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Blanket bog vegetation response to wildfire and drainage suggests resilience to low severity, infrequent burning

Roxane Andersen[1]*, Paula Fernandez-Garcia[1], Alice Martin-Walker[3,4], Daniela Klein[3,4], Chris Marshall[1], David J. Large[3,4], Robert Hughes[1,2,3,4] and Mark H. Hancock[2]

Abstract

Background In 2019, a wildfire impacted an area of blanket bog and wet heath > 60 km^2 in the Flow Country peatlands of northern Scotland, a site of global significance. Unusually the footprint of the wildfire included discrete areas of degraded, restored, and near-natural blanket bogs. Following the wildfire, we surveyed vegetation in 387 quadrats in burnt and unburnt areas. The study aimed to determine whether and how proximity to human-made drains and microtopography affected fire-vegetation interactions and included older wildfire sites and unburnt control sites for context.

Results Overall, our study suggests that the 2019 Flow Country wildfire caused mostly superficial burning; except in the most degraded area, which burned more severely and where we recorded more profound impacts on the vegetation. We found higher cover of litter, which in turn led to increased localized fire damage in quadrats close to drains compared with quadrats away from the influence of drains. We also found greater fire impacts (e.g., proportions of moss burnt and *Sphagnum* discoloration) on hummocks, particularly where they were higher relative to the hollows. Overall, vegetation both near and away from drains largely resembled nearby unburnt sites within 20 years.

Conclusions Overall, our study suggests that the 2019 Flow Country wildfire caused mostly superficial burning, except in the most degraded areas. Vegetation communities of blanket bogs associated with conservation and restoration areas in the region appear to be largely resilient to occasional, low severity wildfires. This implies that management interventions that maintain wet conditions in peatlands have the potential to help reduce the risks of severe wildfires.

Keywords Peatland restoration, *Sphagnum*, Vegetation communities, Post-fire plant succession, Wildfire ecology

*Correspondence:
Roxane Andersen
roxane.andersen@uhi.ac.uk
Full list of author information is available at the end of the article

Resumen

Antecedentes En 2019, un incendio de vegetación impactó un área de pantanos y brezales húmedos de > 60 km2 en las turberas de la región de Flow, en el norte e Escocia, un sitio de significancia global. Usualmente, la marca del incendio incluye áreas discretas degradadas, restauradas, y cuasi-naturales de brezales húmedos. Luego del incendio, relevamos la vegetación en 387 parcelas en áreas quemadas y no quemadas. El estudio tuvo como objetivo determinar cuándo y cómo la proximidad a drenajes artificiales y la micro-topografía afectaron la interacción fuego-vegetación, incluyendo sitios con incendios antiguos y sitios control sin quemar para su contextualización.

Resultados En general, nuestro estudio sugiere que el incendio de Flow fue en gran parte superficial, excepto en el área más degradada, la cual se quemó más severamente y donde registramos impactos más profundos en la vegetación. Encontramos una mayor cobertura de mantillo (broza), que a su vez produjo un daño más localizado en parcelas cercanas a drenajes comparado con parcelas alejadas o sin influencia de los drenajes. Encontramos asimismo mayores impactos del fuego (i.e. mayores porciones de musgos quemados y decoloración de musgos de turberas) sobre montículos, particularmente donde eran más grandes en relación con los huecos. En general, y luego de 20 años de un incendio, la vegetación cercana o alejada de los drenajes tiende a parecerse a los lugares no quemados.

Conclusiones En general, nuestro estudio sugiere que el incendio de Flow de 2019 causó mayoritariamente un fuego superficial, excepto en las áreas más degradadas. Las comunidades vegetales de pantanos del tipo manta (blanquet bogs) asociados a áreas de conservación y restauración en la región aparecen como grandemente resilientes a fuegos ocasionales de baja severidad. Esto implica que las intervenciones de manejo que mantienen condiciones húmedas en las turberas tienen el potencial de ayudar a reducir los riesgos de incendios severos.

Background

Wildfires on peatlands can have important ecosystem effects, altering carbon storage (Turetsky et al. 2004; Ingram et al. 2019; Wilkinson et al. 2023), biodiversity (Kirkland et al. 2023), microtopography (Benscoter & Wieder 2003; Shelter et al., 2008), peat properties (Kuhry 1994; Sillasoo et al. 2007; Wilkinson et al., 2020), and water availability and quality (Brown et al. 2015). These effects are mediated by the way in which vegetation is impacted and responds to fire (Nelson et al. 2021). Showing some commonalities with herbivory (Bond & Keeley 2005), peatland fire impacts on vegetation can vary hugely: at the more extreme end, most propagules and even organic soil horizons can be consumed, leading to very slow vegetation recovery even for fire-associated plants like common heather *Calluna vulgaris* (Maltby et al. 1990). Meanwhile, low severity fires that consume only fine elevated shoots can leave lower growing plants largely unimpacted, and even provide a temporary opportunity for bryophytes sometimes seen as fire sensitive, like *Sphagnum* species (Whitehead et al., 2021).

The spread, severity (organic matter consumed: Keeley 2009), and intensity (energy output: Keeley 2009) associated with wildfire depends on recent and current weather, environmental conditions, and fuel properties (Davies et al. 2016; Arnell et al. 2021). Similarly, post-fire vegetation recovery and succession depends both on fire intensity, severity, and pre-fire and post-fire conditions and management (Kettridge et al., 2019; Davies et al. 2023). In peatlands, wildfires may spread more easily along dry lichen-heather-dominated areas but spare wet depressions (Turetsky et al. 2004; Thompson et al. 2014). Like some

other flammable plants, heather is characterized by elevated dead shoots, which tend to be where fire first develops, given a source of ignition and suitable moisture levels (Davies & Legg 2011). However, where microtopography is less well developed or the water table is lower, even the vegetation in wet depressions may burn (Benscoter & Wieder 2003). On the other hand, where microtopography is well developed, dense *Sphagnum* hummocks have been shown to retain enough moisture to survive fire events (Shetler et al. 2008; Benscoter et al. 2015). Long-term studies also suggest recovery of keystone peatland species like *Sphagnum* sp. and associated functions within decades, i.e., faster than the current fire return interval of 150–350 years estimated from temperate and boreal peatlands (Sillasoo et al. 2011; Turetsky et al. 2004; Wilkinson et al. 2023).

However, human-induced changes in climate could impact peatlands' relationship with fire (Nelson et al. 2021; Wilkinson et al. 2023). Recent climate projections indicate that alongside overall warming, the likelihood of extreme weather events such as droughts will increase over the next century (Arnell et al. 2021). A severe summer wildfire in drought conditions in a UK peatland in northern England in 1976 led to poor recovery of many plant species, with significant areas (~ 30% of a 600 ha site) remaining unvegetated a decade post-fire (Maltby et al. 1990). Fire danger, a series of indices calculated from temperature, relative humidity, wind speed, rainfall, and potential evaporation, are predicted to increase in Europe and across the whole of the UK along with the number of days with "extreme fire danger" (Arnell et al. 2021). In parallel, increases in temperature associated with higher evapotranspiration

are likely to lead to drier fuels (Flannigan et al. 2009). In the UK, where virtually all wildfires are ignited by human action (Glaves et al. 2020), we can therefore reasonably expect greater risk of more frequent, or larger, more impactful wildfires in the future, including on peatlands.

To compound the issue, in the UK, 80% of the peatlands have been substantially modified by a long history of land use conversion, including regular burning, grazing, drainage and afforestation with non-native conifers (Bain et al. 2011). These activities have led to changes in environmental condition that also impact wildfire response. For example, in some degraded areas, the loss of bryophytes has been coupled with increases in biomass of shrubs like *Calluna vulgaris* and/or graminoids like *Molinia caerulea* (Hobbs and Gimingham 1984; Garnett et al. 2000; Ward et al. 2007), which are known to respond to low intensity fires by further increases in biomass and rapid re-sprouting (Mallik and Gimingham, 1983). Degradation also alters hydrology and peat properties, increasing vulnerability to catastrophic deep burning of the peat itself during wildfires (Turetsky et al. 2011, 2015; Wilkinson et al. 2023) and associated with post-fire regime shifts to systems that do not accumulate carbon (Kettridge et al. 2015).

