

Prescribed burning can promote recovery of Atlantic coastal heathlands suffering dieback after extreme drought events

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Abstract

Questions: During the winter of 2014, an intense drought combined with sub-zero temperatures resulted in a massive *Calluna* dieback in Norwegian heathlands. We studied the initial vegetation recovery under two management approaches: natural recovery and prescribed burning. We hypothesized that natural recovery will be slower in more drought-affected sites, whereas burning will facilitate post-fire recovery in all sites by effectively removing dead and damaged heath. Both natural recovery and post-fire succession will be slower in the north.

Location: *Calluna* heath in seven sites spanning an approx. 600-km latitudinal gradient along the coast of Norway (60.22–65.69° N).

Methods: After a natural drought, 10 permanent plots per site were either burnt or left for natural recovery. Vegetation data were recorded annually in 2016 (pre-fire) and 2017–2019 (post-fire) reflecting a factorial repeated-measures design ($n=280$). The data were analyzed using mixed-effects models.

Results: Two years after the drought, we observed high but variable *Calluna* damage and mortality. Over the four years of study, damaged *Calluna* recovered, whereas dead *Calluna* showed little recovery. Both the extent of the damage and mortality, as well as the rate of natural recovery, are only weakly related to site climate or environmental factors. Fire efficiently removed dead and damaged *Calluna* and facilitated post-fire successional dynamics and recovery in a majority of sites.

Conclusions: Extreme winter drought resulted in substantial and often persistent damage and dieback on *Calluna* along the latitudinal gradient. In sites with high mortality, prescribed burning removed the dead biomass and, in some cases, facilitated vegetation recovery. Traditional heathland management, which uses burning to facilitate all-year grazing by Old Norse sheep in Atlantic coastal heathlands, can be an efficient tool to mitigate dieback events and more generally to increase resistance to and resilience after extreme drought events in the future.

KEYWORDS

Arctic browning, *Calluna*, climate change, extreme events, fire, land-use change, resilience, semi-natural vegetation, winter drought

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1 | INTRODUCTION

Land-use change and climate change represent major threats to terrestrial ecosystems across the world, negatively impacting biodiversity ecosystem functioning and benefits to people (IPBES, 2019; IPCC, 2023). Globally, deforestation and agricultural intensification constitute major drivers of land-use change, but in industrialized regions, such as Europe, large areas and important habitats are also negatively impacted by abandonment of traditional and extensive land-use practices (IPBES, 2018, 2019). Land-use changes operate through altering disturbance regimes in ecosystems, and the evidence for consequences of these changes on biodiversity is accumulating, with further changes predicted for the future (Newman, 2019). Managing ecosystems for high resilience (*sensu* Holling, 1973) in the face of changing disturbance regimes has thus become an ecological and socioeconomic imperative of the Anthropocene (Newman, 2019), and resilience has become a key concept for understanding and predicting ecosystem responses to global change.

The Atlantic coastal heathlands of northwest Europe are key habitats threatened by land-use change and abandonment (IPBES, 2018). Heaths once covered several million hectares, but due to tree and shrub encroachment after abandonment of traditional land-use practices combined with pressures from industry, infrastructure, housing developments, and agricultural intensification, their extent has so drastically decreased that this nature type is now classified as greatly endangered in the EU as well as in Norway (Webb, 1998; Tsiripidis et al., 2016; Hovstad et al., 2018). These heaths date back several millennia and were created and maintained by low-intensity land-use regimes involving extensive free-range grazing and prescribed burning, and in some instances also mowing or turf-cutting (Gimingham, 1992). Managed heathlands are typically burnt on a decadal scale to improve fodder quality, resulting in a cyclical successional pattern, where the keystone species *Calluna vulgaris* (L.) Hill (hereafter *Calluna*) passes through characteristic morphological phases (pioneer, building, mature, degenerative) before a new fire is set and the cycle starts again (Gimingham, 1992). These semi-natural cultural landscapes support characteristic biodiversity, provide habitat for pollinators, areas for grazing, fodder, food production, and carbon sequestration along with contributions to the local economy, recreational values, landscape appreciation, and tourism (Walmsley et al., 2021; Cusens et al., 2023). Traditional management practices are crucial to maintain these open landscapes and their biodiversity, benefits, and services. Extreme climatic events (droughts, floods, heat waves, cold snaps) are likely to increase in frequency and intensity in the future (IPCC, 2023). This is of relevance for nature management and conservation, as extreme events are expected to have system-wide impacts on species and ecosystems (Jentsch et al., 2007; Smith, 2011; Ummenhofer & Meehl, 2017; Ploughe et al., 2019) and could drive ecosystems past ecological thresholds (Peñuelas et al., 2007; Knapp et al., 2008; Smith, 2011; Munson et al., 2018; Lamentowicz et al., 2019). Droughts may increase wildfire risk, and particularly so in abandoned heathlands where

successional dynamics and litter accumulation may lead to high fire loads (Davies, Smith, et al., 2010; Log et al., 2017; Grau-Andres et al., 2018).

During the winter of 2013/2014, an intense drought combined with unusually low temperatures resulted in a massive dieback of *Calluna* in the coastal heathlands of Norway. Winter precipitation (Dec–Feb) was less than 50% of normal, and there was a prolonged period of below-freezing temperatures, exposing the evergreen *Calluna* plants to extremely low humidity while at the same time blocking access to groundwater due to frozen ground in the most affected areas (www.met.no). The 2014 winter drought in Norway caused massive *Calluna* dieback in the coastal heathlands, and more generally major damage across the boreal and Arctic heath vegetation zones (Bjerke et al., 2017). With the exception of a minor *Calluna* dieback event in 1991 in Norway (Solberg et al., 1992), massive *Calluna* dieback had previously only been recorded in England (Marrs, 1986, 1993), Scotland (Hancock, 2008), and the Netherlands (Aerts & Heil, 1993), where it has been linked to reduced frost tolerance (Sæbø et al., 2001) due to atmospheric nitrogen pollution (Heil & Diemont, 1983; Aerts & Heil, 1993; Marrs, 1993; Gordon et al., 1999; Southon et al., 2012) and to drought combined with low temperatures (Hancock, 2008). These recent 'Arctic browning events' have been linked to extreme winter climate events, including strong frost and lack of snow, but also winter warming periods (Phoenix & Bjerke, 2016; Parmentier et al., 2018).

