

## Research

### Coastal heathland vegetation is surprisingly resistant to experimental drought across successional stages and latitude

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In the last decade, several major dwarf-shrub dieback events have occurred in northern European coastal heathlands. These dieback events occur after extended periods with sub-zero temperatures under snow-free conditions and clear skies, suggesting that coastal heathlands have low resistance to winter drought. As climate projections forecast increased drought frequency, intensity, and duration, coastal heathlands are likely to experience more such diebacks in the future. There are, however, few empirical studies of drought impacts and responses on plant communities in humid oceanic ecosystems. We established a drought experiment with two distinct levels of intensified drought to identify responses and thresholds of drought resistance in coastal heathland vegetation. We repeated the experiment in two regions, separated by five degrees latitude, to represent different bioclimatic conditions within the coastal heathlands' wide latitudinal range in Europe. As coastal heathlands are semi-natural habitats managed by prescribed fire, and we repeated the experiment across three post-fire successional phases within each region. Plant community structure, annual primary production, and primary and secondary growth of the dominant dwarf-shrub *Calluna vulgaris* varied between climate regions. To our surprise, these wide-ranging vegetation- and plant-level response variables were largely unaffected by the drought treatments. Consequently, our results suggest that northern, coastal heathland vegetation is relatively resistant to substantial intensification in drought. This experiment represents the world's wettest (2200 mm year<sup>-1</sup>) and northernmost (65°8'N) drought experiment to date, thus filling important knowledge gaps on ecological drought responses in high-precipitation and high-latitude ecosystems across multiple phases of plant community succession.

Keywords: arctic browning, Atlantic heathlands, climate change, fire, International Drought Experiment (IDE), rain-out shelter

#### Introduction

Drought is projected to increase in frequency, intensity, and duration in most terrestrial biomes under current and future anthropogenic climate changes (Dai 2013, Shukla et al. 2019), but ecological responses to drought are intrinsically hard to predict



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(Marshall et al. 2008, Zhang et al. 2019). Because of increased temporal and spatial heterogeneity in precipitation patterns with climate change (Knapp et al. 2008, Butcher et al. 2014), intensified drought is projected also in regions with high and increasing mean annual precipitation (Mishra and Singh 2010, Dai et al. 2018). Northern-European coastal heathlands are located in oceanic coastal regions with high annual precipitation (1000–2200 mm annually) and low seasonal amplitude in temperature compared to adjacent inland regions. During the last decade, this heathland region has been subjected to increased precipitation, but also extreme and prolonged winter droughts, the latter of which has been implicated in severe dieback events of the dominant species *Calluna vulgaris* (hereafter *Calluna*) (Hancock 2008, Phoenix and Bjerke 2016, Parmentier et al. 2018). These dieback events have raised considerable concern about how this landscape and its associated ecosystem services will persist in a future climate with increased drought risk.

In recent decades, land-use changes have transformed large tracts of European semi-natural and natural open lowland habitats into either urban developments or arable land (Desender et al. 2010, Exeler et al. 2010), or afforested or naturally reforested habitats (Velle et al. 2014, Wehn and Johansen 2015). As a result of this widespread heathland habitat loss and degradation, coastal heathlands are now considered endangered on both the Norwegian and EU red lists of habitats (EC Habitats Directive 1992, Hovstad et al. 2018). Because of the abandonment of traditional management, current heathlands are disproportionately dominated by old and degenerative successional phases (Moen et al. 2006). The post-fire successional phases differ in community composition, structure and biomass, and hence also in ecosystem functioning (Smith and Knapp 2003, Garnier et al. 2004, Winfree et al. 2015). If different successional phases also differ in resistance and resilience to drought, the cessation of heathland management will have additional implications for conservation and ecosystem functioning. Identifying patterns and thresholds of drought resistance in heathland ecosystems is therefore of key interest for regional economies and culture, nature conservation and climate change mitigation.

During the past two decades, numerous drought experiments attempted to quantify responses and resistance of plant communities and ecosystem functioning to temporary reduction or exclusion of precipitation (Hoover et al. 2018). Recurring responses to intensified experimental drought include reduced plant species richness and primary production (Prieto et al. 2009, Lanta et al. 2012). However, diverging ecological responses to drought between similar ecosystems suggest context-dependencies resulting from e.g. different dominant vegetation types (Cherwin and Knapp 2012, Kimball et al. 2016), land-use legacies (Foster et al. 2003, Bürgi et al. 2017, Karlowsky et al. 2018, Legay et al. 2018) or variation in baseline climatic conditions (Knapp et al. 2017, Slette et al. 2019, Korell et al. 2021). The observed climatic context-dependencies in vegetation responses to drought remain particularly problematic as existing drought experiments are clustered in temperate and relatively

low-precipitation regions in the United States and in central and Mediterranean Europe, and therefore cover limited geographical, ecological, and climatic extent (Hoover et al. 2018, Stuart-Haëntjens et al. 2018). In contrast, few experiments have so far investigated drought impacts in 1) high latitudes, 2) ecosystems with high annual precipitation, and 3) along secondary successional gradients (Prieto et al. 2009, Bretfeld et al. 2018, Hoover et al. 2018), which are all key characteristics of north-European heathlands. Consequently, our current knowledge from existing drought experiments is poorly suited for predicting drought resistance in northern coastal heathlands.

Because of the nature of drought, with high variation in frequency and duration (Mishra and Singh 2010), and because of time-lagged ecological responses, especially in systems dominated by long-lived species (Svenning and Sandel 2013), reports of ‘no effect’ in short-term ecological drought experiments might hide emerging but delayed responses (Magurran et al. 2010, Knapp et al. 2012, Wolkovich et al. 2012). One way to increase the sensitivity of ecological measurements is to focus on demographic parameters and plastic responses in growth or functional traits at different stages in a species life cycle, as these respond to drivers on relatively short timescales (Kimball et al. 2016). Traits related to growth, survival or reproduction of the whole plant community, or of keystone or indicator species, can reveal short-term responses to drought, and thereby predict longer-term community outcomes (Smith and Knapp 2003), even when species abundances remain unaltered during the course of the study (Kimball et al. 2016).