On the other hand, across the UK, large-scale restoration has been undertaken over thousands of hectares of degraded peatlands, with activities such as drain blocking and forestry removal aiming to re-wet the peatlands and enable functions and biodiversity to return (Hancock et al. 2018; Artz et al. 2020). Those interventions have been shown to reduce fire severity in Canada (Blier-Langdeau et al. 2022; Granath et al. 2016), but underpinning evidence supporting this claim in the UK context is mostly anecdotal. Indeed, quantifying the impacts of wildfire across a range of land management regimes is made difficult by the ephemeral and relatively unpredictable nature of this threat, and the need to have existing or readily deployed observation networks in place. As a result, there is a dearth of empirical data to support management decisions and risk mitigation going forward, for a potentially impactful process that is only likely to increase in the future.

In spring and summer 2018, a persistent high-pressure system resulted in a prolonged period of drought across Europe (Buras et al. 2020). In northern Scotland, the months of May, June and July 2018 were nearly 2 °C warmer than the 1981–2010 monthly average and drier, with sustained precipitation deficits (Sterk et al. 2022). This event caused a sustained and widespread water table drawdown (Sterk et al. 2022; Marshall et al 2022) across the Flow Country peatlands of Caithness and Sutherland, northern Scotland, an expanse of 4000 km^2 of largely treeless blanket bog habitat, strongly protected under UK and European law for its global significance (Lindsay et al. 1988). The drought led to varying levels of surface subsidence (ranging between 1 and 10 cm)

in different parts of the landscape (Marshall et al. 2022), and likewise varying impacts on plant-soil processes, ranging from "shut down" of *Sphagnum* to increased productivity in ericoid shrubs and sedges (Sterk et al. 2022).

Following the 2018 drought, in spring 2019, a large wildfire burnt approximately 60 km^2 of wet heath and blanket bog within the same region. The Flow Country is largely a "no-burn" area, where prescribed fire management has not been permitted over blanket bog areas since the 1990s. The Flow Country fire footprint encompassed a well-studied, large area of blanket bog habitat under a range of management regimes and condition: historic and active peat cutting (for domestic fuel) and regularly burned in the past; drained, afforested with non-native conifers, under restoration (through drain blocking and, in places, forestry removal); and near-natural under conservation management.

Here, we aimed to document the effect of the wildfire on vegetation communities across some of these land uses. More specifically, the objectives of the study were to: (1) compare short-term wildfire effects on vegetation assemblages along microtopographic positions and proximity to drains; (2) relate small-scale wildfire effects to local environmental setting such as the presence of drains and microtopography; and (3) contextualize the short-term impacts with a "space-for-time" design using new data from 8- and 20-year-old wildfires sites on nearby blanket bogs. We hypothesized that during the 2019 wildfire, areas closer to active drains and areas on top of higher hummocks would have supported drier vegetation assemblages and would be the most impacted by wildfire. We hypothesized that fire impacts would be more pronounced on areas nearer the start of the fire because it had greater past management impacts as well as on more exposed, windier areas (higher elevation above sea level). Finally, we hypothesized that the vegetation composition in burnt plots would converge towards that of long-unburnt plots over time but would still not be completely undifferentiated after 20 years.

Methods
Site description
The whole 2019 Flow Country fire footprint covered more than 60 km^2, including a large proportion within a Special Area of Conservation (SAC) designated for blanket bog habitat. Within the footprint of the fire, two areas within the SAC were initially selected for the main data collection to reflect the different landownerships, rather than any attempt to stratify by fire severity. The first area is within the privately owned Bighouse estate (hereafter BH) and includes historic, unblocked drains as well as drains blocked as part of restoration management. The second area was within the Forsinard Flows National Nature Reserve (NNR; hereafter FD) managed by the Royal Society for the Protection of Birds (RSPB) (Fig. 1). It includes blanket bog in near-natural
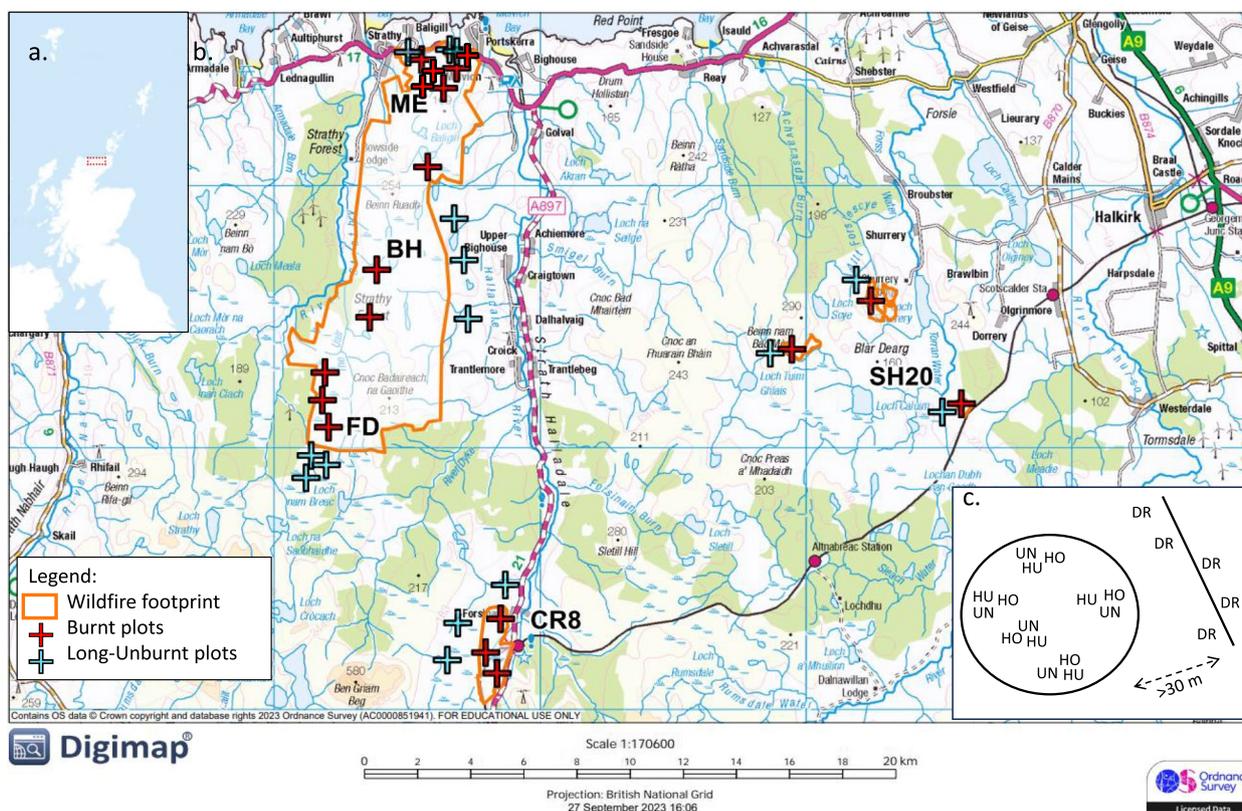
Fig. 1 **a** Region of interest in the north of Scotland. **b** Map displaying the location of the burnt (red crosses) and long-unburnt plots (blue crosses) used as part of the study in relation to the wildfire footprints of the 2019 Flow Country wildfires which includes the Melvich (ME), Bighouse (BH), and Forsinard (FD) sites, the 2011 "Croft 1" wildfire (CR8) and the three ~20-year-old smaller wildfires making up the Shurrery (SH20) sites. **c** Schematic representations (not to scale) of quadrat distribution at each plot represented by a cross in (**b**). All plots included undrained (UN) and drained (DR) quadrats, but plots in BH and FD also included Hummock (HU) and Hollow (HO) quadrats. See dataset and metadata in Martin-Walker et al. (2022) for further details

conditions and areas where more drains have been blocked. Both BH and FD include areas of deep peat (up to 6 m) with well-developed bog pools, as well as shallower (0.3–0.5 m) peat, particularly on sloping ground.

Another area at the northern end of the 2019 fire near the village of Melvich (hereafter ME) was targeted for a separate study conducted in 2020 but included some comparable data, which were integrated to this study where appropriate. This area is outside of the SAC boundary and includes thin peat (0.3–0.6 m) and organo-mineral soil. It is impacted by historic and active peat cutting, grazing by sheep and cattle and past management burning. This is the area where the fire started, and it continued to smolder for several weeks after the main wildfire was considered under control.

In addition to the 2019 Flow Country Fire, we collated records of earlier fires in the same region and on similar blanket bog habitat and identified two areas suitable as older post-fire comparators: an 8-year-old fire area referred to as "Croft 1" (hereafter CR8), and a ~20-year-old area, near the Shurrery estate (hereafter, SH20). CR8

has a 2.98-km^2 footprint and is located west of Forsinard village, encompassing RSPB Forsinard Flows NNR grounds as well as a nearby upland farm. SH20 is within the SAC and includes the footprint of two small wildfires from 2000 (0.36 and 0.9 km^2 approximately 2 km apart) and of a much smaller (0.2–0.3 km^2) wildfire from 1997 (Figs. 1 and 2).