Globally, we lack knowledge of the magnitude, type, and combination of climate extremes under which ecological thresholds are exceeded, and where ecosystem functioning therefore cannot be upheld (Smith, 2011). While a study from lowland heath in the UK finds near full recovery within a year after drought-related dieback (Watson et al., 1966), a Scottish study reports little recovery after three years (Hancock, 2008). Interestingly, a major drought-related dieback in arctic tundra was reported to recover rapidly after wildfire (Bret-Harte et al., 2013). While previous research generally does not consider the pre-drought ecological state, for example successional phase of the damaged heathland vegetation, there is evidence suggesting that successional dynamics may be an underappreciated source of heathland resilience. For example, whereas *Calluna* seedlings have been shown to be drought-sensitive (Gimingham, 1972; Calvo et al., 2005; Meyer-Grünefeldt et al., 2015), *Calluna* in the building phase is more resistant to drought (Meyer-Grünefeldt et al., 2015). In a recent study, Haugum et al. (2021) find that overall, established heathland vegetation is generally resistant to drought, although mature-phase *Calluna* shows signs of being less resistant. Similarly, in a study of a major *Calluna* dieback in England, older stands were more affected by damage compared to younger or uneven-aged stands. Whether the 2014 drought event has driven the coastal heathlands past their ecological threshold depends on the resilience of the ecosystem, which may vary in time and space.

The Norwegian coast provides a particularly suitable system for studying variation in both the immediate response and resilience to extreme events, as this landscape has unusually broad ranges in climate, environment, and land use (Moen, 1998). Along the Norwegian

coast, species composition and abundance (Vandvik et al., 2005; Velle & Vandvik, 2014), seed germination regulation (Måren & Vandvik, 2009; Spindelböck et al., 2013; Vandvik et al., 2014), and regeneration dynamics and growth rates (Nilsen et al., 2005; Velle et al., 2012; Vandvik et al., 2014) all reflect biogeographic variation of relevance to extreme event responses and resilience. For example, an absence of vegetative regeneration in old *Calluna* stands (Mallik & Gimingham, 1985) and in northern heathlands (Velle et al., 2012), and poor seedling recruitment in dry habitats (Calvo et al., 2005; Spindelböck et al., 2013; Velle & Vandvik, 2014) can negatively impact heathland resilience. Regeneration dynamics is therefore generally slower in northern heathlands (Velle & Vandvik, 2014). As *Calluna* is a keystone species in coastal heathlands, drought damage, diebacks, and variation in regeneration rates are likely to have severe repercussions for ecosystem functions and services. For example, *Calluna* is the main fodder resource during winter for the year-round outfield grazing with Old Norse sheep (Buer, 2011), an old livestock type dating back to the first settlement after the last ice age (Kaland, 1986), thus potentially threatening this traditional land use in impacted areas, plus landscape fire risk is likely to increase, especially in areas with high fuel loads (Davies, Smith, et al., 2010).

The current mechanistic understanding of how terrestrial ecosystems are impacted by drought is founded primarily on opportunistic studies and localized experiments (Beier et al., 2004; Jentsch et al., 2007; Smith, 2011). Smith (2011) emphasizes the value of opportunistic studies initiated after a period of extreme climatic conditions as these offer opportunities for assessing ecosystem impacts in realistic ecological settings. Furthermore, such studies can capture the full temporal and spatial magnitude of the extreme climatic event. In this study, we make use of the unique 2014 *Calluna* dieback event in combination with prescribed burning experimental treatments to address critical questions for understanding the role of traditional management (i.e., burning and grazing, see above) in controlling ecosystem resilience after drought damage and dieback along an approx. 600-km north–south gradient. We study the effect

of vegetation recovery in *Calluna*-dominated habitats by following two different approaches. The first approach is to carry out prescribed burns and assess whether the post-fire vegetation development follows the same trajectories as in previous studies when there was no drought damage. The second approach is to leave the vegetation unburnt to recover by itself.

We hypothesize that the rate of recovery after drought is a function of the extent of the damage. This predicts the slowest recovery in the more damaged sites and plots (Figure 1a). We also hypothesize that fire can effectively reset drought-damaged heathland (Figure 1b). This predicts that the rate of post-fire succession will be unaffected by the extent of drought damage pre-fire, but the variation in ecological dynamics along the coast will mean that the rate of regeneration should be higher in southern sites.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was carried out in seven Atlantic coastal heathland sites, spanning a 583-km latitudinal gradient along the west coast of Norway, from 60.22°N, 5.00°E to 65.80°N, 12.22°E (Figure 2, Table 1). All sites are classified as acidic heath vegetation (T34-C-2 and T34-C-4, Nature in Norway), the most common heath type along the Norwegian coast, and a characteristic habitat in the northwestern European heathlands (Loidi et al., 2020). All sites are in oceanic vegetation sections (O1-2); sites A–C are in the boreonemoral vegetation zone and sites D–G in the southern boreal vegetation zone (Moen, 1998). Traditional heathland management along the Norwegian coast involves grazing (often year-round grazing systems) and prescribed burning with burning intervals spanning from 15 years in the south and up to 30 years in the north (Velle et al., 2012; Velle & Vandvik, 2014). In this study, all sites are extensively grazed by Old Norse sheep. The heaths in this study were

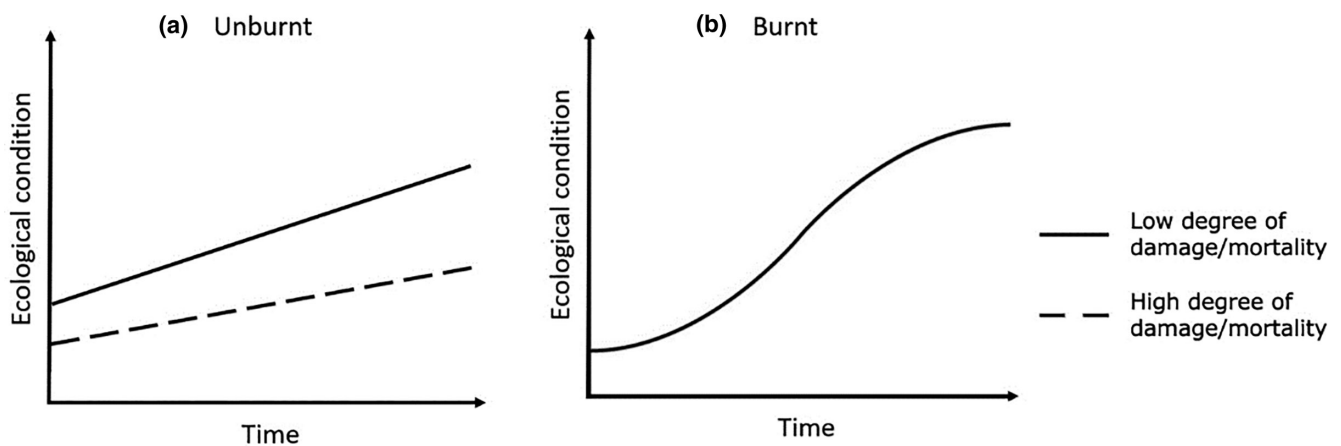


FIGURE 1 Conceptual diagram outlining the predicted recovery after drought damage under the two management approaches: (a) natural recovery in unburnt sites and (b) post-fire vegetation development in burnt sites. In unburnt sites, (a) we expect recovery rates to be higher in sites with a relatively lower degree of drought damage/mortality. After fire, (b) we expect recovery rate to vary over time, but not with degree of pre-fire drought damage.