Here, we present vegetation responses in a four-year intensified drought experiment in Norwegian coastal heathlands. We use rainout shelters (Yahdjian and Sala 2002) to create two levels of drought (60% and 90% shelter cover) in addition to an ambient control treatment, which we repeated within each of the three main post-fire successional phases of coastal heathlands (Gimingham 1988; Fig. 1b) and in two regions – in southern Norway, where coastal heathlands are highly abundant, and in northern Norway, close to the northern range-edge of coastal heathlands. From this experiment we report effects of experimental drought on 1) plant community composition, specifically richness, evenness and Bray–Curtis dissimilarity, 2) aboveground primary production, and 3) annual primary and secondary growth on >400 specimens of the dominant species *Calluna*. We replicated each drought treatment three times. We hypothesised that the coastal heathland plant community will be less resistant to intensified drought in H1) the northern region which is on the colder-climate brim of the coastal heathland distribution, and H2) early successional phases where plants have more acquisitive traits and shorter life cycles. In addition, we hypothesised that H3) *Calluna* growth would be most susceptible to drought in the young successional phase because of the relatively faster growth shortly after the fire, and especially in the north where all new plants originate from seedlings, increasing the shoot : root ratio relative to the vegetative resprouting observed further south (Nilsen et al. 2005,

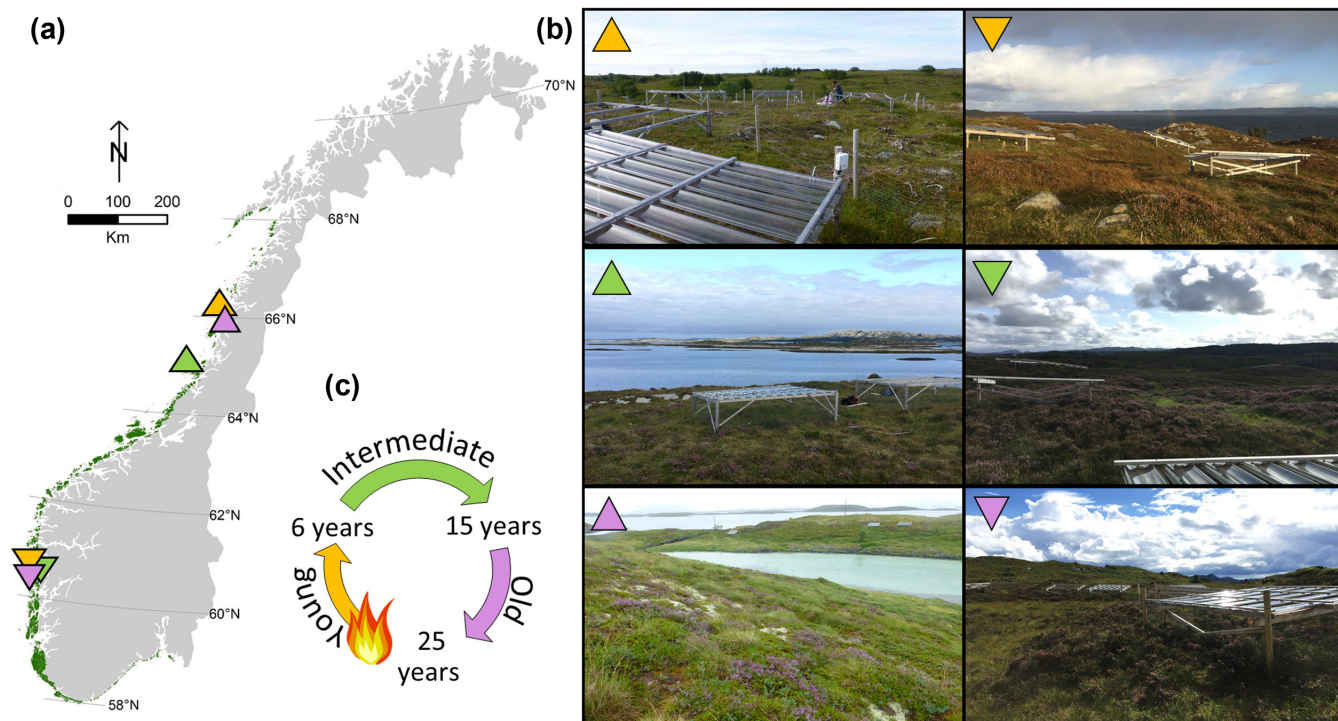


Figure 1. Study system, study sites, and experimental setup. (a) The geographical distribution of coastal heathlands in Norway (dark green area), with the six study sites indicated. Shapes indicate regions (▲ = north, ▼ = south), colours indicate the post-fire successional phase of each site, based on (b) the traditional heathland management cycle (Watt 1947, Gimingham 1988, Velle et al. 2021). (c) The six study sites, representing the successional phases from young (top) to old (bottom) in the north (left-hand photos) and south (right-hand). Table 1 for site details. Within each site, we implemented a DroughtNet rainfall exclusion experiment (using  $3 \times 3$  m roofs) with three treatments (ambient, moderate = 60% roof cover, extreme drought = 90% roof cover) replicated three times, for a total of 54 plots (see text for details). Southern sites are spaced out slightly for visibility.

Velle and Vandvik 2014). Specifically, we expected to observe changes in plant community composition and reduced primary production as symptoms of low drought resistance.

## Material and methods

### Study system

Northern-European coastal heathlands constitute semi-natural landscapes, managed by prescribed fire and low-intensity grazing for millennia (Vandvik et al. 2005, Måren et al. 2010), and they are valued for their ecological and cultural history (Gimingham 1987, Hjelle et al. 2018). *Calluna* is present across the whole post-fire successional gradient but changes morphology from long apex growth in the early post-fire years, to a bushier growth after 6–15 years, before stands grow coarser with reduced canopy density after 15 years. The morphology of *Calluna* is often used to identify the successional phase of the management cycle displayed in Fig. 1b (Gimingham 1988, Velle et al. 2021). This growth pattern is consistent for *Calluna* across its geographical range, but populations show region-specific traits (Vandvik et al. 2014, Meyer-Grünefeldt et al. 2016). For example, whilst *Calluna* frequently resprouts from belowground organs after

fire, only seed germination is observed north of 63 degrees north (Nilsen et al. 2005, Velle and Vandvik 2014). Today, the landscape heterogeneity shaped by post-fire succession supports important habitats have become increasingly important for a range of species, including red-listed birds, plants, invertebrates and fungi (e.g. Eurasian eagle-owl *Bubo bubo*, marsh gentian *Gentiana pneumonanthe*, grey scalloped bar *Dyscia fagaria* and orange waxcap mushroom *Hygrocybe aurantiosplendens*). More recently, coastal heathlands are also acknowledged for their role as a large terrestrial carbon pool (Marrs et al. 2019, Bartlett et al. 2020, Friggens et al. 2020).