Sampling design

Given the prevalence of charcoal in the palaeorecord in the Flow Country (e.g., Lindsay et al. 1988), no areas could be assumed to be truly "unburnt". As a result, for this work, we developed a design where all known "burnt" sites (BH, FD, ME, CR8, SH20) were matched with "long-unburnt" sites (i.e., no recorded wildfires or known management fires since the 1990s), hereafter referred to as "unburnt control" (Figs. 1 and 2). From existing records, we know that the area impacted by the 2019 fires (FD, BH, ME) and some adjacent areas were likely to have burnt 38 years previously, during a large
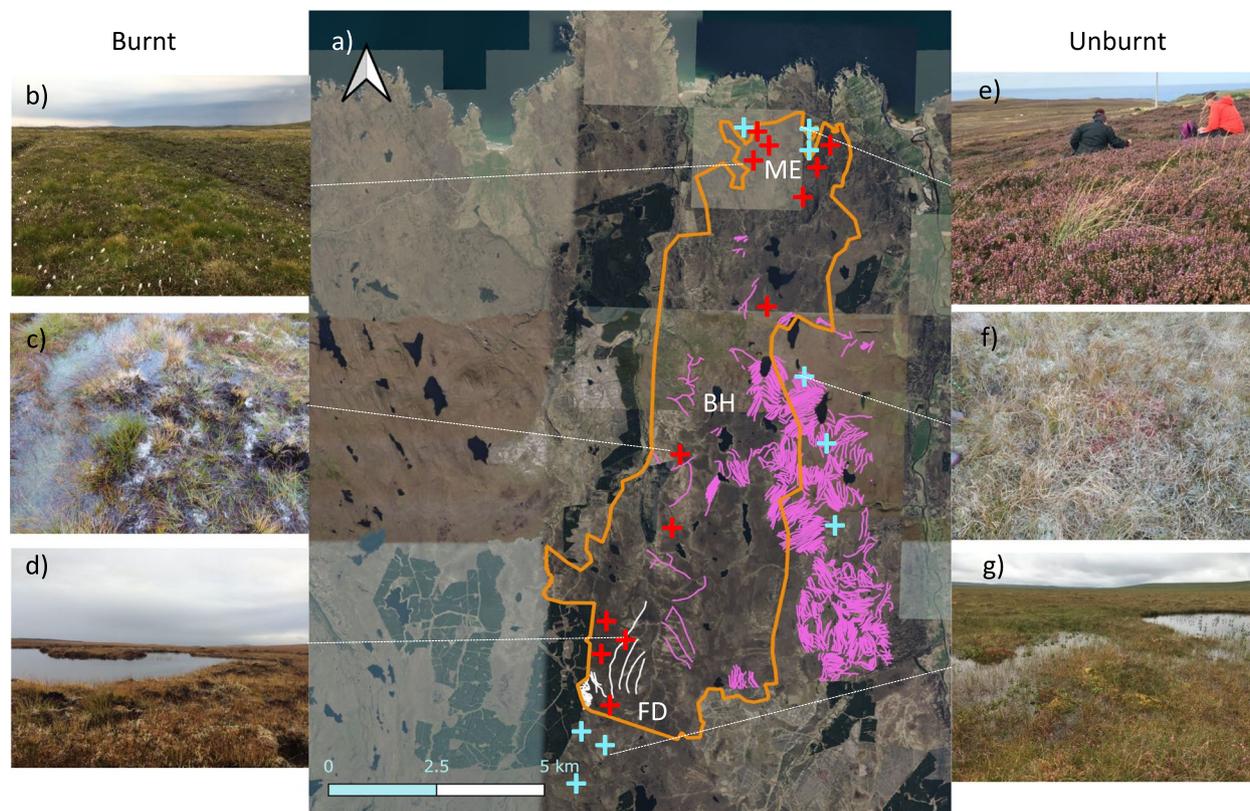
Burnt   Unburnt

Fig. 2 a Map of the 2019 Flow Country Fire scar, including the Melvich (ME), BigHouse (BH), and Forsinard (FD) sites with red crosses depicting burnt plots and blue crosses depicting unburnt plots. **b** Landscape view of the burnt ME site taken from one of the burnt plots looking south. **c** View from above of one of the undrained (UN) burnt quadrats from one of the BH burnt plots. **d** Landscape view of the FD burn site taken from one of the burnt plots looking south-east. **e** Landscape view of the unburnt ME site taken from one of the unburnt plots looking north. **f** View from above of one of the undrained (UN) unburnt quadrats from one of the BH unburnt plots. **g** Landscape view of the unburnt FD site taken from one of the unburnt plots, looking south

wildfire noted for the year 1981. However, the exact footprint of the 1981 fire was unavailable, so areas unimpacted by the 2019 fire were still classified as "(long-) unburnt" for the purpose of this study. The full details of the sampling design, data collection methods, and raw data for this study can be found in the published dataset and metadata (Martin-Walker et al. 2022).

Briefly, for each of the four main "sites" (BH, FD, CR8 and SH20), three pairs of "plots" (A, B, C) were identified and matched for slope between burnt (B)/unburnt(U). Burnt plots in BH, FD, and CR8 were sited at three randomly selected 1-km square centers within the burn scar (out of all the available square centers), while for smaller SH20 site, there was one burn plot centered on each of the three smaller fires comprising the area. The matching unburnt plots were sited at randomly selected 1-km square centers in adjacent (unimpacted) areas. Our target vegetation communities (based on National Vegetation Classification; Rodwell 1991) in the unburnt plots were wet heath (e.g., NVC M15, M16) and blanket mire

(e.g., NVC M17-20) perhaps with some *Molinia*-rich areas (e.g., NVC M25, M26). Streams, lochs (i.e., lakes in Scotland), pools, springs, fens, and flushes as well as other non-bog vegetation classes were excluded. Within each plot, five points were randomly selected out of ten pre-identified on the map, and each sampling point was located with a handheld GPS. Quadrats were then positioned (1) at least 30 m away from drain to avoid influence of drainage as soon as GPS indicated correct location (Undrained, UN); (2) on the nearest hummock (HU, FD and BH only); (3) on the nearest hollow (HO, FD, and BH only); and (4) along the nearest drain (DR), 10 cm either side (chosen at random) of the drain. For the ME site, nine further plots were selected: six randomly selected 1-km square centers within the burn scar equivalent to "burnt bog plots" and three in adjacent unburnt areas of similar slope, equivalent to "unburnt bog plots." At each plot, one 1×1 m quadrat was placed at the correct location indicated by the GPS and two further quadrats were randomly placed at least 10 m away. Following

our design, 240 quadrats were visited in FD and BH, 120 quadrats were visited for CR8 and SH20 and 27 quadrats were visited in ME, leading to a total of 387 quadrats (Table 1).

Vegetation data

All BH, FD, CR8, and SH20 quadrats were visited between October and December 2019 or 5 months post-fire, which was the soonest possible after the urgency grant funding for the research was awarded. Although this might have led to an underestimation of, e.g., flowering species, there was no practical alternative, and the data collection was adapted to the time of year. At each quadrat, the cover estimation of each living species, dead species (litter), burnt species (i.e., showing evidence of burning such as black charring), bare peat, and standing water was recorded. The percent cover of key plant functional types (PFTs; Sphagnum, non-Sphagnum Moss, Lichen, Graminoid, Shrub, Other vascular plants, Bare peat, Burnt vegetation and Litter) was then estimated for each quadrat as the sum of percent cover from individual species within each PFT. The ME quadrats were visited in August 2020 (i.e., 15 months post-fire), and percent cover of the same PFT was noted rather than species, thereby providing a comparable dataset.

In addition, in all the BH and FD burn quadrats ($n = 120$), fire impact measures were collected following Davies et al. (2016), albeit at a smaller scale than their 30 m plots. In the field, a score between 0 (no effect) and 3 (highest severity) was given to variables associated with substrate/ground fuel effects (litter consumed, peat charring, exposed mineral soil cover, *Sphagnum* damage, moss scorch/consumption, moss survival) and to variables associated to surface fuel effects (top-killed vegetation, fine crown consumption, frequency of grass/

sedge/forb and shrub survival, potential for colonizer and species change, shrub frequency re-sprouting). The top-killed vegetation was derived from the total unidentifiable vascular vegetation recorded as "burnt". Fine crown consumption was estimated using the difference in cover of litter and shrub (*C. vulgaris*) between pairs of burnt and unburnt plots. A peat Composite Burn Index (pCBI) value was then calculated for each burnt plot, as the sum of the average scores for substrate/ground fuel and surface fuel effects (Davies et al. 2016).