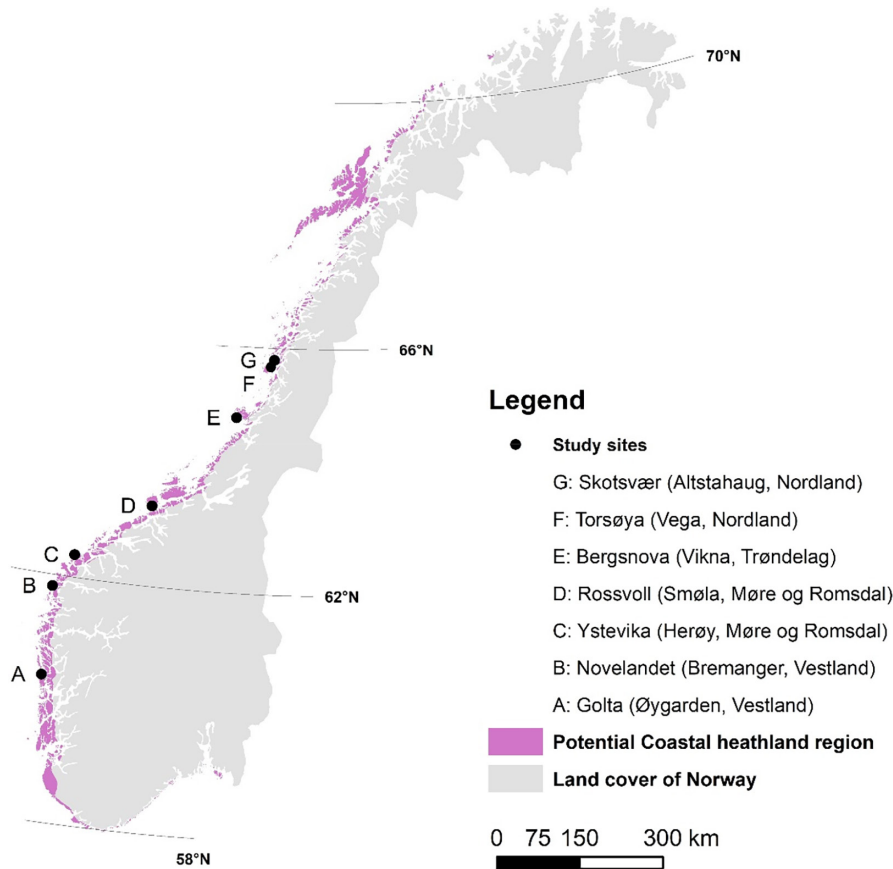


FIGURE 2 Map of study sites and the potential distribution area for Norwegian coastal heathlands (Velle et al., 2023).

Site	Geographical location	Mean annual temp. (°C)	Mean Jan. temp. (°C)	Mean annual precip. (mm)	Bedrock
G	65.80N 12.22E	5.7	-0.3	1309	Mica schist
F	65.69N 12.07E	5.4	-0.4	1131	Mica schist
E	64.84N 10.85E	5.2	-1.5	1535	Granodiorite gneiss
D	63.30N 8.00E	5.7	-0.3	1136	Gabbro
C	62.36N 5.52E	7.1	3.0	2560	Micaceous gneiss
B	61.80N 4.92E	7.3	2.8	2673	Quartzite
A	60.22N 5.00E	7.6	2.5	2080	Amphibolite

TABLE 1 Climatic conditions (temperature (Aune, 1993); precipitation (Førland, 1993)) and bedrock (Sigmond et al., 1984) for the seven study sites along the 583-km gradient from north to south.

selected to be in the late mature phase in all sites, ready to be burnt, according to the traditional land-use management regime. Today, traditional management has been discontinued in many heathlands and, as a consequence, heathlands are now classified as 'endangered' in the Norwegian Red List of habitats (Hovstad et al., 2018) and 'vulnerable' in the European Red List of habitats (Tsiripidis et al., 2016). All our study sites have been subjected to changes in management over recent decades, including both reduced grazing intensity and reduced fire frequency.

2.2 | Data collection

Climate data were obtained from the nearest climate stations to each site. Precipitation, temperature, and air humidity time series were collected from the following meteorological stations: A, Slåtterøy

fyr; B, Ytterøyane; C, Svinøy fyr; D, Sandstad II; E, Rørvik Airport; F, Vallsjø; and G, Tjøtta. The length of the available time series varies among the stations and variables, and all available data for all sites in 2014 were used. Mean annual precipitation ranges from 1100 to 2500 mm (Førland, 1993), mean annual temperature from 5.2°C to 7.6°C, and mean January temperature from -1.5°C to 2.5°C, being above -1.5°C across all sites (Aune, 1993; Table 1).

The data collection in all sites is based on a repeated-measurements design. At each study site, 10 experimental blocks, each of 10 m × 10 m, were randomly positioned within the *Calluna* heath stands. The stands were selected to have as equal a structure as possible (>75% *Calluna* cover, <40 cm height, and at the mature successional stage according to the heathland cycle; Gimingham, 1992). Minimum distance between blocks was 15 m. Within each block, one 1 m × 1 m plot was placed randomly and permanently marked with metal poles in each corner. The plots were selected to avoid marked

depressions and concavities, paths, areas with more than 10% bare rock or bare soil, and less than 5 m from the edge of any previously burnt area. Within each site, half the blocks were dedicated to experimental fires, while the rest were left unburnt as controls. The fires were performed by an experienced team trained to follow traditional burning prescriptions (Kaland, 1999). The prescribed burnings were conducted under conditions as constant as possible along the climatic gradient, between February and April, in dry weather and with wet or frozen ground, downwind under light wind speed ($0.5\text{--}3\text{ m s}^{-1}$). Plant community composition in all plots (seven sites, 10 plots each) was recorded during late summer before burning (2016) and three years after burning (2017–2019).

The cover of species of vascular plants, bryophytes, and lichens was recorded with plant nomenclature following Lid and Lid (2005) for vascular plants, Frisvoll et al. (1995) for bryophytes, and Krog et al. (1994) for lichens. In addition, we recorded the cover of bare soil, graminoids, herbs, mosses, lichens, and litter (total cover of loose dead plant material). To quantify the effect of drought on *Calluna*, we recorded the cover of dead, drought-damaged, and healthy *Calluna* within each plot (Figure 3). This was done according to the observed colouring and texture of the *Calluna* leaves and stems, where green and soft leaves were interpreted as healthy *Calluna*, brown and soft leaves as drought-damaged *Calluna*, and grey, colourless and crispy leaves were interpreted as dead *Calluna* (Figure 3). Each cover was visually estimated to the nearest percentage. For each plot we measured the peat depth (measured from the soil surface to the inorganic substrate), aspect, slope, and recorded the microtopography within the plot as concave, flat, or convex.

