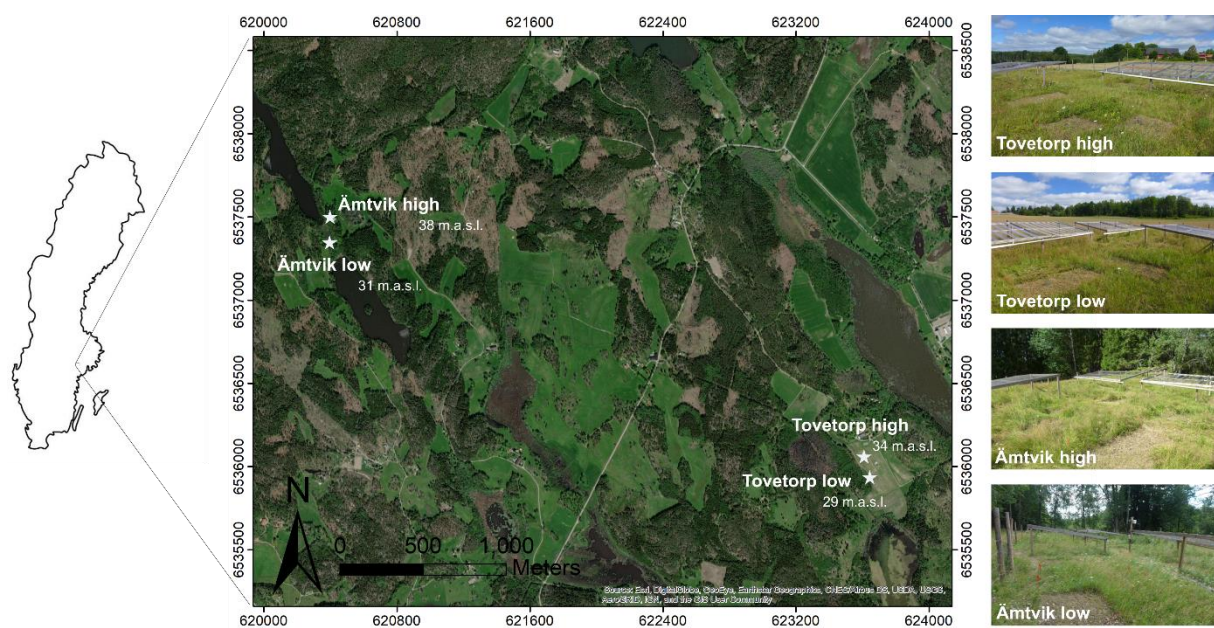


Figure 2: Satellite image of my study area Tovetorp in southern Sweden. The four grassland sites are paired into a higher elevation ('high') and lower elevation ('low') in both Tovetorp and Ämtvik (indicated by white stars). The image was created using ArcGIS® software (Esri et al., 2021). Coordinates are given in SWEREF99. The photos on the right side show the vegetation of each site and the rain-out shelters used to simulate summer drought (Photos: N. Roth).



### 3.2 Teesdale, UK

The study area in Teesdale is located in County Durham in northern England (Fig. 3). The area is part of the Moor House-Upper Teesdale National Nature Reserve. The mean annual precipitation in Moor House was 2012 mm and the mean annual temperature 5.3 °C between 1959 and 2006 (Burt & Holden, 2010), with average wind speeds of 7.3 m/s which often exceeded 10 m/s during winter, measured between 1968 and 1995 on Widdybank Fell (Pepin et al., 2009). The grasslands of my experiment are located on metamorphosed limestone (Pigott, 1956; Johnson et al., 1971) and they have been grazed for centuries (Gilbert et al., 1978), nowadays by free roaming Swaledale sheep and wild rabbits. Teesdale is known for its unique flora, which combines disjunct populations of species at their northern range limit in the UK (e.g. *Helianthemum oelandicum* and *Hippocrepis comosa*) as well as at their southern range limit (e.g. *Bartsia alpina* and *Dryas octopetala*) (Bellamy et al., 1969; Squires, 1971; Turner et al., 1973; Bradshaw, 2023). Some of these locally rare species are relics of a flora that used to be widespread in Britain at the end of the Ice Age ca. 12-15000 years ago (Turner et al., 1973; Squires, 1978; Bradshaw, 2023). Cold winter temperatures have been an important factor restricting biomass growth in my study area (Manley, 1942; Pigott, 1956). With increasing winter temperatures, some plant species can continue to grow during a longer period of the year, potentially suppressing the ‘Teesdale rarities’ because these diminutive plants are light-demanding and sensitive to competition (Squires, 1978; Bradshaw, 2023).

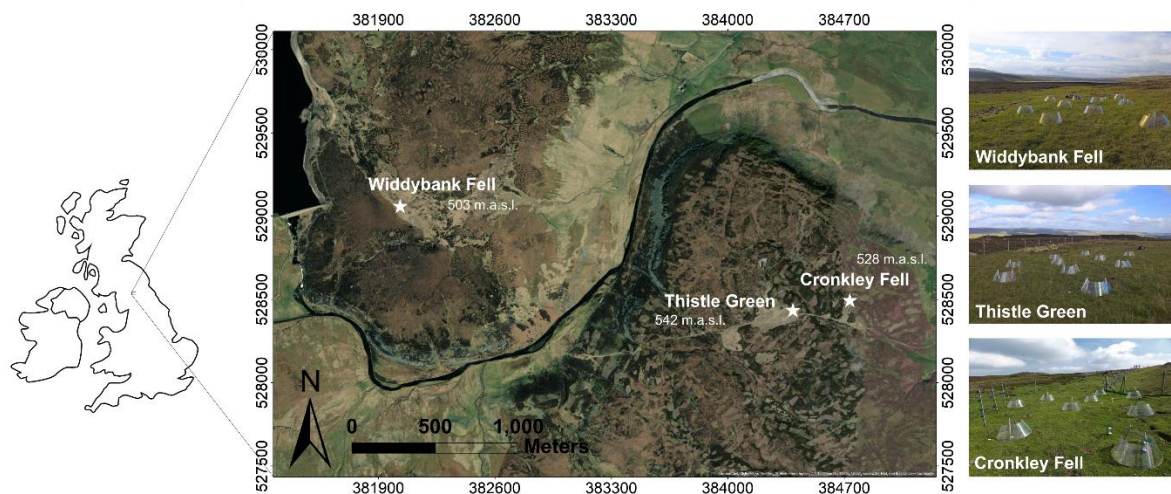


Figure 3: Satellite image of my study area Teesdale in the UK. The three grassland sites are located on Widdybank Fell, Thistle Green, and Cronkley Fell (indicated by white stars). The image was created using ArcGIS® software (Esri et al., 2021). Coordinates are given in the British National Grid. The photos on the right side show the vegetation of each site and the open-top chambers used to simulate winter warming (Photos: N. Roth).  
Reproduction of Figure 1 in **Paper IV**.

## 4 Methods

### 4.1 Literature review

I started my PhD project with a literature review about how different environmental research fields define the terms ‘wetter’ and ‘drier’ in climate change studies (**Paper I**). In the search engine Scopus, I searched for the keywords ‘drier’, ‘wetter’ and ‘climate change’ in articles that were published between 2012 and 2017 under the two subject areas ‘Agricultural and Biological Sciences’ and ‘Earth and Planetary Sciences’. This search string returned 487 articles of 18 research fields, grouped according to CiteScore. For each of these articles, I determined how many and which hydroclimatic variables the authors referred to when using the terms ‘drier’ and ‘wetter’ (it could be none, one or several). I also extracted information on the temporal and spatial scales of the studies. I presented the different hydroclimatic variables used to describe ‘wetter’ and ‘drier’ and how this varies depending on the research field, the temporal and spatial extent of the study, and the number of variables used per study.

### 4.2 *In-situ* experiments

#### 4.2.1 Experimental setup

Both *in-situ* experiments were set up as full factorial designs. In Tovetorp, this includes three factors (presence or absence of ‘summer drought’, ‘soil amendments’, and ‘mowing’) set up in 48 plots of 2x2 m (12 replicates per treatment), blocked into four sites. In Teesdale, two environmental factors were controlled (presence or absence of ‘winter warming’ and ‘sheep grazing’) in 60 plots of 25 cm in diameter (15 replicates per treatment), blocked into three sites. In order not to harm the ‘Teesdale rarities’, I did not set up my experiment where they actually grow, but nearby in the same area. Pictures of the sites can be seen in Fig. 2 and 3 and sketches of the experimental layouts in Fig. 4. The drought experiment in Tovetorp was built together with another PhD student, Daniela Guasconi, who studied belowground effects of the same environmental treatments.

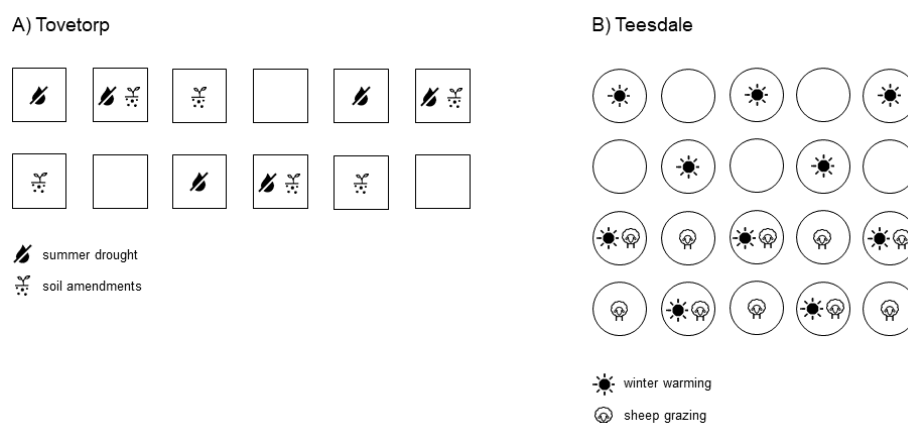


Figure 4: Sketches showing the experimental layouts of one site in A) Tovetorp and B) Teesdale. The sites are replicated four times in Tovetorp and three times in Teesdale. The plot size in Tovetorp is 2x2 m and in Teesdale 25 cm in diameter. The treatments are described below and more details on the experiments can be found in **Paper II, III, and IV**. The mowing treatment is not depicted, but described below, and in **Paper II and III**. Plots without treatment symbols are controls.



### Summer drought (Tovetorp)

Since droughts are an emerging problem in Sweden, as mentioned above, we set up twelve rain-out shelters in Tovetorp in July 2019. These rain-out shelters simulate a local 1-in-100-year drought and they were built in line with the protocol of the Drought-Net Research Coordination Network (Yahdjian & Sala, 2002; Knapp et al., 2017). Polycarbonate strips mounted on wooded structures covered 58% of the roof area. Pictures of the rain-out shelters can be seen in Fig. 2 and more details can be found in **Paper II and III**. Since my focus is on drought effects during the growing season, the polycarbonate strips were taken off over the winter, meaning that the rain-out shelters were in place only from early April until late October each year.



### Soil amendments (Tovetorp)

In order to increase carbon sequestration and to buffer potential negative drought effects on typical, not particularly species-rich Swedish grasslands, we tested soil amendments (i.e. compost) as a novel management method. We applied compost made of maize (*Zea mays*) as a single application on half of all plots (**Paper II and III**). The maize was harvested in September 2019 and composted until late January 2020. In mid-February 2020, we applied ca. 11 kg wet compost per m<sup>2</sup> as an even layer on the grasslands, inspired by the Marin Carbon Project (see Box 1) (Ryals & Silver, 2013). The compost had a carbon (C) to nitrogen (N) ratio of 9.78, a carbon isotope ratio ( $\delta^{13}\text{C}$ ) of -15.39‰ and a nitrogen isotope ratio ( $\delta^{15}\text{N}$ ) of 2.90‰.

### Mowing (Tovetorp)

In Tovetorp, I cut one quarter of each plot (1x1 m out of 2x2 m) every year to mimic grassland management for hay/silage harvest, whereas the other three quarters I cut only once during the experiment. This resulted in treatments of 2, 3, and 4 years of growth without mowing (**Paper II and III**). My mowing treatment differed from normal mowing management for hay or silage as I cut the biomass at ground level and removed litter and bryophytes, in order to measure biomass.



### Winter warming (Teesdale)

To simulate winter warming, I built 30 open-top chambers in September 2019 which can be seen in Fig. 3. Their design was inspired by the International Tundra Experiment (Marion et al., 1997). Chambers were cone-shaped and made of polyethylene terephthalate glycol sheets. They were in place from mid-September until mid-May for three winters to capture the entire period outside of the growing season (Manley, 1942). More information can be found in **Paper IV**.