Ancillary data

For BH, FD, CR, and SH, in each quadrat, the geographical coordinates, height above sea level, number of deer prints, deer dung, and the number of the non-native conifers Sitka spruce (*Picea sitchensis*) and Lodgepole pine (*Pinus contorta*) seedlings and their height were recorded. The maximum depth of standing water, if present, was also noted. In addition to species cover, the height of the tallest species and the canopy height were recorded across a diagonal section of the quadrat. Where applicable, the vertical height difference between the highest point of the hummock quadrat and the lowest point of the hollow quadrat was also measured (see Martin-Walker et al. 2022 for further details).

Statistical analyses

All statistical analyses were done in R Studio using R version 4.2.3 (R core team 2023). We first established whether there were natural gradients in vegetation composition across the whole study area by testing the significance of the differences between vegetation assemblages from the four unburnt sites (BH, FD, CR8, and SH20) with a permutational multivariate analysis of variance (function *adonis2* from the vegan package; Oksanen et al. 2007). We

Table 1 Study design detailing the quadrat types and their distribution at the five study sites

Quadrat type	Plots × points				
	Forsinard (FD)	BigHouse (BH)	Melvich (ME)	Croft (CR8)	Shurrery (SH20)
Undrained Unburnt Bog	3×5 (15)	3×5 (15)		3×5 (15)	3×5 (15)
Undrained Burnt Bog	3×5 (15)	3×5 (15)		3×5 (15)	3×5 (15)
Drained Burnt Bog	3×5 (15)	3×5 (15)	6×3 (18)	3×5 (15)	3×5 (15)
Drained Unburnt Bog	3×5 (15)	3×5 (15)	3×3 (9)	3×5 (15)	3×5 (15)
Hollow Burnt	3×5 (15)	3×5 (15)			
Hollow Unburnt	3×5 (15)	3×5 (15)			
Hummock Burnt	3×5 (15)	3×5 (15)			
Hummock Unburnt	3×5 (15)	3×5 (15)			
Total quadrats	120	120	27	60	60

For each quadrat type, the numbers are presented as Plots × Points within Plot (Total). Here, plots represent spatially independent replicates and points are randomly selected locations within each plot where quadrats are placed, in a ~ 125-m radius or along a 100-m transect (drain quadrat). All ME quadrats were classed as "Drained" (DR) given the lack of microtopography and the extent of peat cutting in this area. For further details, see Martin-Walker et al. 2022

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then investigated differences in vegetation communities in FD and BH using two separate PCAs. First, we used a response matrix of Hellinger-transformed percent cover of species, from all the burnt and unburnt quadrats to visualize the range of fire impact using our "space for time" design. Second, we used only the burnt quadrats to show the range of variation among the post-fire vegetation. In both cases, species with average cover when present < 2% were removed prior to the analysis. To further differentiate the overall fire impact between the sites (FD, BH), and quadrat types (UN, DR, HU, HO) and their interaction, we ran a permutational multivariate analysis of variance, this time with a response matrix of Hellinger-transformed percent cover only for the species that were recorded as "burnt" in the field.

To test differences between sites and quadrat types in pCBI and in individual fire impact measures (Davies et al. 2016), we used linear mixed models (*lmer* function, lme4 package; Bates et al. 2009), with *site*, *quadrat*, and *site × quadrat type* as fixed effects and *plot* as a random effect, checking for normal distribution of residuals. For each response variable, a series of null models (i.e., with only site, quadrat or site + quadrat) were compared to the full model through permutations (*anova* function). Where the contribution of a factor was significant ($p < 0.05$), differences between the levels of that factor were tested using a post hoc Tukey pairwise comparison. We then explored relationships between burnt vegetation cover and Davies' fire impact measures and local environmental setting (Shannon's H, species richness, vegetation height, height difference between hummock/hollow, altitude above sea level, distance from fire ignition), using Pearson's correlations (function *cor.test*).

To contextualize short-term impact with longer-term recovery, we graphically compared the average proportions of PFTs between pairs of burnt/unburnt plots for all sites across the 20-year fire chronosequence (ME, BH, FD, CR8, and SH20) in both undrained and drained (DR) quadrats. To determine whether the vegetation composition of post-wildfire sites converged with long-unburnt areas at different times post-fire, we compared two similarity indices, the Morisita-Horn Index and the Sørensen Index (functions *mh* and *li*, divo package; Sadee et al. 2019) between site pairs (burnt vs. unburnt) for undrained and drained quadrats separately (Magurran 2005). To further characterize the long-term trajectory of post-fire blanket bog vegetation composition, we used principal response curves (PRCs, function *prc*, library vegan), a type of redundancy analysis (RDA) specifically focussing on the time and treatment interaction, commonly used in ecology for time series or space-for-time chronosequences (e.g., Hancock et al. 2018). Here again, we separated undrained and drained quadrats, with unburnt

plots used as a control against which burnt plots of < 1 (FD, BH), 8 (CR8), or ~ 20 (SH20) years since fire were contrasted. Prior to the analysis, species with cover < 2% were removed and the matrix of the remaining 50 species was again subjected to Hellinger pre-transformation. We then graphically compared the actual cover changes across sites and quadrat types for species with the highest loadings on the first PRC axis.
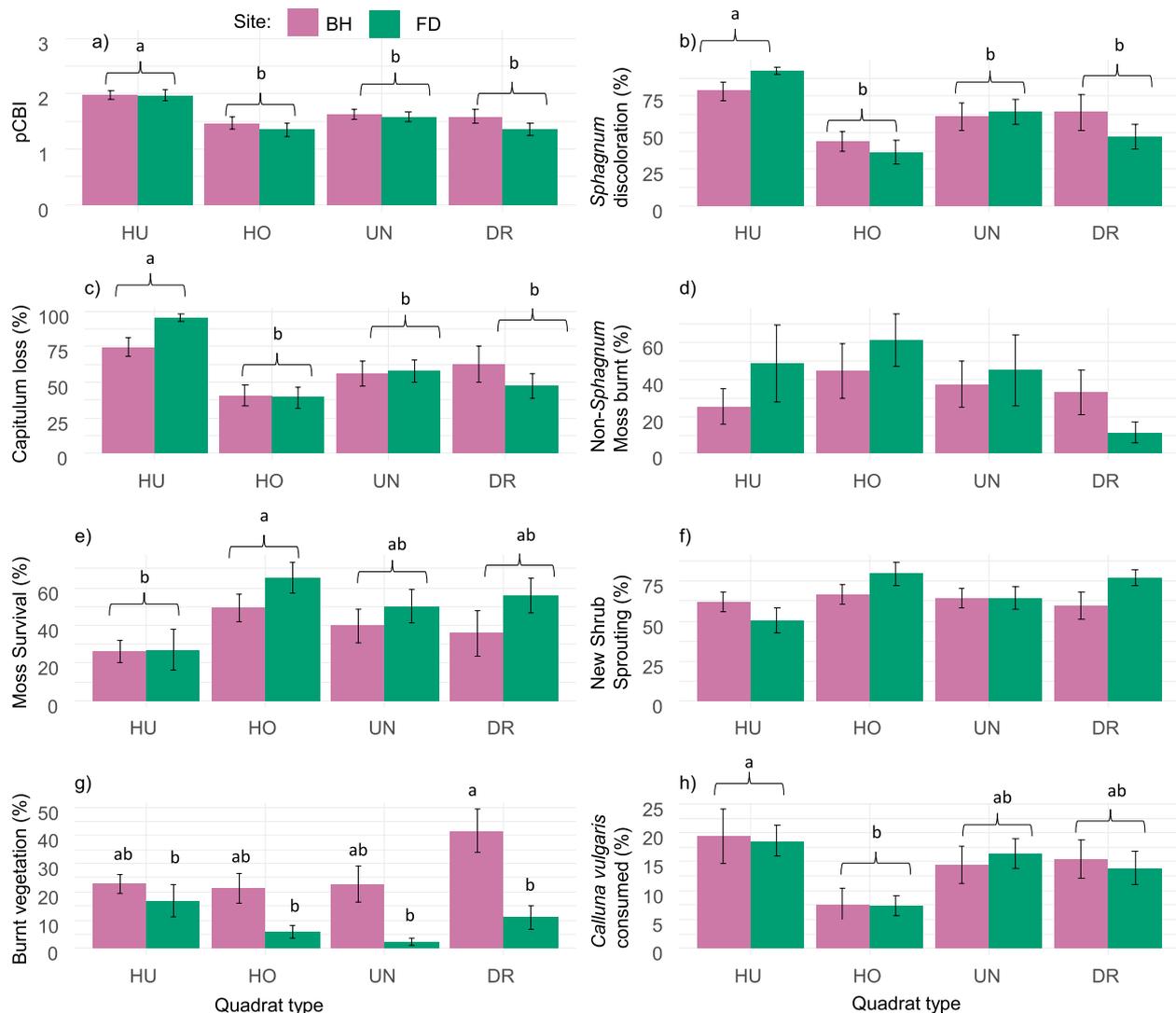
Results