2.3 | Data analysis

We explored the patterns and relationships between climate, environment, *Calluna* damage, and community response data through an exploratory analytical approach and via models. We compared the mean relative humidity, temperature, and precipitation of January 2014 with the same month in other years for the available time series of climate data from the nearest climate stations. We calculated the cover and proportion of the main functional groups, and of dead, damaged, and healthy *Calluna* for each plot and year. These responses were related to climatic and site-level environmental variables reflecting drought severity and soil moisture.

Mixed-effects models were used to regress the proportion of dead *Calluna* in 2016 against drought severity (estimated as January 2014 relative humidity) and local factors (soil depth and aspect). Similarly, the cover of regenerating *Calluna* and number of *Calluna* seedlings in burnt plots were regressed against time and latitude. Latitude was used as a predictor because the 2014 drought damage varied with latitude, and because heathland regeneration dynamics after fire also varies along a latitudinal bioclimatic gradient (Nilsen et al., 2005; Velle & Vandvik, 2014). For all models, we assumed a Gaussian error distribution, except for the number of seedlings where we assumed a negative binomial distribution, and we included

plots within sites as a random factor to capture the nested spatial structure of the data. We used non-parametric multidimensional scaling (NMDS) to summarize community compositional patterns across sites and years.

All analyses were done in R v. 4.3.0 (R Core Team, 2023), using *lme4* v. 1.1.32 (Bates et al., 2015) and *lmerTest* v. 3.1.3 (Kuznetsova et al., 2017) to fit mixed-effect models, *vegan* v. 2.6.4 (Oksanen et al., 2022) for ordination, and *tidyverse* v. 2.0.0 (Wickham et al., 2019) for data manipulation. Packages *targets* v. 1.0.0 (Landau, 2021), *quarto* 1.2 (Allaire et al., 2023), and *renv* v. 0.17.3 (Ushey & Wickham, 2023) were used to ensure reproducibility.

3 | RESULTS

3.1 | Drought severity

All sites experienced droughts beyond the range of the measured climate time series in January 2014, and for the northern sites, this continued into February (Appendix S1). The magnitude and duration of the drought increased northwards, both in terms of mean relative humidity, which decreased from ca 65% in the south to less than 55% in the north in January 2014, and in terms of the magnitude of the difference from the normal range. Precipitation was extremely low across all sites in January 2014, and the three northernmost sites had sub-zero temperatures (Figure 4).

3.2 | Drought damage and recovery of dwarf shrubs

The drought had a pronounced effect on *Calluna* in all sites, with dead or damaged *Calluna* making up on average 20.5%–44.2% of the cover in the sites 2016, with some variation across plots within sites (range 4%–57%) (Figures 5). The sites in the south had less dead *Calluna*, but in return, a greater proportion of drought-damaged *Calluna* (Figure 5). Healthy *Calluna* was still found in all sites, except site F, where the majority of *Calluna* was dead (Figure 5). Other vascular plants were present at all sites, at variable cover. Surprisingly, we do not find any effect of our climatic or environmental variables on the proportion of dead or damaged *Calluna*; specifically, no significant effect of the magnitude of the drought (Figure 4), plot aspect, slope, or peat depth ($p > 0.05$ in all cases, Appendices S2–S4).

Over the four years of study, the unburnt plots showed signs of some natural recovery after drought as the cover of damaged and dead *Calluna* decreased over time, whereas live *Calluna* increased (estimated annual increase 3.06% cover; $F_{1,102,44} = 10.827$, $p < 0.01$). The lowest recovery was observed in plots with dead *Calluna* (E, F) (Figure 5). Prescribed burning efficiently removed the drought-damaged and dead *Calluna* in all sites, and live *Calluna* then emerged and slowly but gradually increased in cover over the three next years in most sites (estimated annual increase 2.34%