### Sheep grazing (Teesdale)

The grasslands in my study area have been grazed for centuries, which promoted plant diversity and in particular the short-statured ‘Teesdale rarities’ (Gilbert et al., 1978; Squires, 1978; Bradshaw, 2023). The Nature Reserve where our study site is located, is grazed by Swaledale sheep (ca. 100 sheep per km<sup>2</sup> from 15<sup>th</sup> May to 1<sup>st</sup> November and less than 25 sheep per km<sup>2</sup> from 2<sup>nd</sup> November to 14<sup>th</sup> May) and by wild rabbits. Since it was unfeasible to experimentally increase the grazing pressure in our study sites, we reduced it instead, in order to manipulate the current grazing regime (**Paper IV**). We set up an electrical fence on each site that excluded sheep (but not rabbits) from half of the sites, see



Fig. 4. The fences were in place between mid-May and mid-September each year. For the rest of the year, the fences were re-arranged so that they encompass the entire sites in order to protect the open-top chambers from animal destruction (there is relatively little grazing activity during winter).

#### 4.2.2 Measurements

In the two experiments described above, I took the following measurements:

- ❖ I recorded the plant community composition of each plot before and after both experiments, i.e. in 2019 and 2022 (**Paper II and IV**). By observing changes in plant communities, I was able to see which species are increasing/decreasing and how plant diversity was affected by our treatments. I visually estimated the cover of each vascular plant species to the nearest 1%. Species that I could not clearly identify because they were grazed or in an early development stage, I grouped to genus level. In Tovetorp, I estimated the aerial cover independently for each species and at different times of the growing season when the respective species had reached its maximum cover, therefore the summed plant cover per plot usually exceeds 100%.
- ❖ I cut the aboveground plant biomass at ground level and collected litter and bryophytes (**Paper II and IV**). The aboveground plant biomass represents how much fodder is available for livestock. I further sorted the collected biomass into the following plant functional groups: graminoids (in Teesdale divided into *Sesleria caerulea* and other graminoids), non-leguminous forbs, legumes, bryophytes, lichens, and litter. The biomass was dried at 60 °C for at least 48 hours before I weighed the dry biomass. This data was used to directly assess the response of biomass in different species groups to the climate/management manipulations, and to compare the responses across the two *in-situ* experiments.
- ❖ In Tovetorp, I counted the floral units in all plots nine times during the 2021 flowering season (between when the first and the last plant flowers; **Paper III**). Floral units are defined as one or multiple flowers that can be visited by a small pollinator (ca. 1 cm long) without having to fly in-between (Carvalho et al., 2008), and it is the common entity to work with in pollination ecology. If the floral units consisted of more than one flower per unit, I counted the number of flowers per floral unit in the field (mean number of open flowers of 10 floral units per species). Based on an existing database (Baude et al., 2016), I derived nectar values for the floral units in order to estimate the amount of nectar that the plant communities provide for pollinating insects. This is important because a lack of nectar is one of the main reasons why insect pollinators are declining. By multiplying the nectar value per flower with the mean number of flowers per floral unit, I calculated the mean nectar sugar production per floral unit ( $\mu\text{g}/\text{floral unit}/\text{day}$ ), which allowed me to assess how the quantity and continuity of floral resources change with the experimental treatments.
- ❖ In Teesdale, I measured the length of the 10 longest leaves of *Sesleria caerulea* in each plot from base to tip, before and after the experiment (**Paper IV**). Only healthy and fully developed leaves were included. *Sesleria caerulea* is known as a particularly competitive species in this study area that has a wide ecological tolerance and can form dense litter layers suppressing other plant species (Lewthwaite, 1999). One indicator trait for its competitiveness is

leaf length (Craine & Dybzinski, 2013). This allowed me to see if winter warming in areas with winter temperatures close to 0 °C favours competitive species, and to draw conclusions on the future of the local ‘Teesdale rarities’.

- ❖ In Tovetorp, I further analysed the C:N ratio of the dry biomass, which can serve as an indicator for its nutritional value (Jentsch et al. 2011; Ryals et al. 2016), carbon isotope ratios ( $\delta^{13}\text{C}$ ) as a proxy for water use efficiency (Farquhar et al. 1989; Snyder et al. 2022) and nitrogen isotope ratios ( $\delta^{15}\text{N}$ ). Interpretation of changes in  $\delta^{15}\text{N}$  is difficult (Craine et al., 2015; Snyder et al., 2022), but in general it reflects N cycling and plants become enriched in  $\delta^{15}\text{N}$  as N availability increases (Dawson et al., 2002; Craine et al., 2015). I prepared samples from each plot and plant group (graminoids, non-leguminous forbs, legumes) from 2019 and 2022, and from *Achillea millefolium* in 2022 (in order to compare the C and N data within one species). The samples were further analysed by the Stable Isotope Facility (University of California, Davis). More details can be found in **Paper II**.
- ❖ In order to monitor how my treatments affected soil moisture and temperature, we installed TOMST TMS-4 loggers (TOMST®, Prague, Czech Republic) which capture the microclimatic conditions experienced by grassland plants (Wild et al., 2019). The loggers were programmed to take measurements every 15 min. In Tovetorp, we additionally measured manually the volumetric soil moisture ca. every three weeks during the growing season down to 100 cm depth with a PR2 profile probe (Delta-T Devices Ltd ©, Cambridge, England). Data on the volumetric soil moisture can be found in **Paper II, III and IV** and on temperature in **Paper IV**.

## 4.3 Data analyses

To analyse the data for this thesis, I used the following approaches:

- ❖ Based on the plant community data, I calculated measures of plant species diversity and of community dissimilarity (**Paper II and IV**). Species diversity was assessed by calculating the Shannon diversity index, which reflects both species richness and evenness (Shannon, 1948). Community dissimilarity was assessed by calculating the Bray-Curtis index, which quantifies the compositional dissimilarity between two plots, based on how many individuals are unique to each plot relative to the summed number of individuals in both plots (Bray & Curtis, 1957).
- ❖ To analyse differences between treatments in aboveground plant biomass, Shannon diversity index, C:N ratio,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , *Sesleria caerulea* leaf length, floral units, and nectar quantity, I used linear mixed effect models (**Paper II, III and IV**). This allowed me to explicitly model the non-independent structure caused by my experimental setup (Zuur et al., 2009), even if the random effects had only few levels in my case (Gomes, 2022; Oberpriller et al., 2022). For calculating pairwise differences between factor levels, I applied the post-hoc Tukey’s test.
- ❖ To investigate nectar continuity over the growing season in Tovetorp, I fitted two generalized additive models, one for each mowing regime (**Paper III**). Generalized additive models are suitable for fitting smooth curves to non-linear data (Zuur et al., 2009). Based on the shapes of these curves I could interpret how the nectar quantity developed over time, and how it differed between treatments.

- ❖ I further analysed treatment effects on plant communities in both Teesdale and Tovetorp with a permutational multivariate analysis of variance, based on a Bray-Curtis dissimilarity matrix of the plant community data (**Paper II and IV**). Permutational multivariate analyses of variance are based on the geometric partitioning of variation across a multivariate data cloud (in my case dissimilarities between plant communities) in response to one or more factors (in my case the experimental treatments) (Anderson, 2017). To visualize dissimilarities between plant communities, I used non-metric multidimensional scaling (**Paper II**). This allowed me to see if the plant communities had become more similar or dissimilar over time depending on the experimental treatments.
- ❖ I used the program R (R Core Team, 2022) for all my statistical analyses. I applied the packages ‘car’ (Fox & Weisberg, 2019), ‘lme4’ (Bates et al., 2015), ‘lsmeans’ (Lenth, 2016), ‘mgcv’ (Wood, 2011), ‘rsq’ (Zhang, 2021) and ‘vegan’ (Oksanen et al., 2023) to analyse my data, and the package ‘ggplot2’ (Wickham, 2016) to create figures. I created the maps with ArcGIS® software (Esri et al., 2021) and graphical illustrations in Inkscape (Inkscape Project, 2020).

## 5 Results and implications

My results confirm that climate change effects are complex, starting with different definitions being used to describe the same words, but also when it comes to seasonally distinct aspects of climate change affecting grassland vegetation in sometimes antagonistic ways. For example graminoid biomass increased more than other plant groups with winter warming, but tended to decrease more than other plant groups with summer drought (**Paper II and IV**). This means that seasonally opposite climate change effects like this could level each other out to some extent. In both of my experiments, the reactions to land use and climate change were species-specific (**Paper II, III and IV**), highlighting the need to know species identity in such experiments. Plant communities did not change much in both experiments, indicating that summer drought and winter warming have little effect on community composition over an initial three years (**Paper II and IV**). This is not surprising considering that it can take several decades until community changes in response to land use and climate change become apparent (Chen et al., 2023). In general, my experiments are likely to underestimate the threats to plant biomass (Kröel-Dulay et al., 2022) and biodiversity (Chen et al., 2023), which is why I expect that under real summer drought and winter warming conditions the effects on grassland vegetation would be more severe.

### 5.1 Definitions in climate change studies

Regarding the terms ‘wetter’ and ‘drier’ in climate change studies, I found that ‘precipitation’ was the main variable that was used to describe these terms in all research fields except for Geology (**Paper I**). However, there were many more hydroclimatic variables that were mentioned to describe changes in water availability, such as ‘temperature’, ‘evapotranspiration’, ‘soil moisture’, ‘runoff’ and ‘proxies’ such as tree rings or lake sediments. Overall, there was no consistency in the use of the words ‘wetter’ and ‘drier’ among the research fields I examined, and most surprisingly the terms were sometimes not clarified at all. This can hinder the synthesis of results across disciplines. Learning from these findings, I made sure to clearly state in my **Papers II, III and IV** what type of ‘summer drought’ and ‘winter

warming’ treatments I applied in my experiments, namely a precipitation reduction during the growing season (simulating a local 1-in-100-year year drought) and an increase in surface temperature outside the growing season (simulating a locally realistic warming scenario). In a broader context, my work on the definitions of ‘wetter’ and ‘drier’ in climate change studies fits well to Slette et al. (2019) who highlighted varying definitions of ‘drought’ in ecological research, and into the general call for a common terminology within climate science (Bowman et al., 2009) and ecology (Herrando-Pérez et al., 2014). While it seems unreasonable to standardize the terms ‘wetter’ and ‘drier’ in climate change studies, because the research fields are so diverse, I emphasized the importance to explicitly state which hydroclimatic variables authors are referring to.

## 5.2 Summer drought, soil amendments and mowing

### Abiotic effects

In the drought experiment that we set up 2019 in four grasslands in Tovetorp, Sweden, I found that the rain-out shelters reduced the volumetric soil water content by ca. 24% (compared to the control plots), measured every three weeks during the growing season in the centre of each plot in the upper 30 cm (**Paper II**). The literature review (**Paper I**) sharpened my awareness that the precipitation exclusion in the Tovetorp experiment (58%) was higher than the volumetric soil water decrease we measured and this could differ again from how much water is available to the plants since that also depends on factors such as soil type, soil depth, seasonal distribution of rainfall, air humidity and temperature (Signarbieux & Feller, 2012; Moles et al., 2014; Kröel-Dulay et al., 2022). Since I was only able to manipulate precipitation in my experiment, my results are conservative representations of real drought conditions. In a real local 1-in-100-year drought event, I expect effects on grassland vegetation to be even stronger than in my experiment. Soil amendments did not increase the soil water content, neither could they buffer the drought-induced soil moisture decrease. This is contrary to what Ryals & Silver (2013) found in the Marin Carbon Project (see Box 1), where they observed a higher volumetric soil water content in the soil amendment plots compared to control. It may be that in our case, the increased plant growth and hence greater water requirement of the plant communities obscured positive compost effects on the soil water content (Baude et al., 2011). Our compost treatment did not significantly alter the calcium, magnesium, pH, phosphorus or potassium content of the soil. Bulk density decreased in the topsoil (upper 10 cm) in response to the compost treatment. Details on how the compost altered soil parameters and increased ecosystem carbon storage will be published in Guasconi et al. (*manuscript*).

### Effects on vegetation

In total, I found 63 vascular plant taxa (61 identified to species level and 2 to section level) in the experimental plots. These taxa showed only small changes in abundance in response to drought (**Paper II**). Also the plant communities as a whole did not differ significantly after three years of drought treatment – most of the variation between plant communities was explained by the four sites. The mild drought response is not surprising given the relatively short timeframe of our study and the fact that community reorganization in response to drought is thought to be driven mainly by competition rather than mortality (Stampfli et al., 2018). I observed a slight decrease in plant species diversity, which is in line with other grassland drought studies (e.g. Tilman & El Haddi 1992; Stampfli et al. 2018; Liu

et al. 2021). Given the increasing drought risk, this implies that plant diversity could decrease in Scandinavian grasslands in the future. Soil amendments did not buffer the abovementioned small changes in plant communities. However, since the primary reason for applying soil amendments is to increase carbon sequestration, my main finding is that they did not have detrimental effects on plant diversity, neither by themselves nor in combination with drought. I have graphically summarized the drought effects in Fig. 5A.