(1) 2019 fire effects on vegetation

The 2019 fire markedly impacted the vegetation composition, as seen by a clear split along the first (horizontal) axis of the PCA (Fig. 2a) caused by the appearance and dominance of the "burnt vegetation" and "dead *Sphagnum*" categories in burnt quadrats, not seen in the unburnt ones. In addition, plants that are likely fuels (*C. vulgaris* and litter of *T. cespitosum* and *Eriophorum* spp.) were more abundant in unburnt sites. Our results suggest that both burnt and unburnt areas in BigHouse (BH) and Forsinard (FD) shared many species but also exhibited some differences in their vegetation, reflected by a bigger spread for BH quadrats along the second (vertical) axis of the PCA (Fig. 3a). This is corroborated by the comparison of unburnt sites among themselves (CR8, SH20, FD, BH) where differences in vegetation composition were found to be significant between sites by the permutational ANOVA ($R^2 = 0.11$, $p = 0.001$). A key difference comes from higher covers of lichen, *Racomitrium lanuginosum*, and *T. cespitosum* (recorded as litter, i.e., "dead") at FD than BH, where *C. vulgaris*, *Sphagnum capillifolium*, and *E. vaginatum* have higher covers instead (Fig. 3a). In the fire-only PCA, the quadrats overlap more, but a gradient that may be interpretable as post-fire wetness is visible along the first axis, broadly separating the presumed wetter quadrats (hollows in particular) with higher covers of algae and *S. cuspidatum* (right), from the hummocks and drained quadrats with higher covers of burnt vegetation and lichens (left; Fig. 3b). There were no other obvious patterns of vegetation differences between the four types of quadrats (Fig. 3a, b).

When comparing the percent cover of species with evidence of burning damage at community level, we found significant differences between sites ($R^2 = 0.21$, $p = 0.001$) but not between quadrat types ($R^2 = 0.03$, $p = 0.138$), driven by the percent cover of undifferentiated vascular vegetation/litter with evidence of burning, which was nearly five times higher in BigHouse (24 ± 3%) than in Forsinard (5 ± 1%). Hence, there were broad differences in the character of burnt vegetation

Fig. 3 Biplots representing the first two axes of a principal component analysis using **a** the Hellinger-transformed cover of vegetation species from Forsinard (FD) and BigHouse (BH) sites impacted by the 2019 fire (B) and their respective long-unburnt controls (U) and **b** the Hellinger-transformed cover of vegetation species from the burnt sites (B) only. The vegetation percent covers were recorded in 1 × 1 m quadrats situated near drains (DR) or away from drains (UN) and in adjacent hummocks (HU) and hollows (HO)

between the two 2019 wildfire study sites, while corresponding variation within each site was relatively modest.

In contrast, fire impact measures did not vary significantly between the two sites investigated within the footprint of the 2019 fire but were influenced by quadrat type. The estimated pCBI was significantly higher in hummock quadrats compared to all other types (chi-squared = 32.3, $p = 0.00001$; Fig. 4a). When looking at individual measures, we found that 75% or more of the *Sphagnum* present showed discoloration and capitulum loss in hummock quadrats, significantly more than in all other quadrats, where around half of the *Sphagnum* present were impacted (chi-squared discolouration: 34.3, p-value = 0.00006; chi-squared capitulum loss: 34.8, p-value = 0.00005; Fig. 4b,c). The proportion of non-*Sphagnum* moss with evidence of burn damage was variable (and not significantly different) between sites and quadrat types, while the proportion of shrub re-sprouting was similar overall (Fig. 4d–f). By contrast, the total cover of vegetation with evidence of burning damage was the only variable that differed between sites (chi-squared 14.062, $p = 0.007$) but also between quadrat types (chi-squared = 17.529, $p = 0.007$): the highest cover of burnt vegetation was found in drain quadrats in BH, and the lowest covers of burnt vegetation found in FD undrained and hollow quadrats (Fig. 4g). Finally, in both sites, our derived

value of *C. vulgaris* consumption was highest in hummock quadrats, with intermediate values in drained and undrained quadrats, and lowest values in hollow quadrats (chi-squared 13.0, p-value = 0.04; Fig. 4h).

The small-scale fire impacts measures within the quadrats did not appear to be strongly correlated with quadrats' geographical position (distance from the start of the fire or the elevation above sea level). On the other hand, regardless of quadrat type, both capitulum losses and discoloration generally increased with vertical height (cm) difference between the highest and lowest points within the quadrat, i.e., where microtopography was more pronounced (Pearson's R capitulum loss = 0.37, $p < 0.001$; Pearson's R *Sphagnum* discoloration = 0.38, $p < 0.001$). These two impact measures were also significantly positively related to total burnt vegetation (Pearson' $R_{CapLoss} = 0.45$, $p < 0.001$; Pearson's $R_{SphDis} = 0.47$, $p < 0.001$). The proportion of surviving mosses was not influenced by microtopography but tended to increase with maximum obscured height, a measure of canopy density and height (Pearson's $R_{MossSurvival} = 0.32$, $p < 0.001$), and decreased where more vegetation was burnt (Pearson's $R_{MossSurvival} = -0.53$, $p < 0.001$). In other words, where the fire consumed less vegetation, leaving behind a higher canopy density and height, mosses were less impacted.

(2) Long-term recovery of vegetation post-wildfire communities

Fig. 4 Fire impact measures collected in 1×1 m² quadrats near drains (DR), away from drains (UN), and in adjacent hummocks (HU) and hollows (HO) in the Forsinard (FD) and BigHouse (BH) sites within the 2019 Flow Country fire footprint for **a** peat Composite Burn Index (pCBI) estimated following Davies et al. (2016); **b** proportion of *Sphagnum* displaying evidence of discoloration; **c** proportion of *Sphagnum* displaying a loss of capitulum; **d** proportion of mosses other than *Sphagnum* with evidence of burning; **e** proportion of Moss survival; **f** proportion of vegetation showing signs of re-sprouting; **g** total cover of vegetation species recorded as "burnt"; and **h** estimation of *Calluna vulgaris* consumption from difference between burnt and unburnt plots. In plots **a**), **b**), **c**), **e**), **g**), and **h**), sites and/or quadrat types that do not share the same italicized letter(s) were found to have differences between using linear mixed models and post hoc tests

When comparing the post-fire response in PFTs, the ME site, which was surveyed 15 months post-fire, clearly stands out both in unburnt and burnt plots (Fig. 5). There, the unburnt vegetation was dominated by a single shrub species, *Calluna vulgaris*, and site visits immediately post-fire confirmed that the vegetation was almost entirely consumed during the fire. This is visible in the data collected 1 year post-fire with large proportion of bare peat and a small (<25%) cover of newly sprouting shrubs (*C. vulgaris*) with some sedges (*Eriophorum*

vaginatum and *Carex panicea*). However, this site is not indicative of the trajectory that BH and FD are likely on, given that it was so different prior to the fire as inferred from unburnt controls. Instead, a more appropriate comparison of potential trajectory for FD and BH is with the CR8 and SH20 sites as illustrated by the similarity in the unburnt vegetation when comparing those sites.