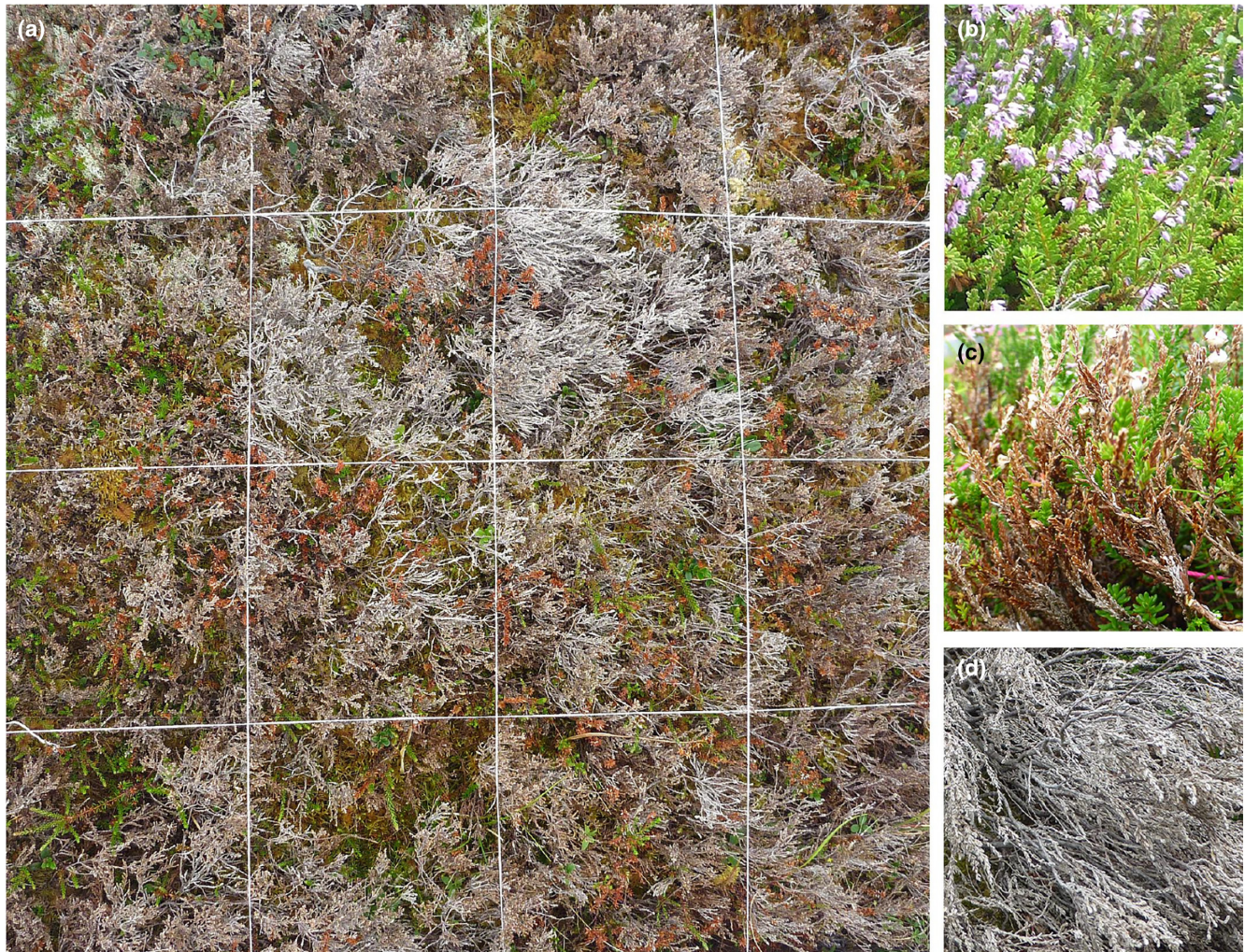


FIGURE 3 (a) A *Calluna*-dominated heathland plot (1 m × 1 m, with 16 subplots) with high cover of dead *Calluna* (site F); (b) healthy *Calluna*; (c) drought-damaged *Calluna*, and (d) dead *Calluna*.

cover; $F_{1,69} = 17.09$, $p < 0.001$) The increase in *Calluna* cover was slower in the two northernmost sites. The cover of other vascular species was variable, with no clear patterns between treatments or among sites (Figure 5).

In all sites, *Calluna* seedlings emerged after fire, with an average of 7.82 seedlings per plot. In contrast, only two seedlings were encountered in the unburnt plots, and the difference is highly significant ($p < 0.001$). In burnt plots, seedling densities decreased sharply towards higher latitudes (with log number of seedlings decreasing by an estimated 0.7 per degree latitude; $p = 0.012$), and very few seedlings emerged from sites F and G (Figure 6).

3.3 | Community-level responses

The total sum of the functional groups' cover in unburnt stands varied over time and space from more than 200% to approx. 100% with especially high cover in site B and in the final year of site E (Figure 7).

The vegetation was generally dominated by Ericales and bryophytes, with lower but variable contributions of graminoids, woody plants, and ferns and forbs. The total vegetation cover, reflected in the sum of the cover of the plant functional groups, was generally relatively constant over time in the unburnt stands, with some low-cover sites and years (2017 for A and E, 2018 and 2019 in F). After fire, total vegetation cover was reduced by ca 30%–90%. In sites where large amounts of bryophytes remained after fire, these generally died in the following 1–2 years (sites D, G, but not E) (Figure 7). The relative abundance of graminoids and ferns and forbs increased after fire, to the extent that these functional groups dominated the vascular vegetation after a few years (e.g., A, C, E, G). Ericales also increased, but more slowly (Figures 5 and 7).

The NMDS diagram reflects the biogeographic gradient from southern sites on the upper right-hand side of the diagram to northern sites on the lower left (Figure 8a). Southern sites are characterized by southernly distributed and drought-tolerant species, such as *Erica tetralix* L. and *Carex pilulifera* L., whereas northern sites are

FIGURE 4 Frequency distribution of mean precipitation, temperature, and relative humidity (%) for January from climate station time series for sites A–G (coloured histograms). The span of each climate time series is given on the plots. More information on sites A–G is given in Figure 2 and Table 1. Climate stations used per site are listed in Section 2.1. Precipitation data for 2014 are missing for site F.

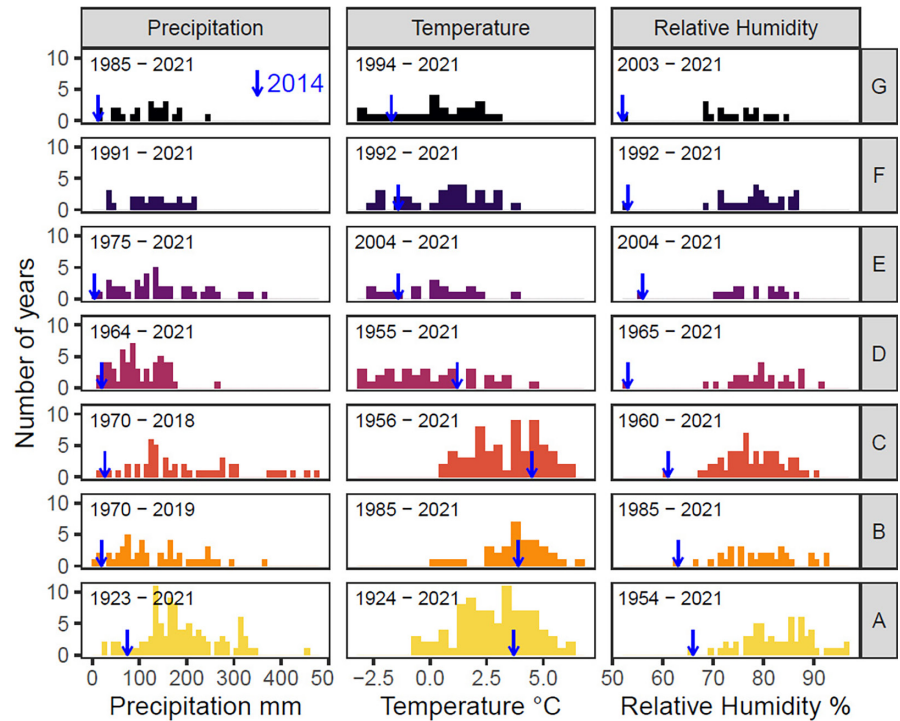
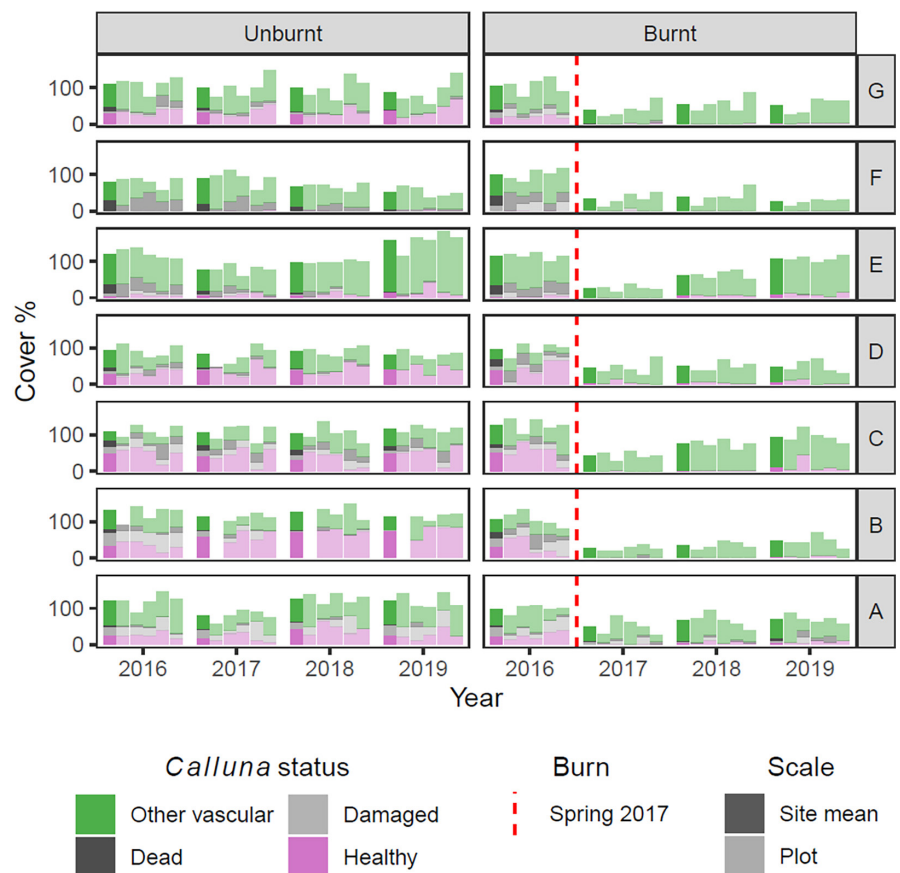