### Study sites

The study is conducted in six coastal heath vegetation sites in Norway. The study sites were selected to represent three successional phases separated by time since last fire each sampled in two distinct geographical regions, at ca 60°N and near the northern brim of the Atlantic heathland distribution at ca 65°N (Fig. 1a). All sites are representative for their post-fire successional phase and the geographical region (Velle and Vandvik 2014). Specifically, the young successional phases have high cover of graminoids (e.g. *Agrostis* spp., *Festuca rubra*) and forbs (*Potentilla erecta*, *Trientalis europea*, *Galium saxatile*), while the cover of dwarf shrubs



*Calluna vulgaris* is initially low but increases with time since fire. The intermediate successional phases have denser cover of dwarf shrubs (*Calluna vulgaris*, *Erica tetralix*, *Vaccinium* spp.) and a few sedges *Carex* spp.. Last, the old successional phases are dominated by taller and coarser *Calluna vulgaris* stands. The bryophyte ground cover (dominated by *Hypnum* spp., *Hylocomium splendens*, *Pleurozium schreiberi*) recovers gradually after fire. In general, the northern sites have more boreal species than the southern sites (e.g. *Trichophorum cespitosum*, *Arctous alpinus* and *Arctostaphylos uva-ursi*). The climatic differences between regions are reflected in higher precipitation and a longer duration of the growing season in the southern region, whereas mean summer and winter temperatures are similar between regions (Table 1). All sites are rich in soil organic matter (30–40% dry weight in the upper 30 cm), acidic (pH 3.8–4.9, except for the young site in the north where pH ranged from 4.4 to 6.3), with a soil depth of 20–30 cm, and high soil water holding capacity ( $-0.7 \text{ g}_w \text{ g}_s^{-1}$ ) (Haugum 2021).

## Experimental design

We installed nine  $2 \times 2$  m permanent plots at each of the six sites in 2016, following the Drought-Net protocol for short-stature vegetation (Drought-Net 2017). In spring 2017, we randomly allocated plots to either moderate drought, extreme drought or ambient controls, resulting in three replicate plots per treatment, successional stage and region, for a total of 54 plots (Fig. 1c). The three levels of drought were implemented by fixed rainout shelters (modified from Yahdjian and Sala 2002) with 60, 90 and 0% roof cover (Icopal Fastlock Uni Clear), respectively. All plots were fenced in spring 2017, except on the northern intermediate site located on a small island, with no large herbivores present during the first two years of the experiment. Here, the plots were fenced in spring 2018.

## Microclimate

Local climate stations with a temperature sensor and precipitation gauge were installed in each site to monitor microclimate and drought effects. Soil moisture sensors were installed at 15 cm depth in all plots from summer 2017. From October 2018 to January 2020, we measured temperature sensors at 8 cm soil depth and at ground level at all sites in the south to

quantify potential warming side effects from the plastic roofs. Moreover, we set up local climate stations to measure quantified photosynthetic active radiation (PAR) inside the plot, and rainwater intercepted by the roof, in one moderate and one extreme drought treatment in the intermediate phase in the south for the same period (Haugum 2021).

## Plant communities

We surveyed vegetation composition in all plots annually from 2016 (pre-treatment year) to 2020. These measurements were made in a permanently marked  $1 \times 1$  m plot. At peak growing season, mid-July to late August, we visually determined the ground cover of all vascular plants and bryophytes on species level, except for liverworts which we registered collectively as one taxon. We followed the nomenclature of (Lid and Lid 2013) for vascular plants and (British Ecological Society 2010) for bryophytes. Because of canopy layering the sum of coverages was frequently  $>100\%$ .

## *Calluna* traits

In each plot, we selected 10 individuals of *Calluna*, targeting five of the shortest individuals and five of the tallest individuals in each plot to maximise variation in size. On each individual, we measured primary growth as stand height in mm (one replicate), current year's growth on three random shoots in mm following (Mohamed and Gimingham 1970), and secondary growth as stem diameter in mm (three replicates). These measurements were made annually in October, which is at the end of the growth season, from 2016 to 2019. Some individuals in the young successional phases in both north and south were lost to grazing in the winter 2016/2017 when the plots were not fenced. In addition, the individual markings on several individuals in the young successional phase in northern Norway were torn off (likely by sheep or birds) to such an extent that we excluded the *Calluna* measurements from this site from the analysis due to low replicate numbers.

## Biomass harvest

We measured standing aboveground biomass by destructively harvesting three randomly placed  $25 \times 25$  cm squares within each  $2 \times 2$  m plot, avoiding the permanent  $1 \times 1$  m plot, in August 2019. All vascular plants rooted inside the square

Table 1. Climatic and ecological site information. Mean annual precipitation (MAP) is based on data from 1990 to 2019, whilst mean summer temperature (MST) and mean winter temperature (MWT) is based on data from 1980 to 2019. Length of growth season (GS) are based on data from 2019. Supporting information for climate data sources (Supporting information). Time since last fire is provided by the local land-owners (Haugum 2021).

Region and successional phase	MAP (mm)	MST (°C)	MWT (°C)	GS (days)	Latitude	Burned (year)
North young	1254 ± 184	13.4 ± 1.3	0.7 ± 1.6	147	65°50'12.4"	2014
North intermediate	1720 ± 461	13.3 ± 1.4	1.5 ± 1.9	150	64°46'44.4"	2010
North old	1254 ± 184	13.4 ± 1.3	0.7 ± 1.6	147	65°47'45.7"	Before 1980
South young	2020 ± 345	13.8 ± 1.5	3.4 ± 1.8	214	60°42'03.0"	2013
South intermediate	2020 ± 345	13.8 ± 1.5	3.4 ± 1.8	214	60°42'03.0"	2004
South old	2020 ± 345	13.8 ± 1.5	3.4 ± 1.8	214	60°42'03.0"	1996

were harvested, in addition to bryophytes, lichens and litter within the square. Vascular plants were sorted into Ericales, graminoids, forbs and bryophytes. Standing dead plant matter, including yellow graminoid leaves, were sorted as 'dead'. Each biomass fraction per square was dried at 65°C for minimum 48 h, before weighing at 0.01 g precision.

## Data analysis

All data analyses were performed in R ver. 4.0.2 (<www.r-project.org>). To assess the drought effect of the rain-out shelters, we quantified both meteorological and ecological drought. Meteorological drought was calculated using standardized precipitation evapotranspiration indices, using the package SPEI (Beguería and Vicente-Serrano 2017). First, historic precipitation and temperature data were retrieved from the nearest public meteorological station (available from Norwegian Centre for Climate Services (NCCS), Supporting information for details). These data were available from approximately 1980 to 2019. To estimate the drought effect of the rain-out shelters, we calculated SPEI values for the moderate and extreme drought intensities by reducing the precipitation data by the amount of rainwater intercepted by the 60% and 90% cover rainout shelters, using measurements of rain interception from the local climate stations. Ecological drought was quantified using the soil moisture measurements.

