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Grant Proposal

The Biodiversity and Climate Variability Experiment (BioCliVE): Quantifying the role of biodiversity in buffering ecosystems against climatic variability

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Abstract

Extreme climate events such as floods and droughts are becoming increasingly frequent and intense across the world. Future climate scenarios predict both an increase in individual extreme events, as well as chronic changes in climatic seasonality. Yet, the combined and relative effects of these pressures on ecosystems remain unknown. Concurrently, human-induced ecological disruption is accelerating species extinction rates, which are estimated to be 100 to 1000 times greater than pre-human levels. This is alarming as greater biological diversity is thought to buffer ecosystem functioning against extreme climate events, thereby safeguarding the provisioning of essential ecological services that contribute to human well-being. However, how and to what extent biodiversity buffers ecosystems against climate variability remains unclear. We recently constructed experimental grassland communities in a mesocosm-based field design representing a realistic gradient of plant diversity. Both extreme events (drought and flood) and a change in seasonality of precipitation are manipulated in a full factorial design to quantify the effects of future seasonal shifts and extremes in precipitation. We will: 1) determine to what extent higher biological diversity ensures that grasslands can continue to provide multiple ecosystem services even in the context of climate change and 2) unravel the fundamental mechanisms by which this is achieved including species asynchrony and positive species interactions. Results of our experimental approach will advance our understanding of the buffering potential of plant diversity and contribute to the development of strategies for sustainable service provisioning of our ecosystems in the face of climate change.

Keywords

biodiversity-ecosystem functioning, biodiversity effects, drought, flood, extreme events, seasonal changes, precipitation, stability, resistance, recovery, resilience, asynchrony, species interactions

Biodiversity and climate change: state-of-the-art

Human activities are triggering unprecedented rates of change to Earth's climatic conditions (Butchart et al. 2010, Diffenbaugh and Field 2013). Increased global temperature is resulting in extreme droughts and floods becoming more frequent and severe across European grasslands (IPCC 2014a). Moreover, seasonal precipitation patterns will be modified with wetter winters and drier summers in northern Europe (Attema et al. 2014). These forecasted changes in precipitation will lead to chronic changes in seasonal water availability (***seasonality***), as well as to increased frequency, intensity and duration of short-term, extreme flood and drought events (***extreme***).

Concurrently and because of this climate change, species extinction rates are accelerating to 100 to 1000 times greater than pre-human levels (Pimm et al. 1995, Diffenbaugh and Field 2013). Yet, biological diversity may serve as a natural buffer against the impacts of both extreme events and chronic manifestations of climate change (McNaughton 1977, Naeem and Li 1997, Yachi and Loreau 1999). If this is true, current human-induced loss of biodiversity threatens the stable provision of essential goods and services from our ecosystems. Understanding and predicting the extent to which future changes in precipitation and biodiversity will interact to impact the functioning of ecosystems is, therefore, one of the most pressing ecological issues of our time. Here, we present the theoretical framework and an experimental design aimed at determining the role of biological diversity in ensuring the provision of multiple ecosystem services in the context of predicted climate changes and quantifying the underlying mechanisms in a grassland ecosystem.

Numerous studies have investigated whether biodiversity buffers ecosystem functioning against climate variability (Tilman and Downing 1994, Pfisterer and Schmid 2002, Caldeira et al. 2005, Kahmen et al. 2005, Ives and Carpenter 2007, Wang et al. 2007, van