Regarding aboveground plant biomass, I found a non-significant tendency for it to decrease under drought (**Paper II**). In the combined drought and compost plots, the aboveground plant biomass remained similar to that seen in control plots, indicating that compost was able to buffer negative drought effects. Yet, given the fact that Ryals & Silver (2013) observed a consistent increase in productivity in response to soil amendments, despite a wide range in precipitation over the years, it is remarkable that in my case soil amendments alone increased biomass significantly more than in the combined treatment with drought. Despite drought not having a strong effect on its own, it seems to reduce the positive effect of soil amendments on biomass. One explanation for my finding could be that the fertilizing effect of our compost treatment aggravates drought effects on grassland productivity (Bharath et al., 2020; Meng et al., 2021; Van Sundert et al., 2021), and therefore levels out if both treatments are combined. Based on these results, I would still recommend the use of soil amendments, but one has to be aware that in the event of a drought they are likely to be less effective in terms of carbon storage and fodder production than in years with sufficient precipitation.

Looking at the plant groups separately, both graminoid and non-leguminous forb biomass non-significantly decreased under drought compared to the control (**Paper II**). Legume biomass did not react significantly or consistently to drought. The higher specific leaf area compared to other forbs (Van Sundert et al., 2021) and reduced nitrogen-fixation due to lack of soil moisture usually puts them at disadvantage under drought (Serraj et al., 1999; Kreyling et al., 2008; Daryanto et al., 2015; Mackie et al., 2019), but it has also been suggested that legumes and forbs can show more varied responses to droughts than graminoids (Zeiter et al., 2016). Looking at the biomass in terms of proportional changes, graminoids decreased more than forbs under drought (with and without compost). Graminoids have generally shallower roots than forbs (Zeiter et al., 2016; Van Sundert et al., 2021) thus forbs should be able to benefit from reduced competition of water-stressed graminoids during droughts (Grant et al., 2017). However, other European drought studies have found the opposite trend of graminoids increasing at the expense of forbs (e.g. Stampfli et al. 2018; Reynaert et al. 2021). In our case, a relative increase of forbs versus graminoids under drought means that plant communities could lastingly shift towards more forbs should droughts become more frequent in Swedish grasslands. Although plant diversity tended to decrease under drought (see above), a relative increase in forbs could have positive effects on other trophic levels, such as maintaining a stable nectar provision for pollinating insects (**Paper III**). Water use efficiency ( $\delta^{13}\text{C}$ ) was slightly higher under drought in all plant groups except graminoids, and the change in  $\delta^{13}\text{C}$  for *Achillea millefolium* was comparable to findings from a drought experiment in Switzerland (Mariotte et al., 2013) (**Paper II**). This elevated water use efficiency implies that the drought treatment, despite excluding only part of the precipitation and only during the vegetation period, caused the plants to be water stressed. It can be expected that plants will be even more water stressed under real drought conditions, since drought events are often coupled with higher temperatures and lower air humidity (Kröel-Dulay et al., 2022).

Regarding floral resources for pollinating insects, I recorded 37 flowering forb species during the sampling campaign in 2021 (**Paper III**). I found no significant drought effect on the amount of floral units in the abandoned plots,

however in the yearly mown plots there were significantly fewer floral units. This implies that grassland patches which are not mown/grazed each year can provide floral resources for pollinators in the event of a drought. Considering that droughts can disrupt plant-pollinator interactions (Descamps et al., 2021) and are seen as one of the major future threats to pollinators (Brown et al., 2016), this is an encouraging finding regarding the opportunity to maintain floral resources under drought by adapting the mowing regime. In combination with soil amendments, the number of floral units remained at levels similar to those seen in control plots, indicating that soil amendments were able to buffer negative drought effects. Unlike the number of floral units, the inferred nectar sugar production (I did not measure nectar production per se but retrieved values from a database) was not significantly affected by drought, irrespective of the mowing regime. This implies that it was mainly species with a low nectar production per floral unit that declined under drought, whereas key species with a high nectar production per floral unit remained stable or even increased with drought. The drought treatment caused a lower nectar sugar production during mid-summer compared to the control treatment (which soil amendments were able to reverse), but a higher production in late summer compared to all other treatments in the abandoned plots. This late nectar sugar production was mainly provided by *Lathyrus pratensis*, which implies that other plant communities without *Lathyrus pratensis* are likely to provide less floral resources during drought events. It is notable that most of the inferred nectar supply across all treatments was provided by only few species, with legumes contributing about half of all nectar (mainly *Lathyrus pratensis*, *Vicia cracca*, *Trifolium medium* and *Trifolium repens*). This highlights the key role of legumes in providing floral resources, both in terms of total amount and for specialized pollinators (Goulson et al., 2005), and it implies that their reaction to environmental changes will have strong subsequent effects on pollinating insects. This may be the case even if plant communities do not change in composition and diversity.

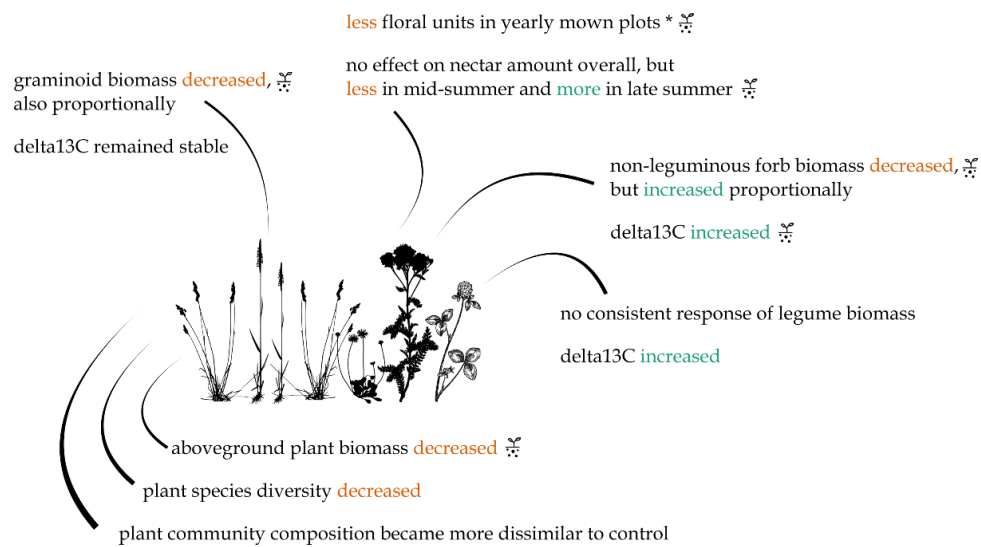
The plant communities did not change significantly in response to the soil amendment treatment alone (without drought) (**Paper II**). Slight changes that did occur pointed towards plant communities becoming more similar to the control plots, and towards an increase in plant species diversity (which is opposite to the drought effects described above). We can therefore confirm the findings of Ryals et al. (2016) that compost with organic nitrogen does not alter plant communities as much as fertilizers with inorganic nitrogen are known to do, and that compost amendments do not reduce plant diversity. This is a promising result regarding the application of soil amendments for carbon sequestration in grasslands without impairing biodiversity, potentially even increasing it. A graphical summary of the soil amendment effects can be seen in Fig. 5B.

Soil amendments alone, i.e. without drought, caused an increase in aboveground plant biomass (**Paper II**), which became stronger each year, when comparing the compost and control plots of the same year. Given that the compost was applied only once, it suggests a long-term effect which is in line with the results of the Marin Carbon Project (see Box 1), where they observed a persistent positive effect of biomass production over four years following a one-time compost application (Ryals et al., 2015). If compost was applied on grasslands on a larger scale, it could lead to a substantial and long-lasting increase in fodder production for livestock. While both graminoids and non-leguminous forbs (the latter non-significantly) increased in biomass with compost (**Paper II**), legumes increased (non-significantly) only in the first year after compost application but decreased in the following years, compared to the control of the same year. Also in terms of proportional biomass changes, legumes decreased slightly with compost. This could be an early warning sign that legumes might lose their competitive advantage of fixing atmospheric nitrogen if organic nitrogen is added to the soil. Legumes were also the only plant group that had a (non-significantly) lower  $\delta^{15}\text{N}$  in the compost plots compared to control, whereas  $\delta^{15}\text{N}$  was elevated in graminoids, non-leguminous forbs and *Achillea*

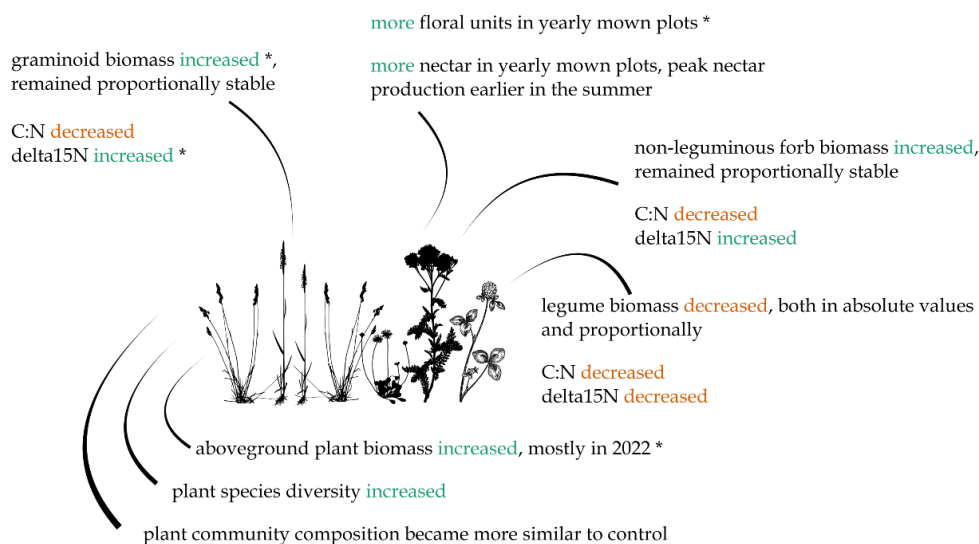
*millefolium* (the latter two groups non-significantly). I therefore see a risk that soil amendments could promote primarily graminoids and non-leguminous forbs, which could eventually outcompete legumes. Since legumes play a key role in plant communities (Felton & Smith, 2017), their decline might have subsequent effects on other plant groups. Moreover, it would have consequences for other trophic levels, since about half of the inferred nectar supply for pollinating insects in my study grasslands was provided by legumes, as described above (**Paper III**). The C:N ratio decreased non-significantly in the compost plots (with and without drought) in all plant groups except *Achillea millefolium* (**Paper II**). From an agricultural point of view, a higher biomass production coupled with a lower C:N ratio of the plant material suggests that compost can increase both fodder quantity and quality.

Soil amendments had an overall positive effect on the number of floral units and the nectar sugar production (non-significant) in the yearly mown plots (**Paper III**). It was mostly species associated to nutrient-rich grasslands such as *Anthriscus sylvestris* and *Cerastium fontanum* that increased their flower production, whereas other species produced fewer flowers, such as the legumes *Vicia cracca* and *Vicia tetrasperma*. Bearing in mind that legumes slightly decreased in biomass and  $\delta^{15}\text{N}$  (see above and **Paper II**), this finding adds to the signs of a detrimental effect of soil amendments on legumes. Since legumes are the major pollen source for most bumblebee species, especially for long-tongued bumblebees such as *Bombus humilis* or *Bombus ruderatus* that specialize in gathering pollen from legumes with deep corollae (Goulson et al., 2005), a decrease in legume flowers would further accelerate their decline. Interestingly, the individual species that increased or decreased their flower production in response to my experimental treatments (**Paper III**) did not show obvious changes in the plant community data (**Paper II**), which suggests that they adapt their resource allocation towards more or less flowers without changing much in abundance. The inferred nectar sugar production in response to soil amendments was shifted towards earlier in the season, which was mainly driven by *Anthriscus sylvestris*. As for the role of *Lathyrus pratensis* under drought (see above), this prominent role of just a single species implies that other plant communities are likely to show a different temporal pattern in response to soil amendments, and it highlights the key role of certain species.

## A) Summer drought



## B) Soil amendments



\* statistically significant

☄ soil amendments buffered drought effects to some extent

Figure 5: Graphical summary of my findings from an *in-situ* experiment in Tovetorp (Sweden), studying the effects of summer drought, soil amendments, and mowing in four grasslands between 2019 and 2022. Text in orange color indicates decreases, and in green color increases in the response variables.



## 5.3 Winter warming and sheep grazing

### Abiotic effects

The open-top chambers increased the surface temperature by 0.48 °C, measured every 15 min at ground level between September 2021 and May 2022 (**Paper IV**). Originally, we had installed more temperature loggers since the beginning of the experiment, however they turned out to be not reliable, which is why my measurements are restricted to the last winter during which I installed additional loggers. Most of the warming happened in autumn and spring, whereas the chambers had almost no warming effect during November, December and January. None of our experimental plots experienced soil frost during the winter we measured, and I detected no open-top chamber effect on soil moisture.