The variation in species composition within and between sites was visualised as a non-metric dimension scaling plot using the *metaMDS* function in the *vegan* package (Oksanen et al. 2019). The *anosim* function was used to test for differences in species composition between regions and successional stages (999 permutations, Bray–Curtis dissimilarity). Evenness ( $E_{var}$ ) was calculated for the fourth year of the drought treatment (2020) using the *community\_structure* function in the *codyn* package (Hallett et al. 2020).

The effects of drought, successional phase, region and their interactions on plot-level plant community structure, plot-level standing biomass and individual-level *Calluna* growth were assessed parametrically with linear mixed-effects models with restricted maximum likelihood in the *lme4* package (Bates et al. 2015). We based these models on the data collected in the fourth year, except for Bray–Curtis distance and *Calluna* height and stem diameter, which were quantified as the difference between the first and the fourth year. To reduce model complexity, we analysed regions and successional phases individually instead of building full models with nested designs. Specifically, two-way interactions between drought and successional phases as fixed factors were explored within regions (north versus south;  $n=27$  per region), and interactions between drought and region as fixed factors were explored within successional phases (young, intermediate and old;  $n=18$  per successional stage). For *Calluna* models, plot was specified as a random factor. We ran all models as full-factorial hypothesis tests without model optimization. To explore to what extent non-significant results were due to low power, we also ran a stepwise backwards model selection to explore if other factors were significant if higher-order terms

were dropped. Biomass for individual functional groups was Log10 or square root transformed to achieve normality and homogeneity of variances.

## Results

### Experimental drought effects on microclimate

The rainfall interception by the roofs were  $32.1 \pm 10.3\%$  and  $43.5 \pm 20.3\%$  for the moderate and extreme drought treatment, respectively. This increased frequency and intensity of meteorological drought in two distinguishable levels below the ambient (control) level (Fig 2a). Specifically, the extreme drought treatments incurred meteorological drought (SPEI  $< -1$ ) and extreme drought (SPEI  $< -2$ ) both more frequently and with longer duration than the controls. Overall, the annual precipitation during the study period was between 77% and 98% of the normal rainfall based on the 1981–2016 climate normal (Supporting information), with high annual and interannual variability, where winter and early growth season tended to be drier than the climate normal, especially in the northernmost sites.

The roof cover also reduced soil moisture, but with considerable variation between sites and over time (Fig. 2b). The effect was more pronounced in dry than wet periods, indicating that the treatments resulted in increased drought intensity and frequency, rather than in lower mean soil moisture overall. Specifically, the moderate and extreme drought treatment reduced daily mean soil moisture during summer (June–August) with  $2.3 \pm 3.9\%$  ( $p < 0.001$ ) and  $26.5 \pm 4.2\%$  ( $p < 0.001$ ), respectively, across sites and successional phases. However, in July 2018, when a natural drought occurred, soil moisture was  $14.2 \pm 36.9\%$  and  $32.0 \pm 26.2\%$  lower in the moderate and extreme drought, respectively. In contrast, no significant effect of the drought treatments was observed on mean soil moisture through winter (December–February) (Fig. 2b).

### Plant community composition and structure

Species composition varied between regions and successional stages in accordance with the overall study design (Fig. 3;  $R=0.72$ ,  $p=0.001$ ). Specifically, the post-fire successional phases clustered chronologically with post-fire time from low to high axis 1 score, whereas the two regions were separated on axis 2 (Fig. 3). The NMDS successfully captured the main compositional variation in the vegetation (stress=0.12). The species composition within sites was more variable over both space and time in the north, and in the younger successional stages within each region (Supporting information, Table 2). In contrast, plant community composition was not affected by drought treatments, as reflected in the relatively minor shifts overtime of the drought treatments in the NMDS plot (Fig. 3) and in the minor and non-significant changes in Bray–Curtis dissimilarity over time in response to drought treatments (Table 2).