From this comparison, we observed that lichens were still present in both burnt and unburnt plots at FD and BH, but they are notably absent in burnt only plots at CR,
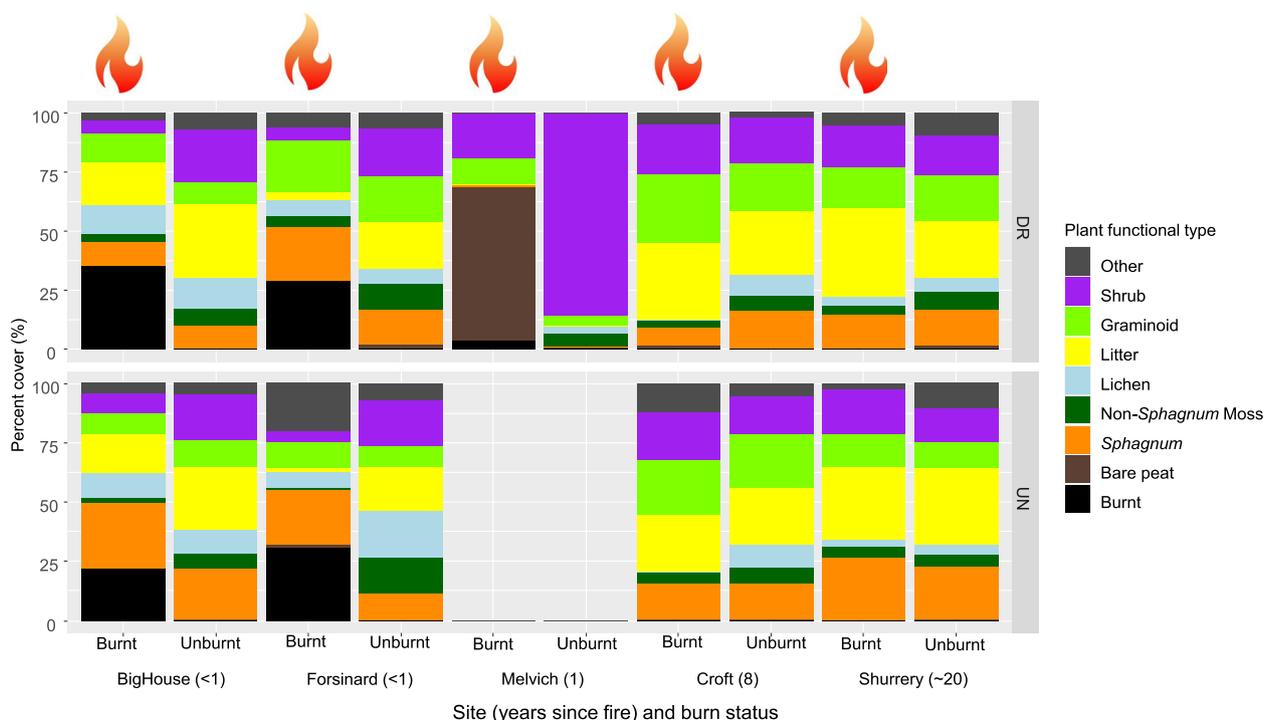
Fig. 5 Comparison of average percent cover for different plant functional types (PFTs) in burnt and unburnt plots from the five study sites. Note that Melvich only has drained quadrats

suggesting no post-fire recovery for that PFT during that timeframe at that site. Eight years post-fire at CR, we also observe slightly smaller *Sphagnum* covers, but higher covers of graminoids (inc. litter) in burnt drained plots compared with unburnt controls. Twenty years on based on the SH20 site, the PFT composition is largely similar, though post-fire covers remains slightly lower for lichen (both drain and undrained plots) and higher for litter (drain plots only) (Fig. 5).

The relative change in species assemblages over time in burnt plots compared to unburnt control was also overall small but significant and similar for undrained (PRC$_{axis1}$ = 6.1%, $p < 0.001$) and drained (PRC$_{axis1}$ = 5.4%, $p < 0.001$) quadrats (Fig. 6). The recovery in vegetation composition towards unburnt state took place rapidly at first before slowing, leading to a near-convergence over 20 years (Fig. 6). This is echoed by values of both the Morisita-Horn and Sørensen similarity indices (Table 2). After 20 years, indices were close to, or within the range observed between pairs of unburnt plots from different sites in both quadrat types (Morisita-Horn$_{drained}$ 0.73–0.79; Morista-Horn$_{undrained}$ 0.60–0.79; Sørensen$_{drained}$ 0.67–0.78; Sørensen$_{undrained}$ 0.69–0.74).

From the species driving these patterns (i.e., high absolute PRC scores in Fig. 6) and indicating a strong link with recovery towards unburnt controls, *Calluna*

vulgaris, the dominant shrub species, has burnt in both BigHouse and Forsinard sites and makes a progressive recovery over the 20-year period to reach similar level to unburnt plots, and never exceeding 20% cover (Fig. 7a). Interestingly for sedges, *Eriophorum vaginatum* is largely consumed in BigHouse but not in Forsinard, whereas *Trichophorum cespitosum* shows the opposite (Fig. 7b, c). The two species follow somewhat different recovery trajectories: *E. vaginatum* appears to recover slowly at first, before reaching or exceeding covers seen in long-unburnt sites after 20 years. *T. cespitosum* appears to recover quickly, before stabilizing or dropping below levels found in the long-unburnt sites after 20 years. For non-vascular plants, *Hypnum* sp., was dominant in BH and was consumed, but does not seem to be as prevalent at other site regardless of burnt status, with overall cover generally much smaller (Fig. 7e). By contrast, the covers of *R. lanuginosum*, as seen for lichen in the PFT analyses, are variable between unburnt sites but appears to lag in their post-fire recovery after 20 years, thus being rare among recorded taxa present in showing some residual differences between burnt and unburnt areas even in the oldest post-fire study site (Fig. 7f). While not displaying a high score on the PRC axis, we also looked at the grass *Molinia caerulea* cover, owing to its known association with fire. Interestingly, and explaining the lack of

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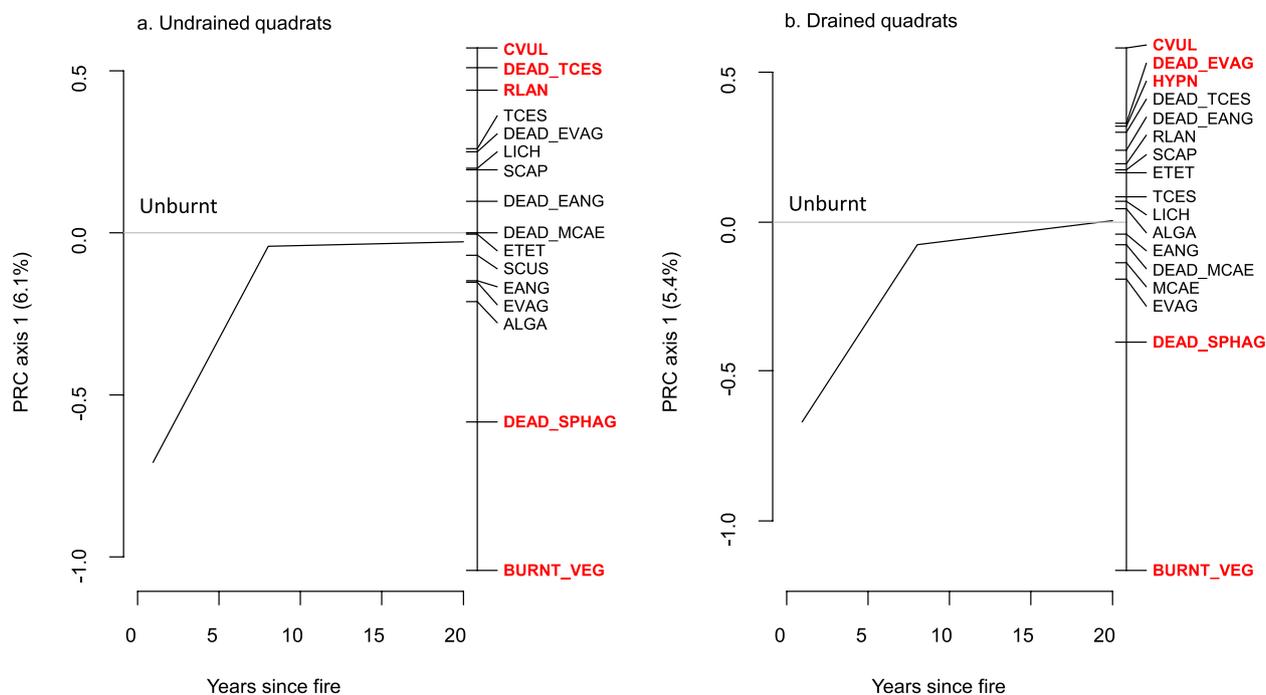
Fig. 6 Change over time in vegetation communities in burnt plots relative to unburnt controls as measured by the first axis of a principal response curve (PRC) for **a** Undrained quadrats and **b** Drained quadrats. Species with the highest scores (i.e., corresponding to the largest response to the time × site interaction) are shown on the vertical axis, species with an absolute value > 0.5 are in bold red character, as they represent species most associated with the time × treatment trend displayed

Table 2 Morisita-Horn and Sørensen similarity indices for pairwise comparison of burnt and unburnt vegetation communities in Undrained and Drained quadrats at the four sites along a fire chronosequence

Quadrat type	Undrained				Drained			
Site (year post-fire)	BH (< 1)	FD (< 1)	CR (8)	SH (20)	BH (< 1)	FD (< 1)	CR (8)	SH (20)
Morisita-Horn index	0.48	0.20	0.71	0.67	0.28	0.31	0.57	0.71
Sørensen Index	0.67	0.48	0.69	0.74	0.65	0.61	0.75	0.77

Sites: Bighouse (BH), Forsinard (FD), Croft (CR8), and Shurrery (SH20). Time since fire is indicated in brackets. Values range from 0 to 1, with 0 being completely different and 1 completely identical

relationship with the PRC curve, it has a high but variable cover (31 ± 13%) in burnt quadrats at the CR8 site only and is not a dominant component of the flora anywhere else, with covers of between 1 and 12% (Fig. 7d).