### Effects on vegetation

In total, I found 36 vascular plant taxa (31 identified to species level and 5 to genus level) in the experimental plots (**Paper IV**). Changes in plant communities in response to warming and grazing were overall small. Taxa that increased in abundance with winter warming were for example *Thymus polytrichus*, *Viola* spp., *Helianthemum nummularium* and *Sesleria caerulea*, the latter two species even more so if coupled with no grazing. Plant species diversity, as reflected in the Shannon diversity index, was not affected by winter warming apart from a slight increase in variability, which indicates that community shifts are happening but with no clear direction. Natural turnover between the survey years can contribute to these community shifts. A graphical summary of the winter warming effects on the vegetation can be seen in Fig. 6A.

Bryophyte biomass decreased, whereas graminoid biomass increased with winter warming (**Paper IV**). These biomass changes were broadly consistent between the two grazing treatments, indicating that grazing could not buffer warming induced changes. The biomass changes imply that with continuing winter warming, taller graminoids might outcompete bryophytes, which would be 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; Nüttynen et al., 2020). Also the leaves of *Sesleria caerulea* became non-significantly longer in the combined warming and no grazing plots (**Paper IV**). This could imply an increase in *Sesleria caerulea* with future climate scenarios if the grasslands are not grazed regularly, which is concerning because *Sesleria caerulea* is known as a particularly dominant grass species in our study area that can form dense litter layers (Lewthwaite, 1999). In my study area in particular, a longer growing season that promotes competitive graminoid species would have negative effects on the ‘Teesdale rarities’, since they are known to be sensitive to competition (Squires, 1978; Bradshaw, 2023). In a comparable experiment in upland grasslands in the UK, bryophyte cover had decreased (non-significantly) with winter warming, supporting my findings, however the response depended on the bryophyte species in question (Bates et al., 2005). Species-specific responses were also emphasized by several summer and all-year warming studies (Lett et al., 2022; van Zuijlen et al., 2022; Hollister et al., 2023). Since bryophytes can impede the germination and establishment of vascular plants by altering light and moisture conditions (Bates et al., 2005), changes in bryophyte cover can subsequently also alter the vascular plant community composition. In real life, the trends I observed will happen in parallel with other drivers such as nitrogen deposition, which is predicted to promote graminoids in British grasslands and to affect bryophytes in various ways depending on species identity (Stevens et al., 2016). This could amplify the changes that I found with subsequent effects on the entire plant community. With increasing winter temperatures in the British Uplands, I see the risk of graminoids

outcompeting other plant species and/or the possibility that open gaps due to reduced bryophyte cover will allow more vascular plants to germinate – both of these processes have the potential to lastingly alter the local plant communities.

The absence of sheep grazing (without warming) caused no significant effects on any of the vegetation parameters I measured (**Paper IV**). Partly, it can be explained by rabbits being present, which continued to graze even in the fenced areas where sheep were excluded. Also, the study period is fairly short and plant communities in the British Uplands have been shown to change very slowly when grazing is excluded (Alday et al., 2021). However, without grazing, plant diversity showed a tendency to decrease across both warming levels which highlights the need for continued grazing in these grasslands in order to maintain biodiversity. The summarized effects of excluding sheep grazing can be seen in Fig. 6B.

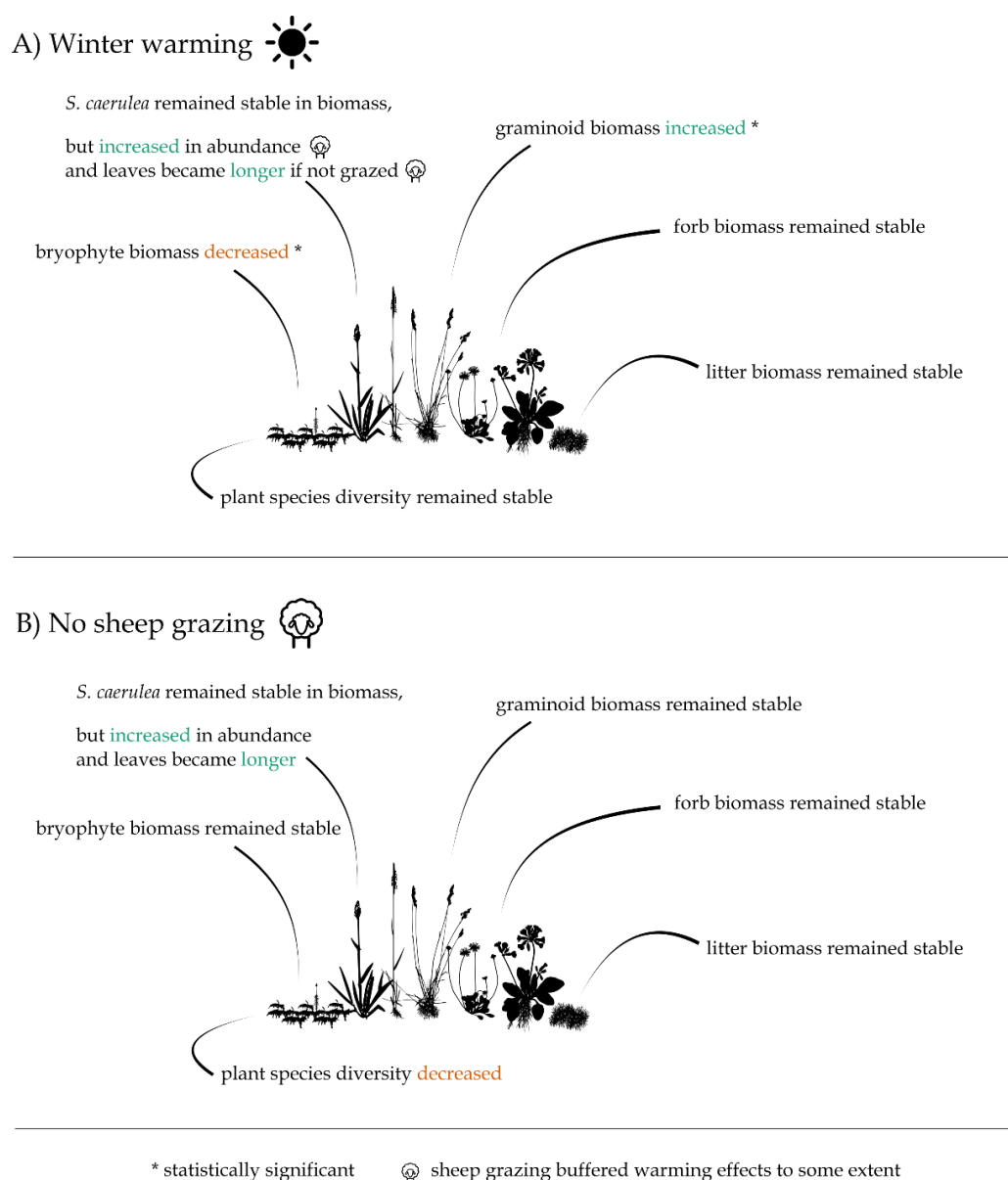


Figure 6: Graphical summary of my findings from an *in-situ* experiment in Teesdale (UK), studying the effects of winter warming and sheep grazing in three grasslands between 2019 and 2022. Text in orange color indicates decreases, and in green color increases in the response variables.

## 5.4 My research in a larger context

### How do my experiments compare to other study approaches?

In order to better understand plant responses to climate change, several study methods can be used, each coming with their own strengths and weaknesses. Observational studies are generally seen as useful to study changes in mean climate (as opposed to extreme events), to capture large spatial and temporal scales, to include many drivers, and they have the advantage of being realistic (Smith, 2011a; Adler et al., 2013; Reyer et al., 2013). However, they do not provide much mechanistic understanding because too many factors are involved and not all of them are measured. Moreover, they often lack replication. Modelling studies have their main strength in predicting future conditions, based on experimental or observational studies, but they can be restricted by their temporal/spatial resolution and by missing explanatory variables. Experimental studies like mine are considered suitable to simulate extreme events, to test individual mechanisms under controlled and novel conditions, and to gain mechanistic understanding, but they can only test a limited number of drivers, are imposed at small spatial scales, and they often have unrealistic artefacts which makes their translation into the ‘real world’ difficult. In my case, I was able to test novel conditions including the interactions between climate change and management (**Paper II, III and IV**), but I could not test all drivers simultaneously that would exist in reality. For example regarding droughts, field experiments like mine are known to underestimate responses of aboveground plant biomass, since a real drought would be typically coupled with less air humidity, higher temperatures and clear skies (Kröel-Dulay et al., 2022). This links back to my literature review on definitions in climate change studies (**Paper I**), meaning that depending on the variables used to define and simulate drought events, effects on plant biomass will differ. Regarding winter warming, the effects would in reality be coupled for example with changes in the phenology of pest and pollinating insects and changes in snow cover. Still, my experiments were more realistic compared to greenhouse or artificial plant community experiments, since they were set up in grasslands with an established vegetation and natural soil conditions. However, in order to gain better mechanistic understanding of the processes related to climate change and management effects on grassland ecosystems, additional greenhouse experiments under more controlled conditions could provide useful insights since there would be less confounding variables and it would be feasible to create more replicates. In conclusion, I chose the most suitable method for my situation (*in-situ* experiments to simulate novel conditions), however, all approaches add useful insights and should ideally be combined.

### How does my work contribute to large-scale, long-term knowledge?

I set up my experiments and took measurements in ways to make the data comparable to other networks, such as the Drought-Net Research Coordination Network (Knapp et al., 2017), the Nutrient Network (<http://www.nutnet.org>) and the Marin Carbon Project (Ryals et al. 2016, <https://marincarbonproject.org/>). This will allow for comparing my results to findings from related *in-situ* experiments in other grassland sites (e.g. use it in meta-analyses) in order to generalize and scale up trends in grassland responses and to better understand the larger implications of climate change.

Both experiments are designed to be long-term experiments that will be continued by colleagues in the coming years. The experimental setups can also be used to ask additional questions, e.g. on the effects of winter warming on seedling emergence after biomass removal in Teesdale. So even though I was only able to evaluate the first three years after

establishing the experiments within my thesis, both the physical structures of the experiments and my baseline data can serve as a basis for further studies. The plant community changes in both experiments should be continued to be monitored, in order to distinguish natural fluctuations from directional change. In Tovetorp, this is particularly relevant regarding the long-term effects of soil amendments, and in Teesdale regarding the fact that vegetation is known to change slowly in such cold and nutrient-poor environments (Grime et al., 2008; Damgaard et al., 2016; Alday et al., 2021). By getting this experimental information as an early warning system, local land managers can proactively adapt grassland management and add novel practices in order to prevent/counteract negative climate change impacts.

### **How would I continue this research?**

Since the vegetation in my study sites reacted quite differently to the experimental treatments, despite being similar in climate, soil type, land use and plant communities within each experiment, I see the need for installing replicates on even more **grassland sites**. Also other authors have pointed out the difficulty to scale up local, species-specific results (e.g. Rustad et al. 2001; Rumpf et al. 2014; Schuerings et al. 2014; Krab et al. 2018). Expanding my experiments to a variety of grasslands would yield more robust results, thus allowing to generalize results and eventually to give practical management recommendations. However, compared to many other *in-situ* experiments that have been performed in only one grassland site, my experimental setup stretches across four respective three grasslands, thus aiding to understand the effects of climate change across a variation of grasslands.

Moreover, it would be helpful to test additional types and levels of **treatments**, such as different timings, durations, and intensities of precipitation exclusion and temperature increases, additional types and quantities of soil amendments, and other grazing and mowing regimes. In order to understand the effects of my treatments better, a life cycle analysis of the compost treatment would be helpful to estimate its full carbon balance (DeLonge et al., 2013). Regarding the use of open-top chambers for winter warming experiments (which are usually used to simulate summer or all-year warming), their abiotic effects could be further investigated, e.g. on snow cover and air humidity.

Finally, I would focus on the **grassland responses** in more detail, such as how legumes are affected by soil amendments and bryophytes by winter warming. For that, it would be helpful to understand mechanistic processes and indirect effects better, such as if air humidity or competition caused the bryophyte decrease in my winter warming experiment, or how soil amendments and winter warming change soil properties and nutrient availability, and how that in turn affects competitive interactions between plants. Climate change and management effects on other trophic levels could be investigated too, despite vascular plants being a good indicator of total biodiversity in an ecosystem (Brunbjerg et al., 2018) – so far I only focused on pollinating insects.

## **5.5 Recommendations for future grassland management**

Since there can be **time lags** of several years to decades between climatic changes to occur and responses in the vegetation to become apparent, climate-smart grassland management requires a long-term and observant approach. Even if we do not notice alarming declines in biodiversity or ecosystem services immediately, environmental changes may still have detrimental consequences in the near future (Chen et al., 2023). On a positive note, these time lags offer

the opportunity to implement adequate conservation measures as long as the plant species predicted to decrease or disappear still persist (Chen et al., 2023). While it is always advisable to base management recommendations on long-term studies, I anticipate that with ongoing climate change, there will not be enough time to wait for such results and that land managers will need to adapt management practices to a large extent based on their own knowledge and observations.