FIGURE 5 Percent *Calluna* cover over time by health status (dead, damaged, healthy) and sum of other vascular plant species. Bars are given for average values per site and each of five individual plots within sites. For further information on sites A–G see Figure 2 and Table 1.



characterized by arctic–alpine species such as *Empetrum nigrum* L., *Betula nana* L., *Arctostaphylos alpinum* (L.) Spreng., and *Carex nigra* (L.) Reichard (Figure 8b). Whereas unburnt plots were stable over time and dominated by dwarf shrubs and bryophytes (upper part

of the diagram), the burnt plots shifted after fire towards communities dominated by early-successional graminoids and forbs such as *Agrostis capillaris* L., *Carex binervis* Sm., *Luzula multiflora* (Ehrh.) Lej., and *Potentilla erecta* (L.) Raeusch. (Figure 8a,b).

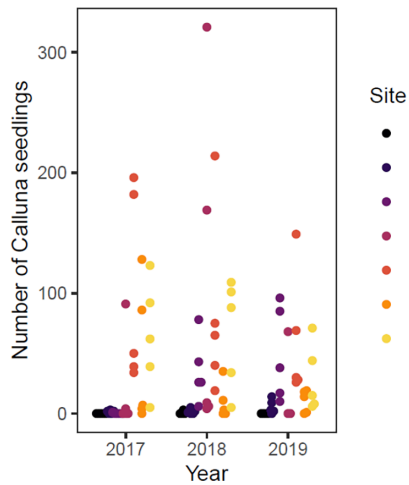


FIGURE 6 Number of *Calluna* seedlings per 1 m × 1 m plot over the three post-fire years (2017–2019) in the burnt plots within each site. For further information on sites A–G see [Figure 2](#) and [Table 1](#).

4 | DISCUSSION

4.1 | Northern sites are most strongly affected by drought

Two years after the severe winter drought in 2014, we observed major but variable *Calluna* dieback, with considerable amounts of dead and damaged heather, especially in some of the northern sites. Dieback of *Calluna* and other evergreen dwarf-shrub heathland vegetation has previously been reported from throughout the Arctic, including Norway (Bjerke et al., 2017; Parmentier et al., 2018). Interestingly, regarding the *Calluna* dieback that followed the 2014 winter drought, Bjerke et al. (2017) suggest that low precipitation and hence very little snow cover caused a frost drought, resulting in the observed *Calluna* mortality. In our more southern coastal heathlands however, lack of snow cover during winter is a common feature; indeed, this forms the basis for the characteristic year-round-grazing

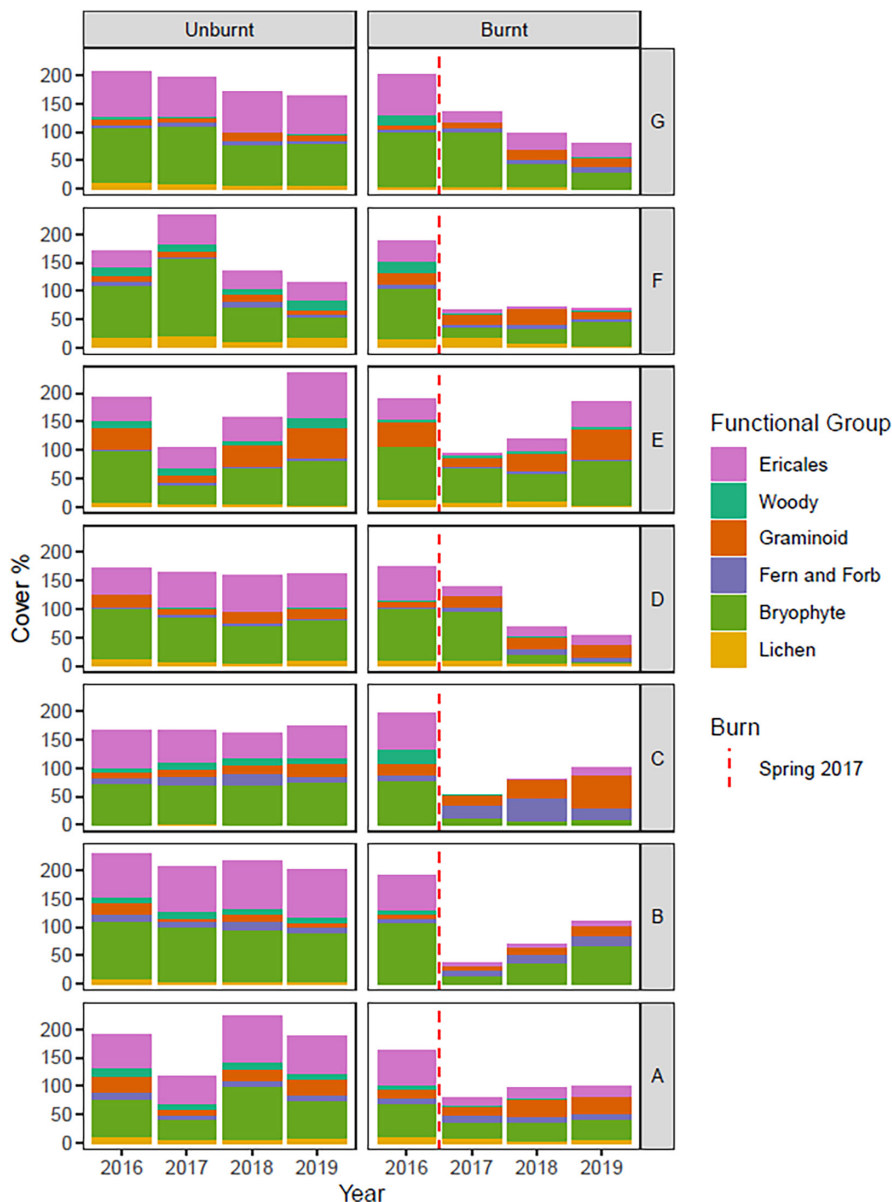


FIGURE 7 Community cover over time by taxonomic group. For further information on sites A–G see [Figure 2](#) and [Table 1](#).