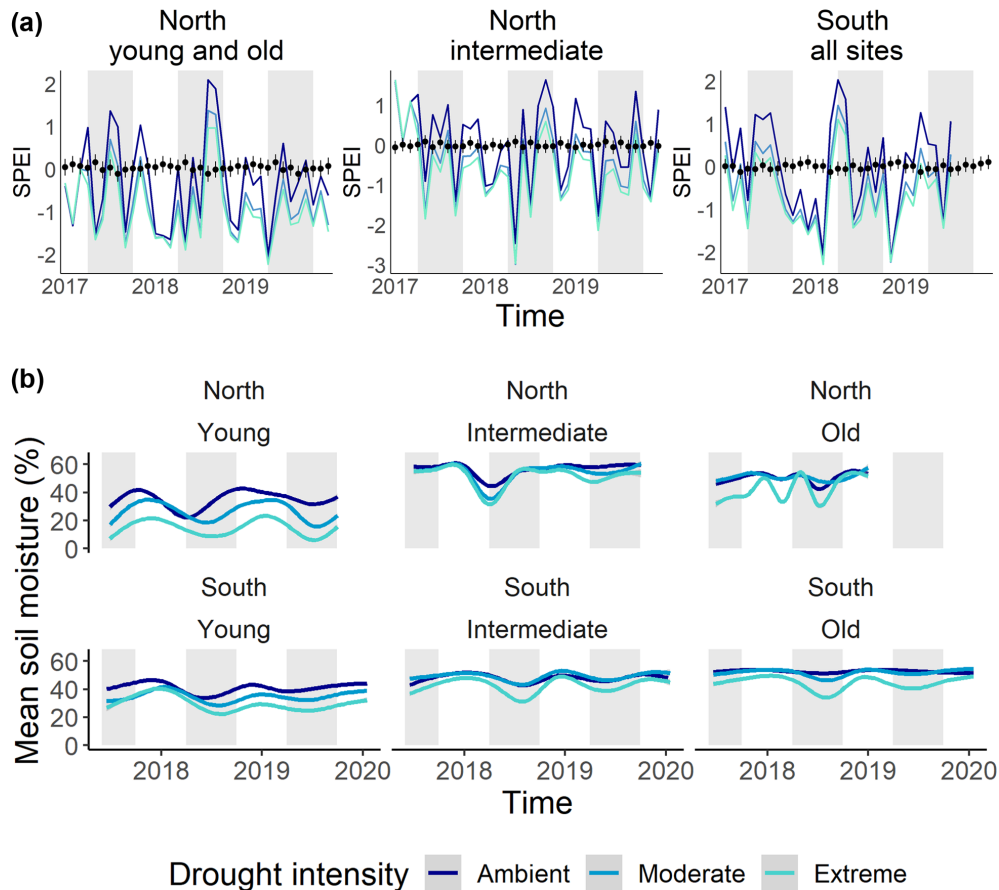


Figure 2. Drought treatment effects on precipitation and soil moisture. (a) Average standardized precipitation evapotranspiration index (SPEI) in the three drought treatments (dark blue = ambient; pale blue = moderate drought, 60% roof cover; turquoise = extreme drought, 90% roof cover) over the study period 2017–2019 compared to long-term monthly averages (black symbols  $\pm$  1 SE) from 1981 to 2019 in the south and 1991 to 2019 in the north. (a) Mean soil moisture in the three drought treatments in each site across the study period. Values are means of replicates ( $n = 3$ ) of the same drought treatment and successional phase combination. Soil moisture is recorded at 15 cm depth every 20th minute. Grey shades indicate the growing season (April–September).

Plant community structure also differed between regions, and between successional phases within regions. Specifically, the northern region had greater species richness than the southern region, and species richness and evenness decreased with time since fire within both regions (Table 2). Experimental drought generally did not affect the community structural parameters, however, except for the intermediate successional phase in the southern region, where evenness decreased in response to the extreme drought treatment (Table 2).

### Biomass

Total biomass increased with post-fire age ( $p < 0.001$  in the north and  $p = 0.02$  in the south; Fig. 4), and was also higher in the south than the north for the young successional phase ( $p < 0.001$ ) and the intermediate successional phase ( $p = 0.041$ ). Generally, the biomass harvested in 2019, three years after the start of drought manipulation, was not affected by the drought treatment. Litter increased with drought in the old successional phase in the south. See the Supporting information for details on responses for each functional group.

### *Calluna* traits

*Calluna* stands in the old successional phase in the north responded to the extreme drought treatment by increasing annual shoot length growth by 76% and 83% compared to the moderate drought treatment and the ambient control, respectively (Fig. 5a). We did not observe any other responses to drought on *Calluna* primary or secondary growth. Height and stem diameter growth over the 2016–2019 period declined from the intermediate successional phase to the old successional phase in the north (Fig. 5b–c), while stem diameter growth showed the opposite response in the south. Primary growth was much higher in the south than in the north. Specifically, annual shoot increment was 83% ( $p < 0.001$ ) and 226% ( $p < 0.001$ ) higher in the intermediate and old successional phase, respectively, and increase in stand height was 75% ( $p = 0.040$ ) and 624% ( $p < 0.001$ ) higher, respectively. However, the increase in stem diameter was 296% higher in the north than in the south in the intermediate phase ( $p = 0.003$ ), and 227% higher in the south than in the north in the old successional phase ( $p = 0.002$ ).

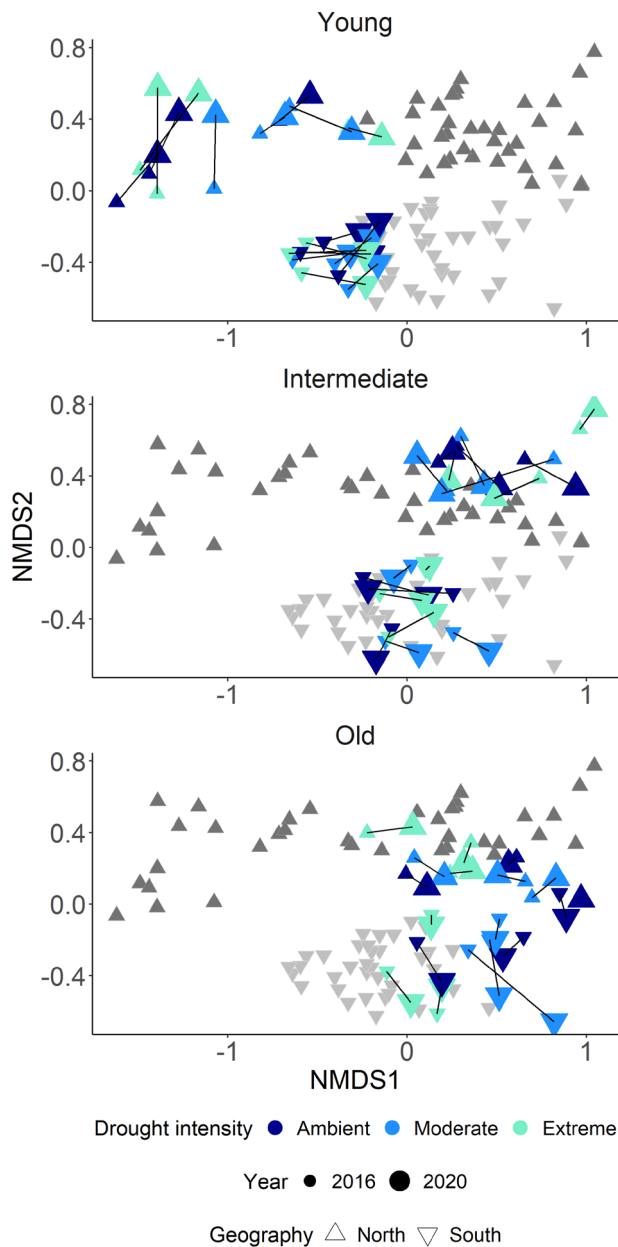


Figure 3. Changes in species composition across all sites and treatments over time, based on a non-metric dimensional scaling (NMDS) of the vascular and non-vascular plant community composition across all sites, treatments and years. For clarity, the NMDS is displayed three times, highlighting patterns in the (a) young, (b) intermediate and (c) old successional phases, with only first and last years are shown. Within each plot, the drought treatments of the highlighted phase are represented by the blue scale (dark blue = ambient; pale blue = moderate drought, 60% roof cover; turquoise = extreme drought, 90% roof cover) and the last year is indicated using larger shapes. On all plots, shapes indicate regions ( $\blacktriangle$  = north,  $\blacktriangledown$  = south), grey shading displays non-focal site plots; pale grey for the south, dark grey for the north. Stress = 0.12.