Based on my results, I see great potential in soil amendments as a novel practice in European grasslands with the main aim to sequester carbon, and which also increase **fodder quantity** (i.e. more aboveground plant biomass) as well as **fodder quality** (i.e. lower C:N ratio of plant biomass, even though not significant). Soil amendments can help to keep productivity stable in the event of a drought, but in general the benefits of soil amendments were strongly reduced under drought. Soil amendments furthermore tended to increase **plant species diversity** in our experiment, but there were signs of negative effects on legumes. Overall, I would recommend the application of soil amendments only on common, not particularly species-rich grasslands like the four study sites in my experiment in Sweden, and not on high nature value grasslands as the latter are sensitive to additional nutrient input.

To support **pollinating insects** in the light of climate change, I can give three management recommendations that are likely to promote floral resources in grasslands, according to the results of my experiment in Sweden. First, soil amendments applied to yearly mown/grazed grasslands are likely to increase the amount of floral units, nectar quantity and shift the peak nectar production towards earlier in the season. Second, if grasslands are managed less frequently (like road verges), they can contribute to a stable nectar supply in late summer in the event of a drought. Saving part of the vegetation from yearly mowing/grazing would also increase the survival of other life stages of pollinating insects, such as larva and pupa (Noordijk et al., 2009). Thirdly, species that contribute high amounts of nectar (in my case *Lathyrus pratensis*, *Vicia cracca*, and *Anthriscus sylvestris*), or that are flowering during periods of nectar deficit (in my case e.g. *Taraxacum* sect. *Ruderalia* and *Lathyrus pratensis*), or that increase the local floral diversity could be promoted specifically, e.g. by sparing their populations from mowing/grazing during the time of their flowering. However, this is probably not feasible in many cases because it requires species knowledge and fine-scale management.

In order to maintain current levels of **plant diversity in British Uplands** and to protect the ‘Teesdale rarities’ in my study area, grazing regimes will probably have to be adjusted towards higher intensity and duration, before the winter warming trends that I observed become apparent in the general vegetation. Even though I found no significant effects caused by the absence of sheep grazing, plant species diversity tended to be higher with grazing and winter warming effects on *Sesleria caerulea* (increases in abundance and leaf length) less strong when grazed. An increase in *Sesleria caerulea* abundance and/or height caused by warmer winter temperatures would threaten the diminutive ‘Teesdale rarities’ which are sensitive to competition, and *Sesleria caerulea* could furthermore form dense litter layers that would hamper the germination of other species.

## 6 Concluding remarks

In my thesis, I have shown that definitions of climate change related terms can differ between research fields and I highlighted the importance of stating clearly how such terms are defined in a given context in order to facilitate

comparisons between studies. Otherwise, inconsistent definitions can lead to low confidence in predictions and add to the complexity of climate change effects. Moreover, I have set up two *in-situ* experiments in Swedish and British grasslands to study seasonally specific aspects of climate change that are locally relevant, and how these interact with varying grassland management practices.

Overall, I detected only small climate change effects during the first three years after establishing the experiments. Regarding aboveground plant biomass, summer drought tended to have a neutral to negative impact on the different plant groups and winter warming a neutral to positive impact. Floral resources for pollinating insects were negatively impacted by drought in yearly mown grassland plots. Plant species diversity slightly decreased under summer drought but did not change with winter warming. In summary, grasslands will be exposed to novel climatic conditions, and I have shown that this can have complex effects (sometimes opposing, sometimes enhancing) on grassland ecosystem services and biodiversity. This highlights the importance of identifying the locally most relevant climatic changes, in order to predict their potential effects on the grassland system in question and on different plant functional groups. What can be done to counteract negative climatic effects is to adapt grassland management.

So, is there such thing as ‘climate-smart management’? In my opinion yes, since management has a strong influence on vegetation, and therefore has the potential to determine how grasslands respond to future climate shifts. Moreover, grasslands can contribute to the global efforts to store and sequester carbon, if they are managed accordingly. My results show that specific management practices interact with seasonal climate changes in a range of ways. Mowing frequency affected the flower provision for pollinating insects under drought, and sheep grazing helped to regulate competitive species and to maintain plant species diversity. My findings suggest that soil amendments could be a promising novel practice in European grasslands. While their main purpose is to increase carbon sequestration, they can be also beneficial for other grassland properties. The management practice best suited to maintain grassland ecosystem services and biodiversity is likely to depend upon the climate change effects that are going to be most relevant in a given area, and how the individual grasslands react to them. Based on the subtle effects that I found after only three years of experimental summer drought and winter warming, I expect that in the long term, climate change will have a substantial impact on biodiversity and ecosystem services in grasslands.

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## References

- Adler, P. B., Byrne, K. M., & Leiker, J. (2013). Can the past predict the future? Experimental tests of historically based population models. *Global Change Biology*, 19, 1793-1803. <https://doi.org/10.1111/gcb.12168>
- Alday, J., O'Reilly, J., Rose, R. J., & Marrs, R. H. (2021). Effects of long-term removal of sheep-grazing in a series of British upland plant communities: Insights from plant species composition and traits. *Science of The Total Environment*, 759, 143508. <https://doi.org/10.1016/j.scitotenv.2020.143508>
- Anderson, M. J. (2017). Permutational Multivariate Analysis of Variance (PERMANOVA). In *Wiley StatsRef: Statistics Reference Online* (pp. 1-15). John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781118445112.stat07841>
- Bardgett, R. D., Bullock, J. M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., Chomel, M., Durigan, G., Fry, E. L., Johnson, D., Lavelle, J. M., Le Provost, G., Luo, S., Png, K., Sankaran, M., Hou, X., Zhou, H., Ma, L., Ren, W., Li, X., Ding, Y., Li, Y., & Shi, H. (2021). Combatting global grassland degradation. *Nature Reviews Earth & Environment*, 2, 720-735. <https://doi.org/10.1038/s43017-021-00207-2>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1-48. <https://doi.org/10.18637/jss.v067.i01>
- Bates, J. W., Thompson, K., & Grime, J. P. (2005). Effects of simulated long-term climatic change on the bryophytes of a limestone grassland community. *Global Change Biology*, 11, 757-769. <https://doi.org/10.1111/j.1365-2486.2005.00953.x>
- Baude, M., Leloup, J., Suchail, S., Allard, B., Benest, D., Mériguet, J., Nunan, N., Dajoz, I., & Raynaud, X. (2011). Litter inputs and plant interactions affect nectar sugar content. *Journal of Ecology*, 99, 828-837. <https://doi.org/10.1111/j.1365-2745.2011.01793.x>
- Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A. K., Morton, R. D., Smart, S. M., & Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, 530, 85-88. <https://doi.org/10.1038/nature16532>
- Beier, C., Beierkuhnlein, C., Wohlgemuth, T., Penuelas, J., Emmett, B., Körner, C., Boeck, H. de, Christensen, J. H., Leuzinger, S., Janssens, I. A., & Hansen, K. (2012). Precipitation manipulation experiments – challenges and recommendations for the future. *Ecology Letters*, 15, 899-911. <https://doi.org/10.1111/j.1461-0248.2012.01793.x>
- Bellamy, D. J., Bridgewater, P., Marshall, C., & Tickle, W. M. (1969). Status of the Teesdale Rarities. *Nature*, 222, 238-243. <https://doi.org/10.1038/222238a0>
- Bengtsson, J., Bullock, J. M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P. J., Smith, H. G., & Lindborg, R. (2019). Grasslands - more important for ecosystem services than you might think. *Ecosphere*, 10, e02582. <https://doi.org/10.1002/ecs2.2582>
- Bharath, S., Borer, E. T., Biederman, L. A., Blumenthal, D. M., Fay, P. A., Gherardi, L. A., Knops, J. M. H., Leakey, A. D. B., Yahdjian, L., & Seabloom, E. W. (2020). Nutrient addition increases grassland sensitivity to droughts. *Ecology*, 101, e02981. <https://doi.org/10.1002/ecy.2981>
- Bokhorst, S. F., Bjerke, J. W., Tømmervik, H., Callaghan, T. V., & Phoenix, G. K. (2009). Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event. *Journal of Ecology*, 97, 1408-1415. <https://doi.org/10.1111/j.1365-2745.2009.01554.x>
- Bowman, T. E., Maibach, E., Mann, M. E., Moser, S. C., & Somerville, R. C. J. (2009). Creating a common climate language. *Science*, 324, 36-37. <https://doi.org/10.1126/science.324.5923.36b>
- Bradshaw, M. E. (2023). Teesdale's special flora - Places, plants and people (288 p.). Princeton University Press.
- Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, 27, 325-349. <https://doi.org/10.2307/1942268>
- Brown, I. (2019). Snow cover duration and extent for Great Britain in a changing climate: Altitudinal variations and synoptic-scale influences. *International Journal of Climatology*, 39, 4611-4626. <https://doi.org/10.1002/joc.6090>
- Brown, M. J. F., Dicks, L. V., Paxton, R. J., Baldock, K. C. R., Barron, A. B., Chauzat, M.-P., Freitas, B. M., Goulson, D., Jepsen, S., Kremen, C., Li, J., Neumann, P., Pattemore, D. E., Potts, S. G., Schweiger, O., Seymour, C. L., & Stout, J. C. (2016). A horizon scan of future threats and opportunities for pollinators and pollination. *PeerJ*, 4, e2249. <https://doi.org/10.7717/peerj.2249>
- Brunbjerg, A. K., Bruun, H. H., Dalby, L., Fløjgaard, C., Frøslev, T. G., Høye, T. T., Goldberg, I., Læssøe, T., Hansen, M. D. D., Brøndum, L., Skipper, L., Fog, K., & Ejrnæs, R. (2018). Vascular plant species richness and bioindication predict multi-taxon species richness. *Methods in Ecology and Evolution*, 9, 2372-2382. <https://doi.org/10.1111/2041-210X.13087>
- Bucharová, A., Brabec, J., & Münzbergová, Z. (2012). Effect of land use and climate change on the future fate of populations of an endemic species in central Europe. *Biological Conservation*, 145, 39-47. <https://doi.org/10.1016/j.biocon.2011.09.016>
- Burt, T. P., & Holden, J. (2010). Changing temperature and rainfall gradients in the British Uplands. *Climate Research*, 45, 57-70. <https://doi.org/10.3354/cr00910>