Ruijven and Berendse 2010, Jentsch et al. 2011, Wilsey et al. 2011, Lanta et al. 2012, Wright et al. 2015, Klaus et al. 2016). These studies can be classified into two categories (De Laender et al. 2016). First, indirect biodiversity manipulations create a gradient in diversity by applying different levels of an environmental change driver with biodiversity change as a response variable. However, this approach makes it impossible to disentangle the effects of diversity from other confounding variables (Huston (1997), Hautier and van der Plas (2022)). Second, direct biodiversity manipulations (namely, biodiversity experiments) experimentally create a gradient in diversity by taking different subsets of a species pool examining causal relationships between biodiversity and ecosystem function (Hooper et al. 2005). When crossed with manipulations of an environmental change driver, biodiversity experiments can assess the causal and mechanistic links amongst biodiversity, environmental drivers and ecosystem functioning. While some studies have experimentally crossed direct climatic perturbation with diversity manipulation (Pfisterer and Schmid 2002, Kahmen et al. 2005, Wang et al. 2007, Jentsch et al. 2011, Wilsey et al. 2011, Lanta et al. 2012, Vogel et al. 2012, Craven et al. 2016, Hong et al. 2022), they often focus on drought events and net primary productivity as the sole ecosystem response (Hong et al. 2022). Moreover, while these experiments have provided evidence that biodiversity likely is an important buffer against environmental variation, the vast majority of these experiments use coarse manipulations of precipitation, such as rain-out shelters. These shelters prevent rainfall from entering the plot, but are dependent upon natural rainfall and, therefore, make it impossible to have a true control for future climate conditions because ambient climate conditions have already and are continuing to change.

Considering these limitations, there is an urgent need for direct investigations of how realistic future precipitation scenarios, including altered seasonality and extreme events, impact ecosystem multifunctionality within the context of changing biodiversity patterns. This is particularly critical given that:

1. future climate milis projected to not only increase the frequency of extreme droughts, but especially floods (Rowell 2005, IPCC 2007),
2. these extreme events will take place within the context of changed seasonality of precipitation patterns (Attema et al. 2014),
3. these combined changes in climate will accelerate the already increased extinction rate (Pörtner 2021) and
4. society is critically dependent on multiple ecosystem services provided by biodiversity including the regulation of biogeochemical and water cycles, carbon storage and greenhouse gas emissions (*ecosystem multifunctionality*) (Pasari et al. 2013, Hautier et al. 2018).

More reliable predictions of climate change scenarios (Attema et al. 2014) and recent technical advances facilitating the analysis of ecosystem multifunctionality (Chao et al.

2024, Byrnes et al. 2023) now make this possible. To fill this critical knowledge gap, we propose a novel experimental approach that overcomes previous limitations by:

1. manipulating seasonal precipitation patterns (*seasonality*) according to forecast realistic precipitation scenarios for 2085 (Attema et al. 2014),
2. manipulating punctual extreme precipitation events (*extreme*) of increased frequency and intensity as predicted by the IPCC (IPCC 2014b),
3. combining *seasonality* and *extreme* in a full factorial design with a true historical control mimicking pre-climate change precipitation patterns and
4. applying these precipitation manipulations along a manipulated gradient of plant diversity representing a common, globally distributed grassland vegetation.

Experimental design

The Utrecht University Biodiversity and Climate Variability Experiment, or UU BioCliVE (https://www.uu.nl/en/research/ecology-and-biodiversity/research/uu-bioclive), consists of manipulations of precipitation applied to experimental mesocosms of constructed grassland communities representing a realistic gradient of plant diversity (Fig. 1). Two blocks of 44 mesocosms (hereafter plots) for a total of 88 plots have been installed in summer 2017 at Utrecht University's Botanic Garden (The Netherlands, 52 °13' N, 5°29' E). Each plot consists of four subplots each planted in a large high density polyethylene Intermediate Bulk Containers (HDPE-IBC) of 1.2 x 1 x 1 m (l x w x h) for a total of 352 subplots (Fig. 2). Each plot is filled with river sand and top soil excavated from a nearby *Arrhenatheretum elatioris* association nature reserve in the Rammelwaard (52°10' N, 6°11' E), which represents a common, but threatened, temperate grassland association around the world. Plots contain one of four levels of plant diversity: monocultures of each of the twelve selected species, twelve combinations of four species, twelve combinations of eight species and eight plots with all twelve species (Figs 1, 2). The top level of diversity approximates the average diversity level in the target grassland in the Netherlands (ca. 12 species m^{-2}). Natural colonisation is prevented by selective weeding of non-sown species.