## Discussion

Here we report on plant community responses to experimental drought; specifically on changes in the species composition, richness and evenness of the heathland vegetation, and biomass and species-specific growth of the dominant dwarf-shrub *Calluna* over four growing seasons. The experiment successfully induced two distinct levels of drought across three post-fire successional phases in two climatic different regions. However, we found surprisingly few ecological responses to experimental drought. Moreover, we did not find support for the hypotheses that resistance to experimental drought is lower in (H1) heathland plant communities on the northern brim of the coastal heathland distribution, and (H2) plant communities in early post-fire successional phases. This experiment represents the world's wettest ( $2200 \text{ mm year}^{-1}$ ) and northernmost ( $65^{\circ}8'N$ ) drought experiment to date (Korell et al. 2021), and it therefore adds knowledge about drought responses in understudied climatic and ecological space. Below we discuss the microclimatic changes caused by the drought experiment, our observed responses, and how this study contributes to an improved understanding of ecological drought responses in general.

### Experimental drought conditions

The fixed rainout shelters (following the design in Yahdjian and Sala 2002) successfully imposed two distinct levels of drought in addition to the ambient control, as assessed by our climatic and soil moisture data, but with large intra- and interannual variation. The largest difference in soil moisture between the experimental drought levels was observed during dry periods. Consequently, the drought experiment did not impose one drought lasting four years, but increased the frequency, intensity and duration of droughts. Quantitatively, the reduction in soil moisture in the drought plots relative to ambient controls were comparable to or exceeded the magnitude of the natural drought that occurred in summer 2018 (Skaland et al. 2019, Buras et al. 2020), suggesting that the experimentally imposed drought regimes were climatologically and ecologically realistic. During the study period, droughts occurred primarily in spring and summer and we did not encounter a prolonged drought in sub-zero temperatures.

We did not observe non-drought side-effects from the roofs on soil or ground temperature, and reduction in photosynthetic active radiation (PAR) was negligible (Haugum 2021), paralleling reports of no significant side-effects from a similar rain-out infrastructure in California (Kreyling et al. 2017, Loik et al. 2019). Other studies have found slight changes in air and soil temperature, but also here these changes did not affect primary production (Vogel et al. 2013).

### Comparison to other studies

As studies experimentally manipulating drought conditions via rain-out shelters accumulate, it is becoming increasingly



Table 2. Linear model estimates for community structural variables in the fourth study year as a response to drought, post-fire time and regions. Models with p-value below 0.05 are considered significant and highlighted in bold. Evenness =  $E_{var}$ , BCD = Bray–Curtis dissimilarity between first and last year. \* = significant only in the reduced model.

	Hypothesis	Model term	Evenness	Richness	BCD	
North n = 27	Drought	Intercept	<b>0.74</b>	<b>41.67</b>	<b>0.55</b>	
		Moderate	-0.06	-5.00	0.02	
		Extreme	-0.02	-5.67	-0.05	
	Succession	Intermediate	<b>-0.16</b>	<b>-20.33</b>	-0.04	
		Old	<b>-0.36</b>	<b>-21.00</b>	<b>-0.22</b>	
		Moderate × Intermediate	0.07	6.33	-0.02	
	Drought × Succession	Extreme × Intermediate	-0.07	5.00	0.04	
		Moderate × Old	0.10	4.00	-0.05	
		Extreme × Old	<b>0.15</b>	7.00	-0.17	
		Intercept	<b>0.57</b>	<b>24.67</b>	<b>0.55</b>	
South n = 27	Drought	Moderate	0.03	1.67	-0.07	
		Extreme	0.05	1.67	-0.07	
		Intermediate	-0.11*	-1.33	-0.10	
	Succession	Old	-0.09*	<b>-5.67</b>	<b>-0.25</b>	
		Moderate × Intermediate	-0.02	-4.33	-0.02	
		Extreme × Intermediate	-0.01	-3.67	0-04	
	Drought × Succession	Moderate × Old	0.01	-3.33	0.13	
		Extreme × Old	-0.04	-2.67	0.11	
		Intercept	<b>0.74</b>	<b>41.67</b>	<b>0.55</b>	
		Region	South	<b>-0.17</b>	<b>-17.00</b>	0.00
Young n = 18	Drought	Moderate	-0.05	-5.00	0.02	
		Extreme	-0.02	-5.67	-0.05	
		South × Intermediate	0.08	6.67	-0.09	
	Region × Drought	South × Extreme	0.07	7.33	-0.02	
		Intercept	<b>0.59</b>	<b>21.33</b>	<b>0.51</b>	
Intermediate n = 18	Region	South	<b>-0.12</b>	2.00	-0.06	
		Drought	Moderate	0.01	1.33	0.00
		Extreme	-0.10	-0.67	-0.01	
	Region × Drought	South × Intermediate	-0.01	-4.00	-0.09	
		South × Extreme	<b>0.14</b>	-1.33	-0.02	
		Intercept	<b>0.39</b>	<b>20.67</b>	<b>0.32</b>	
		Region	South	<b>0.10</b>	-1.67	-0.03
Old n = 18	Drought	Moderate	<b>0.04</b>	-1.00	-0.02	
		Extreme	<b>-0.13</b>	1.33	0.12	
		South × Intermediate	-0.00	-0.67	0.09	
	Region × Drought	South × Extreme	<b>-0.12</b>	-2.33	-0.08	

clear that responses to drought are not consistent (Cherwin and Knapp 2012, Knapp et al. 2017, Karlowsky et al. 2018, Legay et al. 2018, Korell et al. 2021). Yet, most studies find that reduced soil moisture leads to reduced aboveground primary production (Peñuelas et al. 2004, Kongstad et al. 2012, Vogel et al. 2013, Alon and Sternberg 2019, Hannusch et al. 2020, Zhang et al. 2020). Some studies also observe changes in the plant community, often driven by a decrease in abundance of dominant species (Hoover et al. 2014, Alon and Sternberg 2019). Most studies are short-term and single-site, which hampers comparison between studies and synthesis of general responses to drought. A few replicated experiments exist, however, and Peñuelas et al. (2004) found that heathland primary production responded most negatively to drought in the most arid site, but found no response in the least arid site, demonstrating context-dependencies in response to drought along a gradient of increasing ambient precipitation. Moreover, a study by Kröel-Dulay et al. (2015), building on Peñuelas et al. (2004), demonstrates

that more responses to experimental drought emerged in the experiments after 7–14 years. The weak responses to drought in our high ambient precipitation systems are consistent with the trend towards weaker responses in wetter climates and on shorter time-scale in these two previous studies as suggested in Bachmair et al. (2018) and Korell et al. (2021).