- Byrne, K. M. (2012). Climate change and plant species composition and community structure in the central grassland region of North America [PhD Thesis, Colorado State University].  
<https://www.proquest.com/docview/1046587112?pq-origsite=gscholar&fromopenview=true>
- Carvalho, L. G., Barbosa, E. R. M., & Memmott, J. (2008). Pollinator networks, alien species and the conservation of rare plants: *Trinia glauca* as a case study. *Journal of Applied Ecology*, 45, 1419-1427.  
<https://doi.org/10.1111/j.1365-2664.2008.01518.x>
- Carvell, C., Roy, D. B., Smart, S. M., Pywell, R. F., Preston, C. D., & Goulson, D. (2006). Declines in forage availability for bumblebees at a national scale. *Biological Conservation*, 132, 481-489.  
<https://doi.org/10.1016/j.biocon.2006.05.008>
- Chang, J., Gais, 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 and Management*, 12, 11. <https://doi.org/10.1186/s13021-017-0079-8>
- Chen, X., Wang, Q., Cui, B., Chen, G., Xie, T., & Yang, W. (2023). Ecological time lags in biodiversity response to habitat changes. *Journal of Environmental Management*, 346, 118965.  
<https://doi.org/10.1016/j.jenvman.2023.118965>
- Conant, R. T., Paustian, K., & Elliott, E. T. (2001). Grassland management and conversion into grassland: effects on soil carbon. *Ecological Applications*, 11, 343-355. [https://doi.org/10.1890/1051-0761\(2001\)011\[0343:GMACIG\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[0343:GMACIG]2.0.CO;2)
- Cook, B. I., Mankin, J. S., Marvel, K., Williams, A. P., Smerdon, J. E., & Anchukaitis, K. J. (2020). Twenty-first century drought projections in the CMIP6 forcing scenarios. *Earth's Future*, 8, e2019EF001461.  
<https://doi.org/10.1029/2019EF001461>
- Cousins, S. A. O., Auffret, A. G., Lindgren, J., & Tränk, L. (2015). Regional-scale land-cover change during the 20th century and its consequences for biodiversity. *AMBIO*, 44, 17-27. <https://doi.org/10.1007/s13280-014-0585-9>
- Cousins, S. A. O., & Eriksson, O. (2001). Plant species occurrences in a rural hemiboreal landscape: Effects of remnant habitats, site history, topography and soil. *Ecography*, 24, 461-469. <https://doi.org/10.1111/j.1600-0587.2001.tb00481.x>
- Craine, J. M., Brookshire, E. N. J., Cramer, M. D., Hasselquist, N. J., Koba, K., Marin-Spiotta, E., & Wang, L. (2015). Ecological interpretations of nitrogen isotope ratios of terrestrial plants and soils. *Plant and Soil*, 396, 1-26. <https://doi.org/10.1007/s11104-015-2542-1>
- Craine, J. M., & Dybzinski, R. (2013). Mechanisms of plant competition for nutrients, water and light. *Functional Ecology*, 27, 833-840. <https://doi.org/10.1111/1365-2435.12081>
- Damgaard, C., Raundrup, K., Aastrup, P., Langen, P. L., Feilberg, J., & Nabe-Nielsen, J. (2016). Arctic resilience: No evidence of vegetation change in response to grazing and climate changes in south Greenland. *Arctic, Antarctic, and Alpine Research*, 48, 531-549. <https://doi.org/10.1657/AAAR0016-005>
- Daryanto, S., Wang, L., & Jacinthe, P.-A. (2015). Global synthesis of drought effects on food legume production. *PLOS ONE*, 10, e0127401. <https://doi.org/10.1371/journal.pone.0127401>
- Dawson, T. E., Mambelli, S., Plamboeck, A. H., Templer, P. H., & Tu, K. P. (2002). Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics*, 33, 507-559.  
<https://doi.org/10.1146/annurev.ecolsys.33.020602.095451>
- De Boeck, H., Bloor, J., Kreyling, J., C. G. Ransijn, J., Nijs, I., Jentsch, A., & Zeiter, M. (2018). Patterns and drivers of biodiversity-stability relationships under climate extremes. *Journal of Ecology*, 106, 890-902.  
<https://doi.org/10.1111/1365-2745.12897>
- Deléglise, C., Meisser, M., Mosimann, E., Spiegelberger, T., Signarbieux, C., Jeangros, B., & Buttler, A. (2015). Drought-induced shifts in plants traits, yields and nutritive value under realistic grazing and mowing managements in a mountain grassland. *Agriculture, Ecosystems & Environment*, 213, 94-104.  
<https://doi.org/10.1016/j.agee.2015.07.020>
- DeLonge, M. S., Ryals, R., & Silver, W. L. (2013). A lifecycle model to evaluate carbon sequestration potential and greenhouse gas dynamics of managed grasslands. *Ecosystems*, 16, 962-979. <https://doi.org/10.1007/s10021-013-9660-5>
- Dengler, J., Birge, T., Bruun, H. H., Rašomavičius, V., Rūsiņa, S., & Sickel, H. (2020). Grasslands of Northern Europe and the Baltic States. In: *Encyclopedia of the World's Biomes*, 689-702. <https://doi.org/10.1016/B978-0-12-409548-9.12433-9>
- Descamps, C., Quinet, M., & Jacquemart, A.-L. (2021). The effects of drought on plant-pollinator interactions: What to expect? *Environmental and Experimental Botany*, 182, 104297.  
<https://doi.org/10.1016/j.envexpbot.2020.104297>
- Dicks, L. V., Breeze, T. D., Ngo, H. T., Senapathi, D., An, J., Aizen, M. A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L. A., Gemmill-Herren, B., Howlett, B. G., Imperatriz-Fonseca, V. L., Johnson, S. D., Kovács-Hostyánszki, A., Kwon, Y. J., Lattorff, H. M. G., Lungharwo, T., Seymour, C. L., Vanbergen, A. J., & Potts, S. G. (2021). A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nature Ecology & Evolution*, 5, 1453-1461. <https://doi.org/10.1038/s41559-021-01534-9>

- Dirmeyer, P. A., Yu, L., Amini, S., Crowell, A. D., Elders, A., & Wu, J. (2016). Projections of the shifting envelope of water cycle variability. *Climatic Change*, 136, 587-600. <https://doi.org/10.1007/s10584-016-1634-0>
- Dracup, J. A., Lee, K. S., & Paulson, E. G. (1980). On the definition of droughts. *Water Resources Research*, 16, 297-302. <https://doi.org/10.1029/WR016i002p00297>
- Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate extremes: Observations, modeling, and impacts. *Science*, 289, 2068-2074. <https://doi.org/10.1126/science.289.5487.2068>
- Edwards, A. C., Scalenghe, R., & Freppaz, M. (2007). Changes in the seasonal snow cover of alpine regions and its effect on soil processes: A review. *Quaternary International*, 162-163, 172-181. <https://doi.org/10.1016/j.quaint.2006.10.027>
- Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, & GIS User Community. (2021). Basemaps. Esri. <https://www.arcgis.com/apps/mapviewer/index.html?webmap=52bdc7ab7fb044d98add148764eaa30a>
- European Environment Agency. (2014). Projected changes in annual, summer and winter temperature. <https://www.eea.europa.eu/data-and-maps/figures/projected-changes-in-annual-summer-1>
- Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology*, 40, 503-537. <https://www.annualreviews.org/doi/pdf/10.1146/annurev.pp.40.060189.002443>
- Felton, A. J., & Smith, M. D. (2017). Integrating plant ecological responses to climate extremes from individual to ecosystem levels. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160142. <https://doi.org/10.1098/rstb.2016.0142>
- Fox, J., & Weisberg, S. (2019). An R companion to applied regression (Third edition). Thousand Oaks CA: Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Fridley, J. D., Lynn, J. S., Grime, J. P., & Askew, A. P. (2016). Longer growing seasons shift grassland vegetation towards more-productive species. *Nature Climate Change*, 6, 865-868. <https://doi.org/10.1038/nclimate3032>
- Gilbert, O. L., Earland-Bennett, P., & Coppins, B. J. (1978). Lichens of the sugar limestone refugium in Upper Teesdale. *New Phytologist*, 80, 403-408. <https://doi.org/10.1111/j.1469-8137.1978.tb01574.x>
- Gomes, D. G. E. (2022). Should I use fixed effects or random effects when I have fewer than five levels of a grouping factor in a mixed-effects model? *PeerJ*, 10, e12794. <https://doi.org/10.7717/peerj.12794>
- Goulson, D., Hanley, M. E., Darvill, B., Ellis, J. S., & Knight, M. E. (2005). Causes of rarity in bumblebees. *Biological Conservation*, 122, 1-8. <https://doi.org/10.1016/j.biocon.2004.06.017>
- Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, 347, 1255-1257. <https://doi.org/10.1126/science.1255957>
- Graae, B. J., Vandvik, V., Armbruster, W. S., Eiserhardt, W. L., Svenning, J.-C., Hylander, K., Ehrlén, J., Speed, J. D. M., Klanderud, K., Bråthen, K. A., Milbau, A., Opedal, Ø. H., Alsos, I. G., Ejrnæs, R., Bruun, H. H., Birks, H. J. B., Westergaard, K. B., Birks, H. H., & Lenoir, J. (2018). Stay or go – how topographic complexity influences alpine plant population and community responses to climate change. *Perspectives in Plant Ecology, Evolution and Systematics*, 30, 41-50. <https://doi.org/10.1016/j.ppees.2017.09.008>
- 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, 1454-1467. <https://doi.org/10.1007/s10021-017-0122-3>
- Grime, J. P., Brown, V. K., Thompson, K., Masters, G. J., Hillier, S. H., Clarke, I. P., Askew, A. P., Corker, D., & Kieley, J. P. (2000). The response of two contrasting limestone grasslands to simulated climate change. *Science*, 289, 762-765. <https://doi.org/10.1126/science.289.5480.762>
- Grime, J. P., Fridley, J. D., Askew, A. P., Thompson, K., Hodgson, J. G., & Bennett, C. R. (2008). Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences*, 105, 10028-10032. <https://doi.org/10.1073/pnas.0711567105>
- Habel, J. C., Dengler, J., Janišová, M., Török, P., Wellstein, C., & Wiczik, M. (2013). European grassland ecosystems: Threatened hotspots of biodiversity. *Biodiversity and Conservation*, 22, 2131-2138. <https://doi.org/10.1007/s10531-013-0537-x>
- Harden, J. W., Hugelius, G., Ahlström, A., Blankinship, J. C., Bond-Lamberty, B., Lawrence, C. R., Loisel, J., Malhotra, A., Jackson, R. B., Ogle, S., Phillips, C., Ryals, R., Todd-Brown, K., Vargas, R., Vergara, S. E., Cotrufo, M. F., Keiluweit, M., Heckman, K. A., Crow, S. E., Silver, E. C., DeLonge, M., & Nave, L. E. (2018). Networking our science to characterize the state, vulnerabilities, and management opportunities of soil organic matter. *Global Change Biology*, 24, e705-e718. <https://doi.org/10.1111/gcb.13896>
- Henderson, B. B., Gerber, P. J., Hilinski, T. E., Falcucci, A., Ojima, D. S., Salvatore, M., & Conant, R. T. (2015). Greenhouse gas mitigation potential of the world's grazing lands: Modeling soil carbon and nitrogen fluxes of mitigation practices. *Agriculture, Ecosystems & Environment*, 207, 91-100. <https://doi.org/10.1016/j.agee.2015.03.029>
- Henry, H. A. L. (2008). Climate change and soil freezing dynamics: historical trends and projected changes. *Climatic Change*, 87, 421-434. <https://doi.org/10.1007/s10584-007-9322-8>

- Herrando-Pérez, S., Brook, B. W., & Bradshaw, C. J. A. (2014). Ecology needs a convention of nomenclature. *BioScience*, 64, 311-321. <https://doi.org/10.1093/biosci/biu013>
- Hisdal, H., & Tallaksen, L. M. (2000). Drought event definition. *Technical Report to the ARIDE project No.6: Supplement to Work Package 2 Hydro-meteorological Drought Activity 2.1 Event Definition*. [https://www.droughtmanagement.info/literature/UNIVERSITYofOSLO\\_Drought\\_Event\\_Definition\\_2000.pdf](https://www.droughtmanagement.info/literature/UNIVERSITYofOSLO_Drought_Event_Definition_2000.pdf)
- Holden, J., & Rose, R. (2011). Temperature and surface lapse rate change: a study of the UK's longest upland instrumental record. *International Journal of Climatology*, 31, 907-919. <https://doi.org/10.1002/joc.2136>
- Hollister, R. D., Elphinstone, C., Henry, G. H. R., Bjorkman, A. D., Klanderud, K., Björk, R. G., Björkman, M. P., Bokhorst, S., Carbognani, M., Cooper, E. J., Dorrepaal, E., Elmendorf, S. C., Fetcher, N., Gallois, E. C., Guðmundsson, J., Healey, N. C., Jónsdóttir, I. S., Klarenberg, I. J., Oberbauer, S. F., Macek, P., May, J. L., Mereghetti, A., Molau, U., Petraglia, A., Rinnan, R., Rixen, C., & Wookey, P. A. (2023). A review of open top chamber (OTC) performance across the ITEX Network. *Arctic Science*, 9, 331-344. <https://doi.org/10.1139/as-2022-0030>
- Hoover, D. L., Knapp, A. K., & Smith, M. D. (2014). Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology*, 95, 2646-2656. <https://doi.org/10.1890/13-2186.1>
- Inkscape Project. (2020). Inkscape: Open source scalable vector graphics editor. <https://www.inkscape.org>
- Inouye, D. W. (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, 89, 353-362. <https://doi.org/10.1890/06-2128.1>
- IPCC (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.
- IPCC (2023). Sections. In: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland, pp. 35-115, doi: 10.59327/IPCC/AR6-9789291691647
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruehlheide, H., De Luca, E., Ebeling, A., Griffin, J. N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S. T., Mori, A. S., Naeem, S., Niklaus, P. A., Polley, H. W., Reich, P. B., Roscher, C., Seabloom, E. W., Smith M. D., Thakur, M. P., Tilman, D., Tracy, B. F., van der Putten, W. H., van Ruijven, J., Weigelt, A., Weisser, W. W., Wilsey, B., & Eisenhauer, N. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, 526, 574-577. <https://doi.org/10.1038/nature15374>
- Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment*, 5, 365-374. [https://doi.org/10.1890/1540-9295\(2007\)5\[365:ANGOCE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[365:ANGOCE]2.0.CO;2)
- Jentsch, A., Kreyling, J., Elmer, M., Gellesch, E., Glaser, B., Grant, K., Hein, R., Lara, M., Mirzae, H., Nadler, S. E., Nagy, L., Otieno, D., Pritsch, K., Rascher, U., Schädler, M., Schlöter, M., Singh, B. K., Stadler, J., Walter, J., Wellstein, C., Wöllecke, J., & Beierkuhnlein, C. (2011). Climate extremes initiate ecosystem-regulating functions while maintaining productivity. *Journal of Ecology*, 99, 689-702. <https://doi.org/10.1111/j.1365-2745.2011.01817.x>
- Johnson, G. A. L., Robinson, D., & Hornung, M. (1971). Unique bedrock and soils associated with the Teesdale flora. *Nature*, 232, 453-456. <https://doi.org/10.1038/232453a0>
- Jones, M. B., & Donnelly, A. (2004). Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO<sub>2</sub>. *New Phytologist*, 164, 423-439. <https://doi.org/10.1111/j.1469-8137.2004.01201.x>
- Kahmen, S., & Poschlod, P. (2008). Effects of grassland management on plant functional trait composition. *Agriculture Ecosystems & Environment*, 128, 137-145. <https://doi.org/10.1016/j.agee.2008.05.016>
- Kapás, R. E., Plue, J., Kimberley, A., & Cousins, S. A. O. (2020). Grazing livestock increases both vegetation and seed bank diversity in remnant and restored grasslands. *Journal of Vegetation Science*, 31, 1053-1065. <https://doi.org/10.1111/jvs.12956>
- Klein, J. A., Harte, J., & Zhao, X.-Q. (2004). Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters*, 7, 1170-1179. <https://doi.org/10.1111/j.1461-0248.2004.00677.x>
- Klein, J. A., Harte, J., & Zhao, X.-Q. (2007). Experimental warming, not grazing, decreases rangeland quality on the Tibetan Plateau. *Ecological Applications*, 17, 541-557. <https://doi.org/10.1890/05-0685>
- Knapp, A. K., Avolio, M. L., Beier, C., Carroll, C. J. W., Collins, S. L., Dukes, J. S., Fraser, L. H., Griffin-Nolan, R. J., Hoover, D. L., Jentsch, A., Loik, M. E., Phillips, R. P., Post, A. K., Sala, O. E., Slette, I. J., Yahdjian, L., & Smith, M. D. (2017). Pushing precipitation to the extremes in distributed experiments: Recommendations for simulating wet and dry years. *Global Change Biology*, 23, 1774-1782. <https://doi.org/10.1111/gcb.13504>