Discussion

Short-term impacts of wildfires on vegetation at the Flow Country fire site

Although ideal, it is often unrealistic to expect datasets with both pre- and post-fire data, given wildfires' unpredictable nature. In this study, we chose to match unburnt plots in all sites as closely as possible (distance, slope aspect, peat depth) to the burnt plots. We found that despite a large overlap in the unburnt assemblages from our four main sites (FD, BH, CR, SH) some significant

site differences existed. For instance, compared to all the other quadrats and sites, the undrained quadrats from the Forsinard had a notably high cover of *R. lanuginosum* and lichens (*Cladonia* sp.), which both appeared to have largely been scorched and/or consumed by the fire. Without the local long-unburnt control sites, we might have underestimated or missed this particular effect. While vegetation assemblages differed among sites, they did not systematically vary between quadrat types within each site, therefore partially rejecting our hypothesis that drained quadrats would support drier species assemblages. Although all drains were still visible on the ground, they are historic, some have not been actively maintained and some have been blocked by restoration intervention, potentially leading to a smaller-than
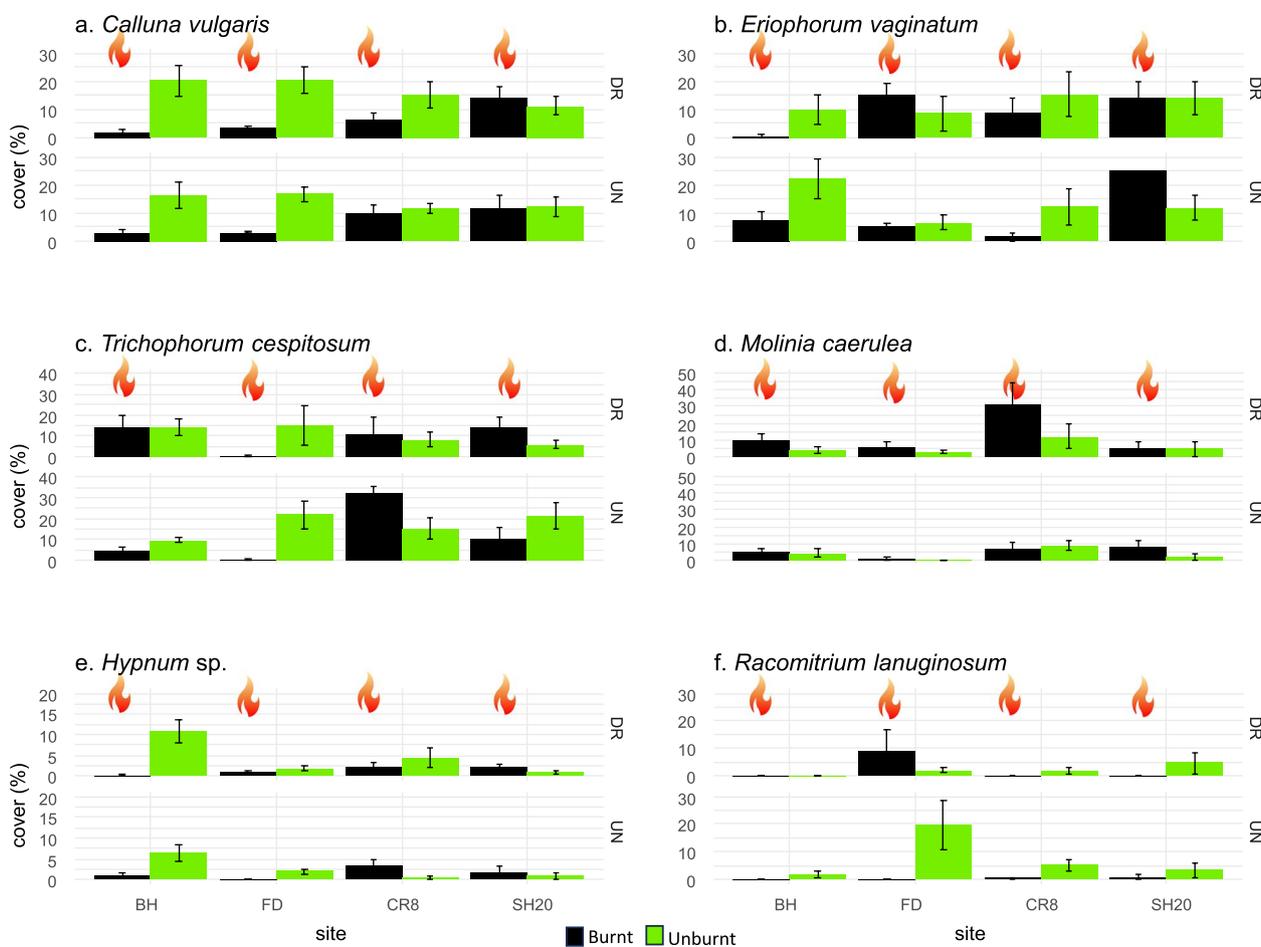
Fig. 7 Percent cover of combined live and litter for **a** Calluna vulgaris, **b** *Eriophorum vaginatum*, **c** *Trichophorum cespitosum*, **d** *Molinia caerulea*, as well as percent cover of **e** *Hypnum* sp., and **f** *Racomitrium lanuginosum* in the drained (DR) and undrained (UN) quadrats from the two sites impacted by 2019 wildfire, i.e., BigHouse (BH), Forsinard (FD), and the two sites used in the chronosequence, Croft burnt 8 years prior to the study (CR8) and Shurrery burnt 20 years prior to the study (SH20), displaying both burnt (black) and unburnt control (green) plots

expected effect on vegetation (van Seters and Price 2002). The influence of these drains would have also varied depending on the length, orientation relative to the slow, and depth of the drain, the slope steepness, and the position of any point upslope or downslope from the drains (Holden et al. 2004).

The wildfire in May 2019 preceded the annual greening up and growth of fresh vegetation, and it also occurred immediately after the European drought of 2018 (Buras et al. 2020), which had reduced surface moisture and water table depth across the Flow Country (Lees et al. 2021; Sterk et al. 2022). In Forsinard and in the parts of BigHouse where the peat is deep, where pool systems are present and where drains are rare or ineffective, the drought in 2018 is likely to have led to a significant surface subsidence, as observed in other similar sites in the Flow Country (Marshall et al. 2022). In other words, during the drought, as peat pores collapsed with dewatering,

the surface likely "tracked" the water level (Whittington & Price 2006). This may have not only mitigated against drought conditions, but may have also reduced the impacts of wildfire by allowing higher water content to be sustained at the peat surface (Price 2003) and increasing water availability for the blanket bog vegetation (Lapen et al. 2000).

Across the blanket bog landscape, this mechanical feedback also known as "bog breathing" (Glaser et al. 2004), is reduced in marginal, thin, or degraded areas (Bradley et al. 2022). In our study, the BigHouse (BH) site included more drains that remain unblocked and generally steeper slopes, both leading to "stiffer," less responsive peat. Instead of the surface tracking the water table, at those sites, only the water table would have dropped during the 2018 drought (Marshall et al. 2022). With lower moisture within the upper peat layers and with increased aeration and temperatures, vegetative growth of vascular

plants above- (Breeuwer et al. 2009; Sterk et al. 2022) and below-ground (Malhotra et al. 2020), and thus litter production, could have been enhanced. In turn, this could explain the higher cover of vascular vegetation and litter with evidence of burning in BH drain quadrats compared to all the other BH and FD quadrats.