Species selection has been based on the *Arrhenatheretum elatioris* association, selecting geographically wide-spread species of importance for agriculture and nature conservation. *Arrhenateretum elatioris* meadows typically occur across west and central Europe on moist to neutral, relatively nutrient-rich soils and play a major role in extensive farming systems (Schaminée et al. 1996). In areas with intensive farming, they are replaced by more productive, less species-rich vegetation. Species selection has been constrained to two functional groups comprising six graminoids and six forbs (Table 1) with the two functional groups being equally represented across the diversity treatments (except in monoculture plots). Legumes were not included because they represent a small fraction of the relative abundance of the *Arrhenatherum elatioris* association, but a dominant role in biodiversity experiments. Each functional group includes species that represent a soil moisture gradient (species Ellenberg values ranging from 3-7). Ellenberg values per species were averaged from databases SynBioSys v.3.6.16 for the

Netherlands (www.synbiosys.alterra.nl) and ECOFACT for the UK (ECOFACT report Volume 2: Technical Annex - Ellenberg's indicator values for British plants). Plots have been sown with commercially supplied seeds from natural populations (Cruydt-Hoeck and MediGran, the Netherlands). Due to the nitrogen leaching from our containers and removal of biomass during the harvest in July, we fertilised each subplot twice per year in April and in July with small amounts of time release fertiliser corresponding to 10 $gm^{-2}y^{-1}$ of nitrogen, 6 $gm^{-2}y^{-1}$ of phosphorus and 9 $gm^{-2}y^{-1}$ of potassium. To activate this fertiliser, we watered the plots with a hose once per week, three times after the fertiliser had been added.

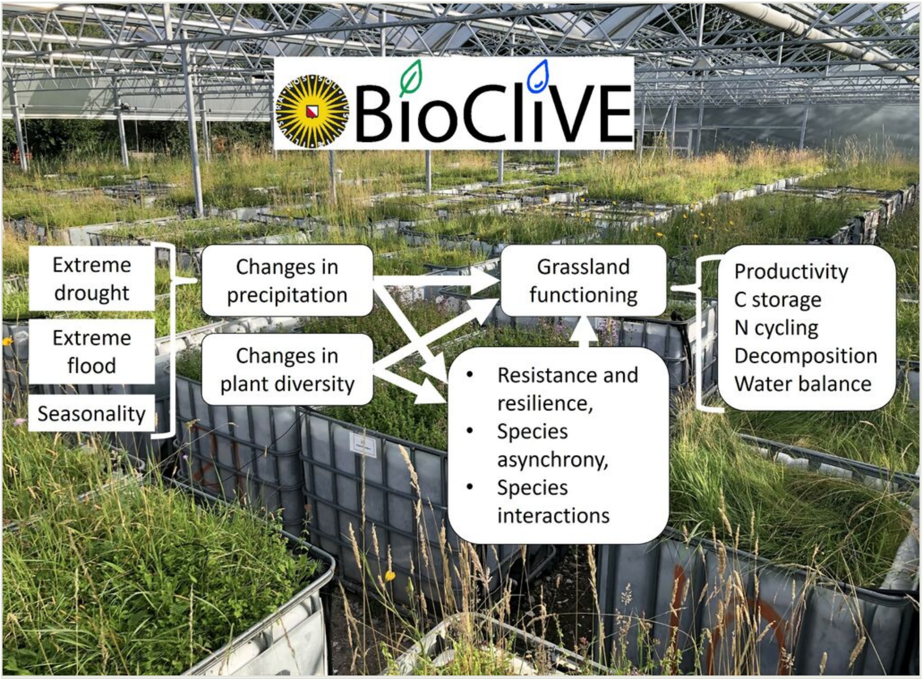

Figure 1. doi

Overview of the project. We investigate whether biodiversity buffers the multifunctionality of grassland ecosystems against realistic changes in precipitation (drought, flood and seasonality). We further assess the contribution of asynchronous plant responses, resistance and resilience and species interactions to grassland stability. Photo credit: Yann Hautier.