- Körner, C., & Hiltbrunner, E. (2018). The 90 ways to describe plant temperature. *Perspectives in Plant Ecology, Evolution and Systematics*, 30, 16-21. <https://doi.org/10.1016/j.ppees.2017.04.004>
- Krab, E. J., 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. *Journal of Ecology*, 106, 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, 1939-1948. <https://doi.org/10.1890/09-1160.1>
- Kreyling, J., Grant, K., Hammerl, V., Arfin-Khan, M. A. S., Malyshev, A. V., Peñuelas, J., Pritsch, K., Sardans, J., Schloter, M., Schuerings, J., Jentsch, A., & Beierkuhnlein, C. (2019). Winter warming is ecologically more relevant than summer warming in a cool-temperate grassland. *Scientific Reports*, 9, 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 Ecology & Diversity*, 4, 13-21. <https://doi.org/10.1080/17550874.2011.558125>
- Kreyling, J., Wenigmann, M., Beierkuhnlein, C., & Jentsch, A. (2008). Effects of extreme weather events on plant productivity and tissue die-back are modified by community composition. *Ecosystems*, 11, 752-763. <https://doi.org/10.1007/s10021-008-9157-9>
- Kröel-Dulay, G., Mojzes, A., Szitár, K., Bahn, M., Batáry, P., Beier, C., Bilton, M., De Boeck, H. J., Dukes, J. S., Estiarte, M., Holub, P., Jentsch, A., Schmidt, I. K., Kreyling, J., Reinsch, S., Larsen, K. S., Sternberg, M., Tielbörger, K., Tietema, A., Vicca, S., & Peñuelas, J. (2022). Field experiments underestimate aboveground biomass response to drought. *Nature Ecology & Evolution*, 6, 540-545. <https://doi.org/10.1038/s41559-022-01685-3>
- Lenth, R. V. (2016). Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software*, 69, 1-33. <https://doi.org/doi:10.18637/jss.v069.i01>
- Lett, S., Jónsdóttir, I. S., Becker-Scarpitta, A., Christiansen, C. T., During, H., Ekelund, F., Henry, G. H. R., Lang, S. I., Michelsen, A., Rousk, K., Alatalo, J. M., Betway, K. R., Rui, S. B., Callaghan, T., Carbone, M., Cooper, E. J., Cornelissen, J. H. C., Dorrepaal, E., Egelkraut, D., Elumeeva, T. G., Haugum, S. V., Hollister, R. D., Jägerbrand, A. K., Keuper, F., Klanderud, K., Lévesque, E., Liu, X., May, J., Michel, P., Mörsdorf, M., Petraglia, A., Rixen, C., Robroek, B. J. M., Rzepczynska, A. M., Soudzilovskaia, N. A., Tolvanen, A., Vandvik, V., Volkov, I., Volkova, I., & van Zuijlen, K. (2022). Can bryophyte groups increase functional resolution in tundra ecosystems? *Arctic Science*, 8, 609-637. <https://doi.org/10.1139/as-2020-0057>
- Lewthwaite, K. J. (1999). An investigation into the impact of environmental change upon the vegetation of Widdybank Fell, Upper Teesdale [PhD thesis, Durham University]. <http://etheses.dur.ac.uk/4407/>
- 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. *Current Opinion in Environmental Sustainability*, 33, 124-135. <https://doi.org/10.1016/j.cosust.2018.05.008>
- Liu, D., Zhang, C., Ogaya, R., Fernández-Martínez, M., Pugh, T. A. M., & Peñuelas, J. (2021). Increasing climatic sensitivity of global grassland vegetation biomass and species diversity correlates with water availability. *New Phytologist*, 230, 1761-1771. <https://doi.org/10.1111/nph.17269>
- Liu, Q., Piao, S., Janssens, I. A., Fu, Y., Peng, S., Lian, X., Ciais, P., Myneni, R. B., Peñuelas, J., & Wang, T. (2018). Extension of the growing season increases vegetation exposure to frost. *Nature Communications*, 9, 426. <https://doi.org/10.1038/s41467-017-02690-y>
- Loeser, M. R. R., Sisk, T. D., & Crews, T. E. (2007). Impact of grazing intensity during drought in an Arizona grassland. *Conservation Biology*, 21, 87-97. <https://doi.org/10.1111/j.1523-1739.2006.00606.x>
- Mackie, K. A., Zeiter, M., Bloor, J. M. G., & Stampfli, A. (2019). Plant functional groups mediate drought resistance and recovery in a multisite grassland experiment. *Journal of Ecology*, 107, 937-949. <https://doi.org/10.1111/1365-2745.13102>
- Manley, G. (1942). Meteorological observations on Dun Fell, a mountain station in Northern England. *Quarterly Journal of the Royal Meteorological Society*, 68, 151-166. <https://doi.org/10.1002/qj.49706829502>
- Marion, G. M., Henry, G. H. R., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H., Lévesque, E., Molau, U., Mølgaard, P., Parsons, A. N., Svoboda, J., & Virginia, R. A. (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, 3, 20-32. <https://doi.org/10.1111/j.1365-2486.1997.gcb136.x>
- Mariotte, P., Vandenbergh, C., Kardol, P., Hagedorn, F., & Buttler, A. (2013). Subordinate plant species enhance community resistance against drought in semi-natural grasslands. *Journal of Ecology*, 101, 763-773. <https://doi.org/10.1111/1365-2745.12064>
- Meng, B., Li, J., Maurer, G. E., Zhong, S., Yao, Y., Yang, X., Collins, S. L., & Sun, W. (2021). Nitrogen addition amplifies the nonlinear drought response of grassland productivity to extended growing-season droughts. *Ecology*, 102, e03483. <https://doi.org/10.1002/ecy.3483>

- Moeslund, J. E., Arge, L., Bøcher, P. K., Dalgaard, T., Ejrnæs, R., Odgaard, M. V., & Svenning, J.-C. (2013). Topographically controlled soil moisture drives plant diversity patterns within grasslands. *Biodiversity and Conservation*, 22, 2151-2166. <https://doi.org/10.1007/s10531-013-0442-3>
- Moles, A. T., Perkins, S. E., Laffan, S. W., Flores-Moreno, H., Awasthy, M., Tindall, M. L., Sack, L., Pitman, A., Kattge, J., Aarssen, L. W., Anand, M., Bahn, M., Blonder, B., Cavender-Bares, J., Cornelissen, J. H. C., Cornwell, W. K., Díaz, S., Dickie, J. B., Freschet, G. T., Griffiths, J. G., Gutierrez, A. G., Hemmings, F. A., Hickler, T., Hitchcock, T. D., Keighery, M., Kleyer, M., Kurokawa, H., Leishman, M. R., Liu, K., Niinemets, Ü., Onipchenko, V., Onoda, Y., Penuelas, J., Pillar, V. D., Reich, P. B., Shiodera, S., Siefert, A., Sosinski Jr. E. E., Soudzilovskaia N. A., Swaine, E. K., Swenson, N. G., van Bodegom, P. M., Warman, L., Weiher, E., Wright I. J., Zhang, H., Zobel, M., & Bonser, S. P. (2014). Which is a better predictor of plant traits: Temperature or precipitation? *Journal of Vegetation Science*, 25, 1167-1180. <https://doi.org/10.1111/jvs.12190>
- Morecroft, M. D., Bealey, C. E., Beaumont, D. A., Benham, S., Brooks, D. R., Burt, T. P., Critchley, C. N. R., Dick, J., Littlewood, N. A., Monteith, D. T., Scott, W. A., Smith, R. I., Walmsley, C., & Watson, H. (2009). The UK Environmental Change Network: Emerging trends in the composition of plant and animal communities and the physical environment. *Biological Conservation*, 142, 2814-2832. <https://doi.org/10.1016/j.biocon.2009.07.004>
- Niittynen, P., Heikkinen, R. K., Aalto, J., Guisan, A., Kemppinen, J., & Luoto, M. (2020). Fine-scale tundra vegetation patterns are strongly related to winter thermal conditions. *Nature Climate Change*, 10, 1143-1148. <https://doi.org/10.1038/s41558-020-00916-4>
- Noordijk, J., Delille, K., Schaffers, A. P., & Sýkora, K. V. (2009). Optimizing grassland management for flower-visiting insects in roadside verges. *Biological Conservation*, 142, 2097-2103. <https://doi.org/10.1016/j.biocon.2009.04.009>
- Oberpriller, J., de Souza Leite, M., & Pichler, M. (2022). Fixed or random? On the reliability of mixed-effects models for a small number of levels in grouping variables. *Ecology and Evolution*, 12, e9062. <https://doi.org/10.1002/ece3.9062>
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., & Weedon, J. (2023). *vegan: an R package for community ecologists*. <https://github.com/vegandevs/vegan>
- O'Mara, F. P. (2012). The role of grasslands in food security and climate change. *Annals of Botany*, 110, 1263-1270. <https://doi.org/10.1093/aob/mcs209>
- Pärtel, M., Bruun, H. H., & Sammul, M. (2005). Biodiversity in temperate European grasslands: origin and conservation. *Grassland Science in Europe*, 10, 1-14. [http://www.planteco.lu.se/people/hhb/Partel\\_Bruun\\_Sammul\\_2005\\_Grassland\\_Science\\_in\\_Europe\\_10.pdf](http://www.planteco.lu.se/people/hhb/Partel_Bruun_Sammul_2005_Grassland_Science_in_Europe_10.pdf)
- Paustian, K., Lehmann, J., Ogle, S., Reay, D., Robertson, G. P., & Smith, P. (2016). Climate-smart soils. *Nature*, 532, 49-57. <https://doi.org/10.1038/nature17174>
- Pepin, N. C., Adamson, J. K., & Benham, D. (2009). Creation of a homogenous climate record for Widdybank Fell in the Upper Teesdale National Nature Reserve, northern England: 1968-2006. *Theoretical and Applied Climatology*, 98, 47-56. <https://doi.org/10.1007/s00704-008-0090-9>
- Pigott, C. D. (1956). The vegetation of Upper Teesdale in the North Pennines. *Journal of Ecology*, 44, 545-586. <https://doi.org/10.2307/2256835>
- Poschlod, P., & WallisDeVries, M. F. (2002). The historical and socioeconomic perspective of calcareous grasslands - Lessons from the distant and recent past. *Biological Conservation*, 104, 361-376. [https://doi.org/10.1016/S0006-3207\(01\)00201-4](https://doi.org/10.1016/S0006-3207(01)00201-4)
- Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences*, 105, 12353-12358. <https://doi.org/10.1073/pnas.0802421105>
- R Core Team. (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. <https://www.R-project.org/>
- Reyer, C. P. O., Leuzinger, S., Rammig, A., Wolf, A., Bartholomeus, R. P., Bonfante, A., de Lorenzi, F., Dury, M., Gloning, P., Abou Jaoudé, R., Klein, T., Kuster, T. M., Martins, M., Niedrist, G., Riccardi, M., Wohlfahrt, G., de Angelis, P., de Dato, G., François, L., Menzel, A., & Pereira, M. (2013). A plant's perspective of extremes: Terrestrial plant responses to changing climatic variability. *Global Change Biology*, 19, 75-89. <https://doi.org/10.1111/gcb.12023>
- Reynaert, S., De Boeck, H. J., Verbruggen, E., Verlinden, M., Flowers, N., & Nijs, I. (2021). Risk of short-term biodiversity loss under more persistent precipitation regimes. *Global Change Biology*, 27, 1614-1626. <https://doi.org/10.1111/gcb.15501>
- Rumpf, S. B., Semenchuk, P. R., Dullinger, S., & Cooper, E. J. (2014). Idiosyncratic responses of high arctic plants to changing snow regimes. *PLOS ONE*, 9, 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, 543-562. <https://doi.org/10.1007/s004420000544>
- Ryals, R., Eviner, V. T., Stein, C., Suding, K. N., & Silver, W. L. (2016). Grassland compost amendments increase plant production without changing plant communities. *Ecosphere*, 7, e01270. <https://doi.org/10.1002/ecs2.1270>
- Ryals, R., Hartman, M. D., Parton, W. J., DeLonge, M. S., & Silver, W. L. (2015). Long-term climate change mitigation potential with organic matter management on grasslands. *Ecological Applications*, 25, 531-545. <https://doi.org/10.1890/13-2126.1>
- Ryals, R., & Silver, W. L. (2013). Effects of organic matter amendments on net primary productivity and greenhouse gas emissions in annual grasslands. *Ecological Applications*, 23, 46-59. <https://doi.org/10.1890/12-0620.1>
- 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 and Soil*, 371, 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. *Ecological Research*, 29, 561-570. <https://doi.org/10.1007/s11284-014-1174-x>
- Schwalm, C. R., Anderegg, W. R. L., Michalak, A. M., Fisher, J. B., Biondi, F., Koch, G., Litvak, M., Ogle, K., Shaw, J. D., Wolf, A., Huntzinger, D. N., Schaefer, K., Cook, R., Wei, Y., Fang, Y., Hayes, D., Huang, M., Jain, A., & Tian, H. (2017). Global patterns of drought recovery. *Nature*, 548, 202-205. <https://doi.org/10.1038/nature23021>
- Seneviratne, S., Nicholls, N., Easterling, D., Goodess, C., Kanae, S., Kossin, J., Luo, Y., Marengo, J., McInnes, K., Rahimi, M., Reichstein, M., Sorteberg, A., Vera, C., Zhang, X., Alexander, L. V., Allen, S., Benito, G., Cavazos, T., Clague, J., Conway, D., Della-Marta, P. M., Gerber, M., Gong, S., Goswami, B. N., Hemer, M., Huggel, C., van den Hurk, B., Kharin, V. V., Kitoh, A., Tank, K., Albert, M. G., Li, G., Mason, S., McGuire, W., van Oldenborgh, G. J., Orłowsky, B., Smith, S., Thiaw, W., Velegrakis, A., Yiou, P., Zhang, T., Tianjun, Z., & Zwiers, F. W. (2012). Changes in climate extremes and their impacts on the natural physical environment. *Chapter 3 of managing the risks of extreme events and disasters to advance climate change adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change (IPCC)*. (pp. 109–230). <https://doi.org/10.7916/d8-6nbt-s431>
- Serraj, R., Sinclair, T. R., & Purcell, L. C. (1999). Symbiotic N<sub>2</sub> fixation response to drought. *Journal of Experimental Botany*, 50, 143-155. <https://doi.org/10.1093/jxb/50.331.143>
- Shannon, C. E. (1948). A mathematical theory of communication. *The Bell System Technical Journal*, 27, 379-423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>
- Signarbieux, C., & Feller, U. (2012). Effects of an extended drought period on physiological properties of grassland species in the field. *Journal of Plant Research*, 125, 251-261. <https://doi.org/10.1007/s10265-011-0427-9>
- Slette, I. J., Post, A. K., Awad, M., Even, T., Punzalan, A., Williams, S., Smith, M. D., & Knapp, A. K. (2019). How ecologists define drought, and why we should do better. *Global Change Biology*, 25, 3193-3200. <https://doi.org/10.1111/gcb.14747>
- Smith, M. D. (2011a). An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology*, 99, 656-663. <https://doi.org/10.1111/j.1365-2745.2011.01798.x>
- Smith, M. D. (2011b). The ecological role of climate extremes: Current understanding and future prospects. *Journal of Ecology*, 99, 651-655. <https://doi.org/10.1111/j.1365-2745.2011.01833.x>
- Smith, P. (2014). Do grasslands act as a perpetual sink for carbon? *Global Change Biology*, 20, 2708-2711. <https://doi.org/10.1111/gcb.12561>
- Snyder, K. A., Robinson, S. A., Schmidt, S., & Hultine, K. R. (2022). Stable isotope approaches and opportunities for improving plant conservation. *Conservation Physiology*, 10, coac056. <https://doi.org/10.1093/conphys/coac056>
- Spinoni, J., Vogt, J. V., Naumann, G., Barbosa, P., & Dosio, A. (2018). Will drought events become more frequent and severe in Europe? *International Journal of Climatology*, 38, 1718-1736. <https://doi.org/10.1002/joc.5291>
- Squires, R. (1978). Conservation in Upper Teesdale: Contributions from the palaeoecological record. *Transactions of the Institute of British Geographers*, 3, 129-150. <https://doi.org/10.2307/622198>
- Squires, R. (1971). Flandrian history of the Teesdale rarities. *Nature*, 229, 43-44. <https://doi.org/10.1038/229043a0>
- Stampfli, A., Bloor, J., Fischer, M., & Zeiter, M. (2018). High land-use intensity exacerbates shifts in grassland vegetation composition after severe experimental drought. *Global Change Biology*, 24, 2021-2034. <https://doi.org/10.1111/gcb.14046>
- Stampfli, A., & Zeiter, M. (2004). Plant regeneration directs changes in grassland composition after extreme drought: A 13-year study in southern Switzerland. *Journal of Ecology*, 92, 568-576. <https://doi.org/10.1111/j.0022-0477.2004.00900.x>
- Stevens, C. J., Dise, N. B., Mountford, J. O., & Gowing, D. J. (2004). Impact of nitrogen deposition on the species richness of grasslands. *Science*, 303, 1876-1879. <https://doi.org/10.1126/science.1094678>