Of all the areas in the study, Melvich (ME) was the most severely impacted by the wildfire, with nearly all the vegetation biomass consumed. This area was dominated by dense, monospecific stand of *Calluna vulgaris* and was thus particularly vulnerable to the wildfire (Davies and Legg 2011). What is more, there, the peat is the shallowest (up to ~0.5 m) and the area has a long history of peat cutting, grazing, and burning, which are likely to have caused the drying and compaction of the peat. During the drought, rather than subsiding, the sustained drop in water table would have caused prolonged aeration of the peat and severe cracking particularly on the sides of peat cuttings, creating hotspots for smoldering observed on the ground days after the fire was extinguished. The denser and drier peat at this site likely burned hotter and longer, causing higher severity and burning deeper into the peat and seed bank (Wuquan et al. 2021), which in turn is linked with long-lasting impact on vegetation (Davies et al. 2013; Kettridge et al. 2015). In other words, as observed by Davies et al., (2016), our study indicates that drier moorland community types are at greater risk of severe burns than wetter blanket bog communities.

At the small scale, we found that vegetation on hummocks (including *Sphagnum* mosses) tended to have more severe fire impacts than in hollows, with stronger impacts apparent where microtopography was more pronounced, as was hypothesized. This appears to contradict Shetler et al. (2008) who found hummocks to burn less severely than hollows, but is in line with theirs, and Benscoter et al.'s, (2011) findings that hummocks do not burn evenly during wildfires, with differences in depth of burn influenced by height but also slope, aspect and complexity of the hummock's surface. For instance, surfaces angled towards the flaming front, like the sides of bigger hummocks, tend to burn deeper than flat surfaces (or lower hummocks) because they receive a greater radiation pulse (Dupuy & Maréchal 2011). In our site, this may also be related to the abundance of flammable species like *C. vulgaris* and lichen sp., which, although variable, were on average twice as abundant on hummock than on hollows and would have allowed wildfire to spread (Turetsky et al. 2004). Anecdotally, we observed localized charring and deep burn scars into hummocks where *C. vulgaris* had entirely been consumed. It will be possible to use our baseline data to determine whether the abundance of microforms (hummock-hollows) changes post-fire, through a range of feedback processes such as autogenic

surface drying, facilitating hummock species expansion into adjacent hollows (Benscoter et al. 2015).

Longer-term effects of known wildfires in the Flow Country and beyond

Twenty years post-fire, only small differences remain between burnt and unburnt plots with some species or functional groups taking longer to recover, such as lichen. Dunford et al. (2006) also recorded an absence of lichens in several 20-year-old post-fire sites in boreal peatlands, with a recovery after 40 years to covers within their natural range at long-unburnt sites (4.6–41.3%). This is interesting as the long-unburnt site at Forsinard (FD), which had the highest cover of lichen, is likely to have burnt in 1981 (38 years prior to the study) during a large wildfire that land managers remember, but for which a documented footprint was not available. Yet, overall, vegetation assemblages in our blanket bog sites have largely recovered to the point that while not being identical, they are no more dissimilar after 20 years to the unburnt controls than the different unburnt areas are among themselves. For nearly all the pairwise comparisons, the abundance-based Morisita-Horn index had a lower value (lower similarity) than the richness-based Sørensen index, with the largest discrepancy between the two indices found in the more recently burnt sites. Given that the Sørensen index is more sensitive to the most abundant species, this suggests that the progressive homogenization between burnt-unburnt plots over time is more likely related to changes in species relative abundances rather than turnover (Jost et al. 2011). This is also reflected by the small proportion of variation (5–6%) explained by the time and treatment interaction in our PRCs, which suggest a high survival rate through the fire, including of keystone genera like *Sphagnum*.

By contrast, higher severity fires have been shown to increase the abundance of ericoids, graminoids and acrocarpous mosses (Grau-Andrés et al. 2019) or even to lead to loss of specialist species (Kelly et al. 2023). In our study, for ericoids, we did not find any evidence of *C. vulgaris* dominance or post-fire increases in covers relative to unburnt sites, with values remaining no higher than 20% at all our sites except the highly degraded ME. Fires have also been shown to stimulate increased invasive spread of the grass *Molinia caerulea* through changes in demographic parameters such as growth of seedling and juveniles and increase in biomass (Jacquemyn et al. 2005). Again, we did not observe this effect except with a marginal increase at our CR sites (8 years post-fire). It may be that in areas of the Flow Country such as the ones studied here, where historical burning management has not been practiced for several decades, but where occasional wildfires have occurred, vegetation succession could have led

to an ageing and degeneration of the *C. vulgaris* stands (Schellenberg & Bergmeier 2022; Hancock et al. 2018), alongside a progressive replacement by peatland species characteristic of wetter habitats, such as *E. tetralix, M. gale, E. angustifolium*, and *T. cespitosum*. Fires impacting older stands of *C. vulgaris*, such as those that may be present in parts of the Flow Country, have been shown to lead to poor regeneration with limited seedling establishment (Davies et al. 2010). Another important distinction with heather-dominated sites in northern England where much of the UK fire research takes place relates to grazing: while those sites are mostly summer grazed by sheep (e.g., Milligan et al. 2018), the Flow Country sites are subject to year-long grazing by deer, which could further impact heather, particularly with winter grazing (Pérez-Barbería et al. 2013). Together, these processes could explain the lack of *C. vulgaris/M. caerulea* dominance, and in turn contribute to reduction in flammable vegetation and associated risk of severe impacts from wildfire.

On the other hand, like in many upland areas, our sites include large stands of non-native conifers in the landscape, which may also influence peatland fire feedback (Nelson et al. 2021). Over 1 Mha of Western European peatlands were planted with *Picea sitchensis* and *Pinus contorta* during the 1960s–1980s (Andersen et al., 2017) including 67,000 ha of Flow Country (Lindsay et al. 1988), creating large plantation "islands" beyond which trees have spread onto the adjacent open peatlands, often drying the peat around them. There is a known association of *P. contorta* with fire in its native range (Agee 1998) and it is also one of the most invasive conifers in the world owing to its large seed production and rapid juvenile growth (Rejmanek & Richardson 1996). While we did not find seedlings of either species in any of the plots at any of the sites during our surveys in 2019–2020 (less than 1 year post-fire), it is possible that in coming years, conifer regeneration, and particularly *P. contorta* regeneration, may increase more in burnt vs unburnt areas at the BH and FD sites close to existing plantations that continue to act as seed sources. This adds to the risk of alternative, unwanted vegetation trajectories after peatland wildfire, which would not only be detrimental to peatland biodiversity, but would also increase fuel load and thus the susceptibility of these areas to future wildfires. To better understand the feedback between conifer regeneration, peatland biodiversity and wildfire and to inform policy, it will be important to re-visit the 2019 sites over time and use the present study as a post-fire "baseline."

Conclusion
Our study provides further evidence that resilience to occasional wildfires is strongest where peatlands have vegetation assemblages with a mixture of shrubs and sedges with abundant *Sphagnum* cover, typical of wet conditions and high soil moisture. In our study, these conditions were primarily found in "no-burn" areas subject to conservation management, including where restoration interventions such as drain blocking have taken place. On the other hand, we observed more severe impacts where past degradation had enabled drier, flammable species to take hold, close to active drains and on historic peat cutting areas. Our findings support the idea that management interventions that enable wetter vegetation assemblages to persist on peatlands could play an important role in mitigating fire effects and enabling rapid vegetation recovery at the landscape scale. In future research, site(s) with a longer fire-free interval and multi-taxa surveys (including, e.g., microbes) would be needed, to determine whether any true fire refugia exist in the UK peatlands as they do elsewhere (Kuntzemann et al. 2023). In addition, understanding of how internal ecological-hydrological-mechanical feedback mechanisms affect fire severity and post-fire succession will be enhanced by studies at the landscape scale, taking into account other factors that might have impacted fire behavior. Finally, well-designed and well-replicated, long-term fire experiments, e.g., burning matched drained and undrained areas under near-identical conditions, would also help resolve questions around peatland wildfire behavior and impact. These studies are much needed, as we now face a future where wildfires are likely to become more frequent and more severe (Arnell et al. 2021), with potentially profound consequences on global feedback between peatlands and the climate system (Turetsky et al. 2015; Wilkinson et al. 2023).

Author details
[1]Environmental Research Institute, University of the Highlands and Islands, Castle St., Thurso KW14 7JD, UK. [2]Centre for Conservation Science, RSPB, RSPB Scotland, Etive House, Inverness IV2 3BW, UK. [3]RSPB Forsinard Flows National Nature Research, Forsinard KW13 6YT, UK. [4]Faculty of Engineering, University of Nottingham, University Park, Nottingham NG7 2RD, UK.

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