The overwhelmingly non-significant results in our study beg the question of whether we lack the statistical power to detect biologically meaningful results. Several lines of evidence suggest that this is not the case (Schweiger et al. 2016). The ecological reliability of the experiment is enhanced by including gradient designs (three successional phases, three drought treatments) and by replicating the experiment in two regions. Our response variables are also causally linked reflecting the same underlying processes, which gives clear expectations about linkages between the resulting variables. We also note that the absolute effect sizes of the drought treatments in all cases are much lower than the successional effects, and the drought-related parameter estimates tend to



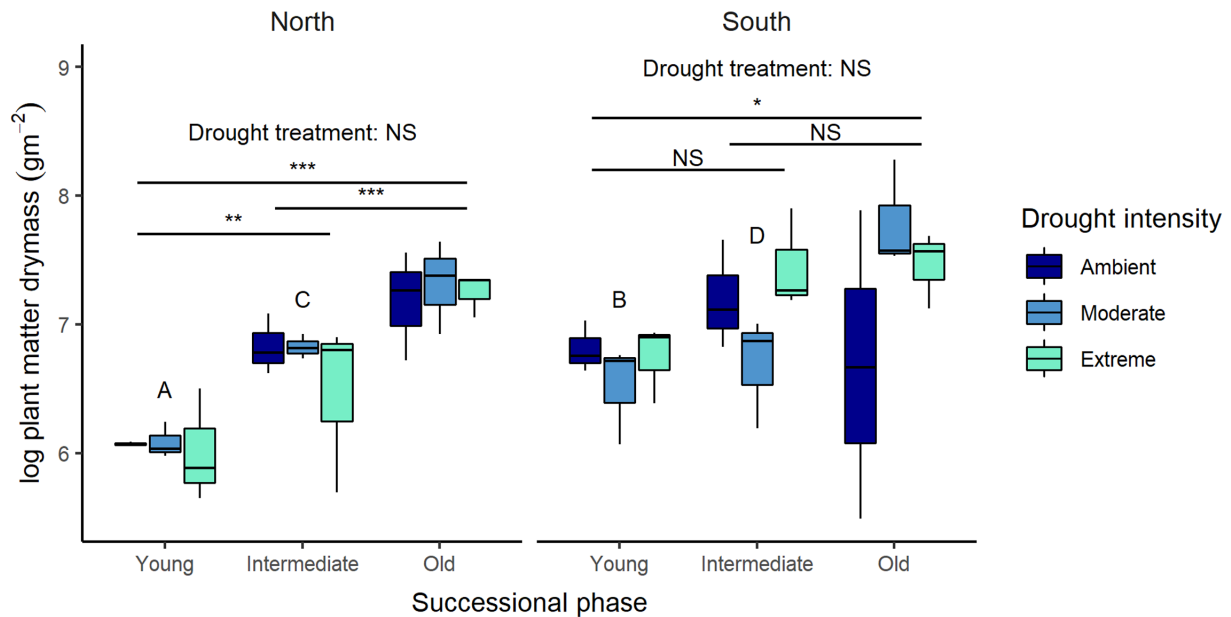


Figure 4. Harvested biomass across drought treatments and post-fire successional phases in the two study regions. We found no significant responses to drought treatments, either as main effects or as interactions with regions or successional phases. Asterisks indicate significant differences between successional phases within regions. Letters annotate significant differences between regions within the young (A:B) or intermediate (C:D) successional phases. Note the log-scaled Y-axis.

cancel each other out, suggesting that the drought effects are not prominent in this system.

Furthermore, the characteristics of northern European coastal heathlands ecosystems may render them relatively resistant to drought. First, the high soil organic content of boreal coastal heaths combined with dense vegetation and bryophyte carpets may provide a mechanistic explanation, as organic soils (Robinson et al. 2016) and dense bryophyte mats (Bates 1998) generally have high water holding capacity. Second, Ericales form mutualistic relationships with ericoid mycorrhiza (Read 1983, Mitchell and Gibson 2006), which have high ability to withstand and adapt to environmental stress, and therefore also reduce stress effects on their host plants (Cairney and Meharg 2003). As Ericales, including *Calluna*, are dominant in the plant community, the symbiotic relationship with ericoid mycorrhiza might buffer community level stress responses (Diaz et al. 2006). Third, experimental drought treatments may be less effective in moist climates. Rain-out shelters reduce or exclude precipitation, which is a key-driver of drought. However, natural drought typically co-occurs with high temperatures and high vapor-pressure deficit (Ibe et al. 2020). These conditions do not necessarily co-occur with the experimental reduction of precipitation, especially in otherwise moist climates, which may partly explain the surprisingly weak effects of drought in our study. Fourth, atmospheric nitrogen deposition is a threat to heathlands (Heil and Diemont 1983, Maskell et al. 2010), partly through lowering drought resistance in heathland plants (Meyer-Grünefeldt et al. 2016). As our study takes place in a part of Europe with relatively low nitrogen deposition (5–8 kg ha<sup>-1</sup> year<sup>-1</sup>) (NILU 2018) compared to the rest of Europe (CCE IMPACT Database, 2004), this

may explain the relatively high drought resistance of our study system. Lastly, we assess drought responses in terms of differences in responses between roofed plots and controls. However, the controls were subjected to the ambient weather through the study period, which may not be representative of the long-term local climate. This is an important, and often underacknowledged shortcoming of many climate manipulation experiments. In fact, Langley et al. (2018) found that species frequently changed their abundance more in the ambient controls than in the treatment plots during long term (>10 years) climate manipulation experiments. Plants in northern-European heathlands are expected to be adapted to consistently wet conditions, rather than droughts (Meyer-Grünefeldt et al. 2016), and their resilience to our quite severe experimental droughts merits further and more detailed investigations into the underlying processes.

## Discussion of hypotheses

We hypothesised that heathlands on the northern brim of the coastal heathland distribution (at 65°8'N) would be less resistant to drought than the populations in the centre of the distribution further south (at 60°7'N). We also hypothesised that the young successional phases would have lower resistance to drought than older phases because species abundant in this phase and younger *Calluna* plants have more resource acquisitive functional traits and can respond sooner to environmental changes than later-successional plant communities and older plants (Grime 1977, Prach et al. 1997). We expected this to be especially evident in the north where *Calluna* is only recruited from seeds, and not vegetative sprouting (Nilsen et al. 2005,