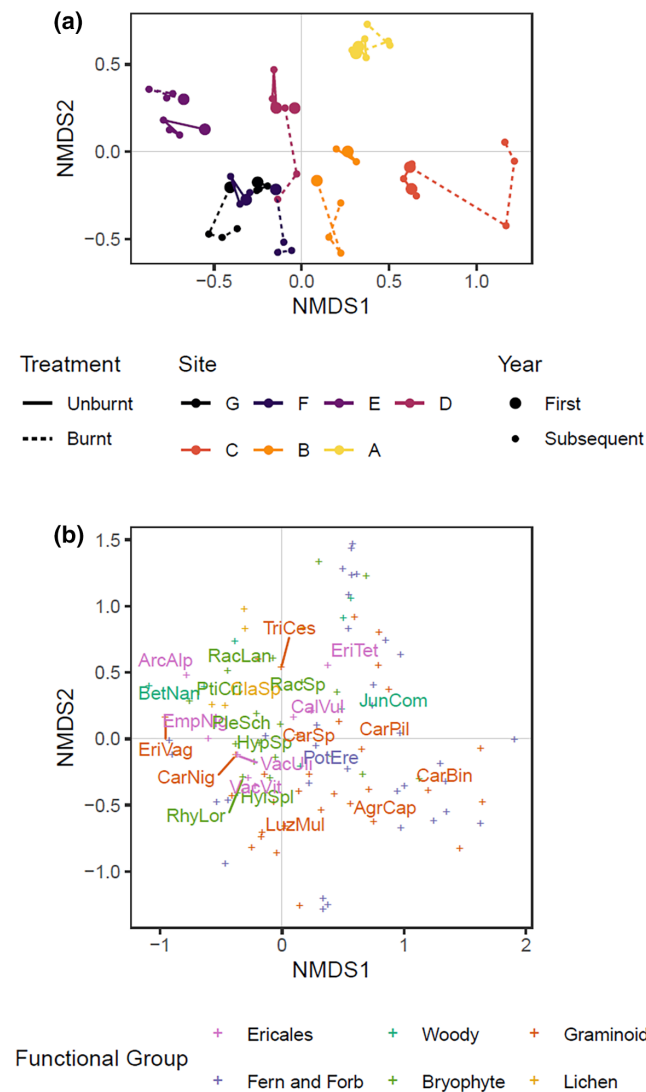


FIGURE 8 Non-parametric multidimensional scaling (NMDS) plot of (a) plots and (b) species. Species names are given as the 3+3 first letters of the genus and species names. Full names are given in Appendix S5.

systems (Buer, 2011; Kvamme et al., 2004). In contrast, long drought spells, with or without sub-zero temperatures, are uncommon. During January and February 2014, our sites were exposed to extremely low air humidity, with the four northernmost sites having reductions that were unprecedented in the available climate time series. In the three northernmost sites, this was combined with periods of sub-zero temperatures. Drought stress is often characterized by passing a threshold in soil water availability (Beier et al., 2012), but it has been argued that models used to measure the impact of drought on ecosystems should be refined to record the role of low air humidity as this is often an underestimated cause of plant stress (Novick et al., 2016). Our study adds further support to this line of argument, as we find no relationship between the proportion of damaged and dead *Calluna* and typical variables that influence soil moisture, such as peat depth, slope, or aspect.

Our heathlands are relatively species-poor and dominated by a single species, *Calluna vulgaris*, hence the ecosystem's dynamics and functioning rely on a single species. According to the biodiversity insurance hypothesis (Yachi & Loreau, 1999), diversity confers ecosystem resilience because more diverse communities potentially harbour a broader range of niches to accommodate environmental perturbation, hence low-diversity systems such as ours should be vulnerable to perturbations (e.g., drought). However, while Gobin et al. (2015) find that *Calluna* from within temperate forests show little drought tolerance, several other studies suggest that *Calluna* may be relatively resistant to drought, possibly with locally adapted responses (Meyer-Grünefeldt et al., 2016; Haugum et al., 2021). Accordingly, Ibe et al. (2020) find provenance- and life-history-specific responses in the morphology and physiology of *Calluna* plants to water pressure deficit. As our northern oceanic heathland study sites have little historic exposure to droughts, these high-latitude heathlands may be particularly susceptible to increased climatic variability, and in particular to increased drought risk (Hanssen-Bauer et al., 2017) under climate change.

4.2 | Varying recovery in unburnt stands

In some sites, drought-damaged *Calluna* was relatively rapidly replaced by live *Calluna* over our three years of study. This happened in three of the seven sites (B, D, E), possibly due to a recovery of drought-damaged tissue, or the emergence of new shoots that replaced damaged tissue. These results may indicate that when the drought damage is below a certain threshold, the plants manage to recover, and conversely, if the damage exceeds this threshold, the damage becomes permanent and the plants may die. There is a knowledge gap related to such thresholds, and the causal relationships of how species and communities respond to stress appear to be complex (Vicente-Serrano et al., 2020). In an experimental drought study in Norwegian coastal heathlands, partial browning on *Calluna* was observed during prolonged summer droughts (Haugum et al., 2021). Most of this browning was reversed in less than three months, demonstrating high resilience at this magnitude of disturbance. Moreover, a study in grassland and heath communities by Backhaus et al. (2014) finds that mild drought events increase the resistance towards extreme drought events and proposes epigenetic changes or soil biotic legacies as possible explanations. The study also shows that the response of a single species to drought may be affected by the presence of other species. Although *Calluna* is the keystone species, *Empetrum nigrum*, which is also typically found in our northern heathlands, is a heathland species with relatively high resistance to climatic variability in the arctic tundra. A study by González et al. (2019) finds that shoot length and berry production are reduced when exposed to freezing temperatures during winter, but less so if the following growing season is warm and long.