The experimental period comprises three phases. In **Phase I** (2017-2022), we exclusively manipulated plant diversity without applying any additional treatments before initiating the precipitation treatments. This timeframe allowed the plant and soil communities to develop before introducing the precipitation treatments. At the end of Phase I, we raised a large retractable roof greenhouse over the experiment, covering all plots. In **Phase II** (2023-2030), during natural precipitation events, the retractable roof automatically closes to prevent plots from unintentional watering outside of the designated amount. The roof remains otherwise open to allow the experiment to be exposed to nearly natural conditions. Precipitation manipulations are applied, based on future precipitation projections developed by the Royal Netherlands Meteorological Institute (KNMI) (Attema et al. 2014) and the IPCC (IPCC 2014b) for the Netherlands and northern Europe. Each plot is divided into four subplots (following a split plot design) with each of the four precipitation treatments, allowing for a full factorial design. The size of the subplots is comparable to those for other grassland experiments that investigate global change impacts (Zavaleta et al. 2010, Pasari et al. 2013) and ensures that precipitation is homogeneous. Each subplot receives a prescribed precipitation treatment by automated drip irrigation watering systems that are programmed to deliver 27 litres of water per hour of watering time directly at the soil surface. This watering system must be shut off when weather is below freezing (i.e. during December, January and February as well as part of March) at the study site. During this time period, the roof remains open allowing natural precipitation to fall on the plots. Containers are equipped with a tap at the bottom to allow flushing and collecting drainage water.

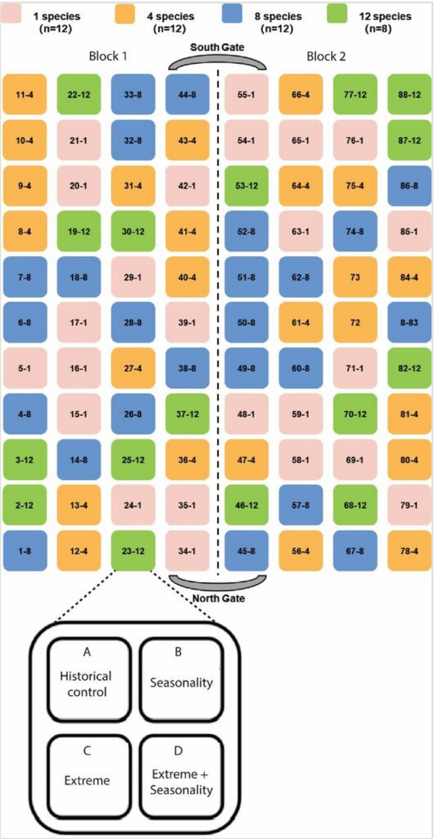

Figure 2. doi

Experimental design representing the plant species richness and precipitation treatment. A) The BioCliVE contains two blocks of 44 plots each for a total of 88 plots. Plots contain one of four levels of plant diversity: 1, 4, 8 or 12 species represented with different colours. Shown are plot numbers followed by their richness level; B) Each plot is divided into four subplots (following a split plot design) with each of the four precipitation treatments.

Table 1.

The BioCliVE species pool. Species frequencies in *Arrhenateretum elatioris* association from SynBioSys v.3.6.16.

Species	**Family**	**Functional group**	**Ellenberg moisture value**	**Frequency in *Arrhenatheretum elatioris***
Arrhenaterum elatius	Poaceae	Grass	5	95
Festuca rubra	Poaceae	Grass	5	66
Rumex acetosa	Polygonaceae	Forbs	5	64
Holcus lanatus	Poaceae	Grass	6	54
Poa trivialis	Poaceae	Grass	6.5	51
Ranunculus repens	Ranunculaceae	Forbs	7	38
Anthoxanthum odoratum	Poaceae	Grass	6	30
Luzula campestris	Juncaceae	Grass	4	14
Tragopogon pratensis	Asteraceae	Forbs	4	14
Veronica chamaedrys	Plantaginaceae	Forbs	5	26
Knautia arvensis	Caprifoliaceae	Forbs	3.5	13
Origanum vulgare	Lamiaceae	Forbs	3.5	8