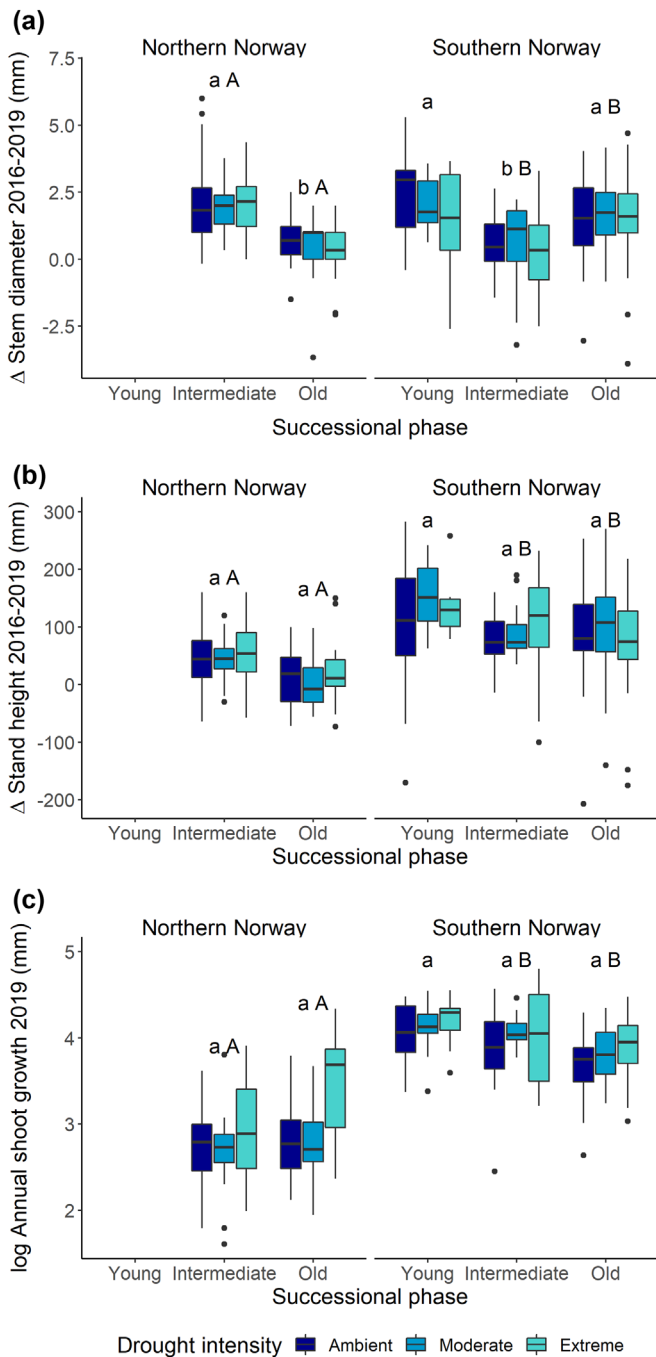


Figure 5. Primary and secondary *Calluna* growth as response to experimental drought across post-fire succession in two regions. (a) Length of growth increment in 2019, (b) change in stand height of 10 tagged *Calluna* specimens per plot from 2016 to 2019 and (c) change in stem diameter of 10 tagged *Calluna* specimens per plot from 2016 to 2019. Annual growth increments were significantly higher in the extreme drought treatment in the north compared to the moderate drought treatment (Tukey HSD  $p < 0.001$ ) and ambient control (Tukey HSD  $p < 0.001$ ). All other drought responses were non-significant. Non-capitalized letters annotate significant differences between successional phases within the same region. Capitalized letters annotate significant differences between regions of sites in the same successional phase.

Velle and Vandvik 2014), and hence have a larger shoot : root ratio (Meyer-Grünefeldt et al. 2015, Ibe et al. 2020). Our data did not support these hypotheses. In contrast, we found increased litter in the moderate and extreme drought treatment compared to the ambient control in the old successional phase in the south, suggesting that old-growth stands of *Calluna* may have lower resistance to experimental drought. Despite having, in general, more extensive roots which facilitate water uptake, old stands also have a large and open canopy that promote evaporation (Gimingham 1988) and lower wood density (Marrs 1986) which increase the risk of cavitation (Hacke et al. 2000, Willson and Jackson 2006).

However, we also note that in the third and fourth year of the experiment, after the onset of the rain exclusion (i.e. 2019 and 2020), we did observe short term browning during summer that was often no longer visible in fall, reflecting low resistance, but high resilience to experimental drought. Photos of the browning are presented in the Supporting information. This temporary browning did not affect the biomass or abundance of species on the timescales covered in this study and was therefore not reflected in our data. We speculate that this could be an early warning of a longer-term drought response which may restore support to H1 in following with other studies that observe ecological drought responses on longer time scales than covered by this study (Peñuelas et al. 2004, Kröel-Dulay et al. 2015). Accordingly, we plan to maintain the experiment to enable follow-up studies to test these hypotheses.

### Understanding the study system

While we found only weak evidence of drought responses across successional phases and latitudes, some general attributes of northern coastal heathlands are apparent. For example, our results add to a series of other studies showing that the heathland plant community composition and structure is changing in predictable ways over the post-fire succession (Mallik and Gimingham 1983, Vandvik et al. 2005, Velle et al. 2014, Måren et al. 2018), but with distinguishable regional patterns (Webb 1998, Moen et al. 2006, Velle and Vandvik 2014). There is a general trend for *Calluna* abundance and biomass accumulation rate increase over succession, and diversity to peak in the young successional phase, but with generally slower dynamics, less resource-acquisitive traits and lower peak biomass in the north (Velle and Vandvik 2014). Because of this heterogeneity, coastal heathlands might respond differently to environmental drivers, even over relatively small spatial scales.

### Conclusions

This study is an important contribution to filling the knowledge gap on ecological drought responses in high-precipitation and high-latitude ecosystems, and the role of secondary plant community succession on these responses. We report

high resistance to four years of experimental drought across six coastal heathland sites. Moreover, the variation in plant community composition and succession between sites demonstrates the role of local climate, as well as land-use history, in shaping vegetation structure and potentially longer-term responses. Upholding landscape heterogeneity of heathlands through management with prescribed fire is therefore not only a means to conserve heathland vegetation and habitat diversity, but also a means to increase drought resistance on the landscape level. More knowledge on the effects of different kinds and intensities of droughts, and over different time-scales, is needed to bridge the gap between these experimental findings and the observations of large-scale dieback on the landscape scale.

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### Author contributions

**Siri V. Haugum:** Conceptualization (supporting); Methodology (equal); Validation (lead); Visualization (lead); Writing – original draft (lead). **Pål Thorvaldsen:** Conceptualization (equal); Methodology (equal); Supervision (supporting); Writing – original draft (supporting). **Vigdis Vandvik:** Conceptualization (equal); Methodology (equal); Supervision (lead); Writing – original draft (supporting). **Liv G. Velle:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (supporting); Writing – original draft (supporting).

### Data availability statement

Data are available from the Open Science Framework (<<https://osf.io/mv84d/>>) (Vandvik et al. 2021).

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