In some of the southern sites, such as A and C, there was little recovery despite a relatively modest drought impact. One possible explanation is higher atmospheric nitrogen deposition in these southern sites, exceeding the critical limit of 5–15 kg N ha⁻¹ year⁻¹ (Bobbink et al., 2022). Nitrogen addition can cause increased drought susceptibility (Power et al., 1998; Carroll et al., 1999; Southon et al., 2012) and slower growth (Barker et al., 2004) in *Calluna* shoots. Generally, the distribution range of *Calluna* is characterized by high precipitation, mild temperatures, and low nutrient availability (Loidi et al., 2020), making it potentially susceptible to both nitrogen enrichment and drought. Drought resistance in *Calluna*, including winter drought because of soil freezing, has been documented to decrease when exposed to elevated nitrogen levels (Britton & Fisher, 2007; Fangmeier et al., 1994). One explanation is linked to an increase in the shoot:root ratio (Meyer-Grünefeldt et al., 2015). Combinations of increased nitrogen deposition and extreme winter droughts can thus be a potential future threat to *Calluna*-dominated heathlands.

In sites E and F drought-damaged and dead *Calluna* disappeared over time, without any recovery of live *Calluna*. In these northern sites, *Calluna* does not resprout vegetatively and thus depends exclusively on seed regeneration for recovery (Velle & Vandvik, 2014). As seed germination is strongly promoted by fire (Måren & Vandvik, 2009), recovery in the absence of fire may be effectively inhibited. The loss of the dominant *Calluna* due to drought impact on older *Calluna* plants may free up niches for new species to establish (Hobbs & Gimingham, 1984; Gimingham, 1992), giving forest successional species opportunities to enter the system (Gimingham, 1972). This reduces the ecological condition of the heathland (Nybø & Evju, 2017) and may speed up secondary succession into forest (Gimingham, 1972; Moen et al., 2006). Despite low relative humidity, precipitation, and temperature, site G had a higher proportion of healthy *Calluna* than the other northern sites. The differences are not explained by peat depth, slope, or aspect. However, one possible reason might be site differences in exposure, as site G is more sheltered from the prevailing winds than E and F. This is compatible with Davies, Legg, et al. (2010), who find significant variation in spatial and temporal moisture content in *Calluna*. They link this to shoots from exposed locations having a lower moisture content when the ground is frozen and that over-winter damage to leaf cuticles reduces the ability of the plant to regulate water loss.

4.3 | Prescribed burning resets the post-fire succession

In this study, we find that fire effectively reset drought-damaged heathland by removing dead or damaged *Calluna* across all sites. The prescribed burning initiated a classical heathland post-fire succession with grasses and forbs, but also *Calluna* seedlings and other Ericales. These post-fire successional trends follow the generalized heathland cycle (Gimingham, 1972, 1992), and we note that the rate of recovery of healthy *Calluna* is similar in burnt and

unburnt plots, at approx. 3% linear increase in cover over the study years. As the burnt plots start from a much lower cover, this suggests greater potential for growth at a *per capita* rate. The latitudinal variation in post-fire development agrees with earlier studies along the same latitudinal gradient (Velle & Vandvik, 2014). In particular, the slow development of the *Calluna* cover after fire in northern sites is explained by the geographical variation in *Calluna*'s regeneration strategy, as it re-establishes from both resprouting stems and from seeds in the south, but only from seeds north of 63°N (Velle et al., 2012; Velle & Vandvik, 2014). Seed germination in *Calluna* is stimulated by exposure to smoke (Vandvik et al., 2014) and *Calluna* typically resumes dominance in the canopy 3–6 years after fire (Velle et al., 2012; Velle & Vandvik, 2014). While we encountered low numbers of seedlings in the two northernmost sites compared to previous studies in western and central Norway (Måren et al. 2010; Måren & Vandvik, 2009; Nilssen et al., 2005; Velle & Vandvik, 2014), the number was comparable to that in late-successional heathlands in Scotland (Hobbs & Gimingham, 1984). In our study, low seeding numbers could be due to bryophytes and lichen left behind after the burning delaying seedling establishment (Figure 7), or because seedlings died before they were recorded during the relatively warm and dry summer of 2018. This drought might have had a more negative impact in the north, as the northern seeds and seedlings are less adapted to drought (Birkeli et al., 2023). Heathland seed banks generally harbour vast numbers of *Calluna* seeds (Måren & Vandvik, 2009), and we can expect additional seedlings to emerge over time, although the majority of new individuals after fire normally establish within the first 2–3 years after burning (Måren et al. 2014; Måren & Vandvik, 2009; Vandvik et al., 2014).

4.4 | Implications for heathland management after drought

Drought damage has implications for heathland biodiversity, ecosystem functioning, and benefits to people. First, drought-damaged and dead *Calluna* generally has lower moisture content compared to healthy *Calluna* (Log et al., 2017; Log, 2020), which might increase the probability of uncontrolled and unwanted wildfires. Wildfires do occur in heathlands, as has recently been experienced in the UK (Grau-Andres et al., 2019) and Norway (Log et al., 2017). Unlike prescribed burning, which takes place under controlled conditions during the autumn and winter to avoid damage to the soil and seed bank (Gimingham, 1972), wildfires will generally occur in dry periods, including during summer, and they are thus more likely to damage seed banks, biodiversity, and carbon pools (Davies, Smith, et al., 2010; Grau-Andres et al., 2018). Our study thus suggests that prescribed burning during winter can be an efficient tool to remove dead biomass after drought, thus decreasing wildfire risk in subsequent years. As we find that natural recovery after drought is unpredictable and can be slow, prescribed burning appears to be a reliable option to reset damaged

heathlands and promote ecosystem recovery. Although *Calluna* recovery after fire was slow in some of our sites, graminoids and forbs increased relatively quickly and reached 50%–100% cover after a few years, supporting ecosystem recovery and functioning, including grazing value. Since drought resistance is lower in older *Calluna* stands (Haugum et al., 2021) and since post-fire regeneration rates are generally higher in younger stands (Marrs, 1986; Davies, Smith, et al., 2010; Velle et al., 2012, many of our sites), heathland management, including burning and grazing, can be efficient mitigation tools to increase resistance to and resilience after future extreme drought events.

AUTHOR CONTRIBUTIONS

Velle, Thorvaldsen and Vandvik conceived the ideas and designed the methodology; Haugum, Thorvaldsen and Velle collected the data; Telford analyzed the data; Velle and Vandvik led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Open Science Framework at DOI [10.17605/OSF.IO/MV84D](https://doi.org/10.17605/OSF.IO/MV84D).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Relative humidity and air temperature for January and February 2014.

Appendix S2. Proportion of dead, damaged, and healthy *Calluna* against mean peat depth across the seven study sites along the ~600 km north–south gradient.

Appendix S3. Proportion of dead, damaged, and healthy *Calluna* against slope across the seven study sites along the ~600 km north–south gradient.

Appendix S4. Proportion of dead, damaged, and healthy *Calluna* against aspect across the seven study sites along the ~600 km north–south gradient.

Appendix S5. List of species names, abbreviations, and functional groups, sampled in the experimental plots.

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