In the ***historical control***, we add precipitation, based on 50 years of climate data from 1920 to 1971 as reported by the KNMI (Fig. 3 – Historical control). For the other precipitation treatments, we follow the predictions of the KNMI ’14 report scenarios (Attema et al. 2014) for a change in temperature of 3.5 degrees (scenario Wg). This model predicts that both the amount of precipitation and the number of days with precipitation will change by 2085, with increasing rainfall during the winter months and decreasing rainfall and number of days with rainfall during the summer months. We apply the percentage change estimates from the KNMI ’14 model (Fig. 4) to our historical control watering regime to create our ***seasonality*** treatment which mimics this change in both the seasonal amount of rainfall and the number of days with precipitation in each month (Fig. 3 – Seasonality). Climate models also predict that some of this change in seasonal precipitation will be driven by an increase in extreme events, such as extreme drought and flooding (IPCC 2014a). To separate the effects of these extreme events from the change in the seasonality of rainfall, we also apply an ***extreme*** treatment. In this treatment, we reduce the number of rainfall events by 75% relative to the historical control during May and June 2023 to create an extreme drought event and we increase the rainfall events by 75% relative to the historical control in May and June 2027 to create an extreme flood event (Fig. 3 – Extreme). After each extreme event, we allow the system to recover for three consecutive years, time during which the extreme treatment receives the same amount of precipitation as the historical control. Finally, we combine these two experimental treatments in an ***extreme+seasonality*** treatment where we reduce/ increase the number of rainfall events by 75% relative to the seasonality treatment rather than the historical control (Fig. 3 – Extreme+Seasonality). In **Phase III** (2030-NA), weeding is discontinued for one of the blocks. This will allow us to assess the role of non-sown species colonisation in buffering against climate change. Furthermore, movement across the landscape will be simulated by seed rain of a mixture of non-planted seeds. This will allow us to assess the importance of priority effects and succession on the buffering capacity against climate change.

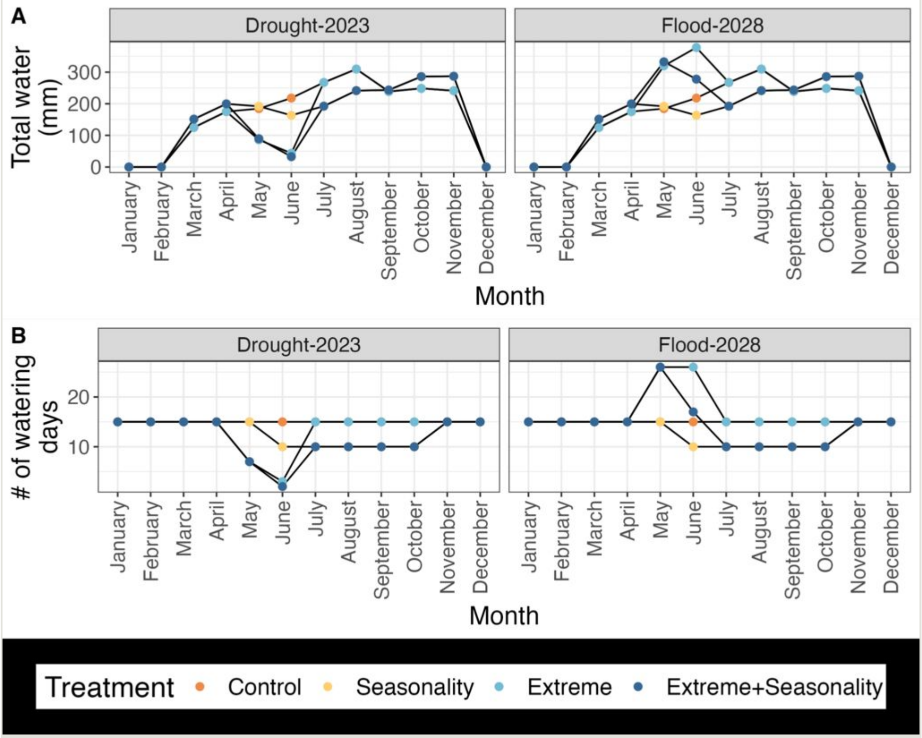

Figure 3. doi

Total amount of water added per month (A) and number of watering days per month (B) across the four BioCliVE precipitation treatments.