- Stevens, C. J., Payne, R. J., Kimberley, A., & Smart, S. M. (2016). How will the semi-natural vegetation of the UK have changed by 2030 given likely changes in nitrogen deposition? *Environmental Pollution*, 208, 879-889. <https://doi.org/10.1016/j.envpol.2015.09.013>
- Swedish Meteorological and Hydrological Institute. (2019). Climate extremes for Sweden - State of knowledge and implications for adaptation and mitigation (75 p.). SMHI. [https://doi.org/10.17200/Climate\\_Extremes\\_Sweden](https://doi.org/10.17200/Climate_Extremes_Sweden)
- Swedish Meteorological and Hydrological Institute. (2022). Normal årsmedeltemperatur. <https://www.smhi.se/data/meteorologi/kartor/normal/arsmedeltemperatur-normal>
- Swedish Meteorological and Hydrological Institute. (2023). Advanced climate change scenario service. [https://www.smhi.se/en/climate/future-climate/advanced-climate-change-scenario-service/met/sodermanlands\\_lan/medeltemperatur/rcp45/2071-2100/spring/anom](https://www.smhi.se/en/climate/future-climate/advanced-climate-change-scenario-service/met/sodermanlands_lan/medeltemperatur/rcp45/2071-2100/spring/anom)
- Tälle, M., Deák, B., Posch, P., Valkó, O., Westerberg, L., & Milberg, P. (2016). Grazing vs. mowing: A meta-analysis of biodiversity benefits for grassland management. *Agriculture, Ecosystems and Environment*, 222, 200-212. <https://doi.org/10.1016/j.agee.2016.02.008>
- Tilman, D., & El Haddi, A. (1992). Drought and biodiversity in grasslands. *Oecologia*, 89, 257-264. <https://doi.org/10.1007/BF00317226>
- Trenberth, K. E. (2011). Changes in precipitation with climate change. *Climate Research*, 47, 123-138. <https://doi.org/10.3354/cr00953>
- Turner, J., Hewetson, P., Hibbert, F. A., Lowry, H., Chambers, C., & West, R. G. (1973). The history of the vegetation and flora of Widdybank Fell and the Cow Green reservoir basin, Upper Teesdale. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 265, 327-408. <https://doi.org/10.1098/rstb.1973.0031>
- Ummenhofer, C. C., & Meehl, G. A. (2017). Extreme weather and climate events with ecological relevance: A review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160135. <https://doi.org/10.1098/rstb.2016.0135>
- Van Sundert, K., Khan, M. A. S. A., Bharath, S., Buckley, Y. M., Caldeira, M. C., Donohue, I., Dubbert, M., Ebeling, A., Eisenhauer, N., Eskelinen, A., Finn, A., Gebauer, T., Haider, S., Hansart, A., Jentsch, A., Kübert, A., Nijs, I., Nock, C. A., Nogueira, C., Porath-Krause, A. J., Radujkovic, D., Raynaud, X., Risch, A. C., Roscher, C., Scherer-Lorenzen, M., Schuchardt, M. A., Schütz, M., Siebert, J., Sitters, J., Spohn, M., Virtanen, R., Werner, C., Wilfahrt, P., & Vicca, S. (2021). Fertilized graminoids intensify negative drought effects on grassland productivity. *Global Change Biology*, 27, 2441-2457. <https://doi.org/10.1111/gcb.15583>
- van Zuijlen, K., Asplund, J., Sundsbø, S., Dahle, O. S., & Klanderud, K. (2022). Ambient and experimental warming effects on an alpine bryophyte community. *Arctic Science*, 8, 831-842. <https://doi.org/10.1139/as-2020-0047>
- Vogel, A., Scherer-Lorenzen, M., & Weigelt, A. (2012). Grassland resistance and resilience after drought depends on management intensity and species richness. *PLOS ONE*, 7, e36992. <https://doi.org/10.1371/journal.pone.0036992>
- Wang, S., Duan, J., Xu, G., Wang, Y., Zhang, Z., Rui, Y., Luo, C., Xu, B., Zhu, X., Chang, X., Cui, X., Niu, H., Zhao, X., & Wang, W. (2012). Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow. *Ecology*, 93, 2365-2376. <https://doi.org/10.1890/11-1408.1>
- Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. <https://ggplot2.tidyverse.org>
- Wilcke, R. A. I., Kjellström, E., Lin, C., Matei, D., Moberg, A., & Tyrlis, E. (2020). The extremely warm summer of 2018 in Sweden – set in a historical context. *Earth System Dynamics*, 11, 1107-1121. <https://doi.org/10.5194/esd-11-1107-2020>
- Wilcox, K. R., Shi, Z., Gherardi, L. A., Lemoine, N. P., Koerner, S. E., Hoover, D. L., Bork, E., Byrne, K. M., Cahill, J., Collins, S. L., Evans, S., Gilgen, A. K., Holub, P., Jiang, L., Knapp, A. K., LeCain, D., Liang, J., Garcia-Palacios, P., Peñuelas, J., Pockman, W. T., Smith, M. D., Sun, S., White, S. R., Yahdjian, L., Zhu, K., & Luo, Y. (2017). Asymmetric responses of primary productivity to precipitation extremes: A synthesis of grassland precipitation manipulation experiments. *Global Change Biology*, 23, 4376-4385. <https://doi.org/10.1111/gcb.13706>
- 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. *Agricultural and Forest Meteorology*, 268, 40-47. <https://doi.org/10.1016/j.agrformet.2018.12.018>
- Wilhite, D. A., & Glantz, M. H. (1985). Understanding the drought phenomenon: The role of definitions. *Water International*, 10, 111-120. <https://doi.org/10.1080/02508068508686328>
- Williams, C. M., Henry, H. A. L., & Sinclair, B. J. (2015). Cold truths: How winter drives responses of terrestrial organisms to climate change. *Biological Reviews*, 90, 214-235. <https://doi.org/10.1111/brev.12105>
- Wilson, J. B., Peet, R. K., Dengler, J., Pärtel, M., & Palmer, M. (2012). Plant species richness: The world records. *Journal of Vegetation Science*, 23, 796-802. <https://doi.org/10.1111/j.1654-1103.2012.01400.x>
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, 73, 3-36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>



- Xia, J., Chen, J., Piao, S., Ciais, P., Luo, Y., & Wan, S. (2014). Terrestrial carbon cycle affected by non-uniform climate warming. *Nature Geoscience*, 7, 173-180. <https://doi.org/10.1038/ngeo2093>
- Yahdjian, L., & Sala, O. E. (2002). A rainout shelter design for intercepting different amounts of rainfall. *Oecologia*, 133, 95-101. <https://doi.org/10.1007/s00442-002-1024-3>
- Zeiter, M., Schärer, S., Zweifel, R., Newbery, D. M., & Stampfli, A. (2016). Timing of extreme drought modifies reproductive output in semi-natural grassland. *Journal of Vegetation Science*, 27, 238-248. <https://doi.org/10.1111/jvs.12362>
- Zhang, D. (2021). rsq: R-Squared and Related Measures. <https://CRAN.R-project.org/package=rsq>
- Zhang, Y., Gao, Q., Dong, S., Liu, S., Wang, X., Su, X., Li, Y., Tang, L., Wu, X., Zhao, H., Zhang, Y., Gao, Q., Dong, S., Liu, S., Wang, X., Su, X., Li, Y., Tang, L., Wu, X., & Zhao, H. (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. *The Rangeland Journal*, 37, 57-65. <https://doi.org/10.1071/RJ14080>
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects models and extensions in ecology with R (574 p.). Springer.