Measurements

We measure the buffering capacity of plant diversity against changes in water availability across a suite of fundamental ecosystem variables that are proxies for ecosystem functions and services classified into three categories of services, based on the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005). Provisioning services are associated with forage fodder quantity (aboveground plant biomass) and quality (fat, mineral, crude protein and fibre fractions). Supporting services are related to nutrient uptake and cycling (plant root production, decomposition, soil plant available nitrogen [total N, nitrate and ammonium] and phosphorus [inorganic P], nutrient leaching). Regulating services are linked to resistance to pathogens, pest control, carbon cycling (soil organic carbon accumulation, leaching of dissolved organic C, N and P, ecosystem respiration, net ecosystem CO_2 exchange, soil invertebrate feeding activity and litter decomposition) and water balance. The functionality of associated soil communities is also included by tracking enzymatic activities, nutrient cycling potential, community respiration and properties related to plant disease suppression (Faust and Raes 2012). The number of measurement campaigns depend on the function measured. For example, plant biomass per species and community root biomass are measured once a year at the peak growing season in July. Plant traits above- and belowground are measured prior to each harvest. High-throughput phenotyping will utilise digital images of plant material analysed for specific traits by Plant Computer Vision (PlantCV) software. Treatment impacts are related to single and multiple functions simultaneously using the average (Hooper 1998, Maestre et al. 2012) and multiple threshold multifunctionality (Zavaleta et al. 2010, Pasari et al. 2013) as described in our recent publication (Hautier et al. 2018). Measurements of changes in functional traits related to resource use and capture (e.g. root diameter, length, volume and distribution, specific leaf area, plant height, leaf nutrient content) in response to the diversity and watering regimes will allow us to assess the role of functional diversity in buffering against climate change.

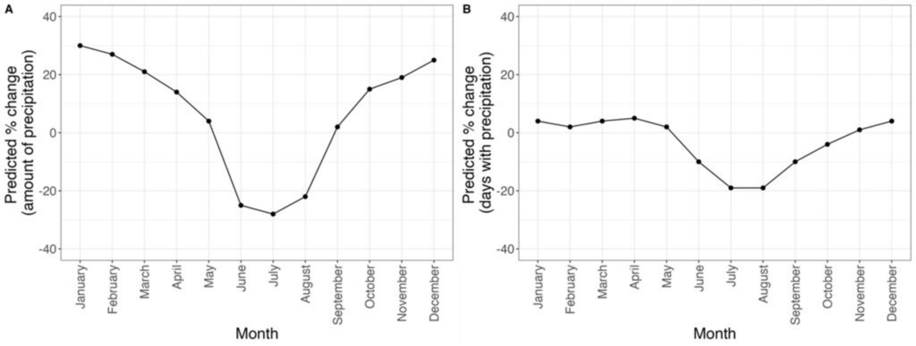

Figure 4. doi

Percent change in precipitation amount (A) and the number of days with precipitation (B). These calculations make use of the predictions in the KNMI ’14 report (Attema et al. 2014).

Objectives

The overarching goal of this project is to **understand and predict the extent to which plant diversity buffers the integrated functioning of grassland ecosystems against future changes in precipitation**. We hypothesise that plant diversity will stabilise ecosystem functioning against variability in precipitation. We hypothesise that the functioning of species-rich communities will be more resistant to extreme events as compared to that of species-poor communities, but that both types of communities will have similar abilities to return to their original functional states (i.e. different resistance, but similar resilience, leading to lower invariability). We hypothesise that the same will be the case for the seasonality treatment, but that the magnitude of change in functioning will be much less as compared to the extreme treatment leading to a higher invariability. We hypothesise that the impact of the combined extreme+seasonality treatment on functioning will lead to additive effects on functioning. We also hypothesise that ecosystem functioning will be strongly linked with species interactions. We will address the following three key objectives (Fig. 1):

***Objective 1*: *Importance of plant diversity to buffer grassland multifunctionality against future changes in precipitation patterns*.** We will fit generalised linear mixed-effects models (GLMM) with block as random effect to test for the effects of plant species richness, precipitation scenarios and their interaction on single and multifunctionality (Hautier et al. 2018). We will further evaluate the buffering effect of plant diversity by analysing changes in ecosystem multifunctionality across precipitation scenarios for each species richness level. Smaller changes in ecosystem multifunctionality in response to change in precipitation at higher species richness level provides evidence for plant diversity buffering against climatic changes.

***Objective 2*: Identify the mechanistic underpinnings that determine whether plant diversity buffers ecosystem functions against the impacts of changing precipitation patterns.**

Objective 2a: In species-rich communities, the decline in the functioning of some species may be compensated for by increases in other species, thereby buffering temporal fluctuation in the functioning of the whole community (species asynchrony) (Yachi and Loreau 1999, Loreau and de Mazancourt 2008, Loreau 2010, Gross et al. 2014). In past studies, we demonstrated the importance of species asynchrony in stabilising ecosystem productivity through time using grassland sites worldwide (Hautier et al. 2014). Here, we will utilise two recently developed asynchrony metrics, as well as high-throughput phenotyping of harvested plant material, in order to explore intra- and inter-specific species asynchrony in traits associated with tolerance to drought and flooding conditions. Relating asynchrony with species richness and variations in ecosystem functioning will allow us to test whether compensatory mechanisms are a determinant of grassland stability against environmental fluctuations.

Objective 2b: More diverse plant communities may also buffer ecosystem functioning against climate events through increased resistance (i.e. functions show little deviation from normal during perturbations), increased resilience (i.e. functions return to normal rapidly after perturbations) or both. Diverse plant communities might be more resistant because they are more likely to contain species that thrive during the disturbance, thus compensating for species that are negatively affected. Similarly, species-rich communities are more likely to contain species that recover faster after the disturbance. Ecosystem multifunctionality will be measured before, during and after application of precipitation scenarios, thus allowing us to assess resistance and resilience according to our recent publication (Isbell et al. 2015). Resistance will be indicated by small changes in ecosystem multifunctionality relative to normal levels during a precipitation scenario and resilience by the rate of return towards normal ecosystem multifunctionality levels after a precipitation scenario.

Objective 2c: We will follow the development of soil-borne microbial communities over time in relation to plant diversity, plant identity and precipitation treatment. High-throughput sequencing will be used to track the microbial community structure (bacteria, archaea and micro-eukaryotes) and quantitative PCR approaches will be used to monitor the density of microbial gene families involved in key activities related to plant disease suppression (e.g. antibiotic production) and carbon and nitrogen cycling (Faust and Raes 2012). Microbial responses to precipitation manipulation treatments will also be monitored by tracking potential enzyme activities of the soil communities and fluctuations in these activities will be related to plant diversity and identity.

Objective 3**: Separate the individual and interactive effects of seasonality and extreme precipitation events on grassland functioning.** A series of modelling experiments carried out in mimicked field conditions of a mesic grassland of the US Great Plains, has recently suggested that extreme drought affects carbon loss at least as much as seasonal drought and that combining a realistic seasonal and extreme drought scenario leads to intermediate effects on carbon loss compared to either seasonal or extreme drought alone (Hoover and Rogers 2016). Our experimental manipulation of *seasonality* and *extreme* precipitation events in a full factorial design will allow us, for the first time, to assess this experimentally and directly compare the magnitude of drought and flood impacts on grassland functioning undergoing changes in extreme or seasonal precipitation events. Additionally, results will establish whether the impact of extreme and seasonality precipitation scenarios are additive or interactive.

Innovative aspects

Our experiment will, for the first time, manipulate both chronic seasonal precipitation patterns and punctual extreme precipitation events that, when combined, simulate forecasted precipitation scenarios in northern Europe. Further, we do this using a state-of-the-art watering system in combination with a retractable roof to overcome the inability of rain-out shelters to make a true historical control. The *seasonality* and *extreme* precipitation scenarios will be applied in a full factorial design allowing unprecedented assessment of individual and interactive effects between chronic and punctual events on grassland functioning. Importantly, precipitation scenarios will occur within a gradient of manipulated plant diversity allowing us to determine whether diverse communities are less affected by these changes than depauperate communities and, thus, whether biodiversity buffers ecosystem multi-functionality against future climate variability. Our study will, therefore, provide a mechanistic understanding of plant diversity impacts on ecosystem stability and function across realistic future precipitation scenarios. This novel integrated approach will provide the much-needed predictive insights on mechanisms and processes governing ecosystem responses to future precipitation changes, thereby providing information for projections of global change impacts on the functioning of grassland ecosystems.

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Grant title

NWO Open Programme

Conflicts of interest

The authors have declared that no competing interests exist.

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