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RESEARCH ARTICLE

Diversification of *Molinia*-dominated blanket bogs using *Sphagnum* propagules

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Abstract

1. Increasing dominance by purple moor grass, *Molinia caerulea* ('*Molinia*') on globally rare and protected blanket bogs of the United Kingdom and the South Pennines is a growing threat to diversity and carbon storage, as well as increasing the risk of wildfire.
2. In a trial to increase diversity using *Sphagnum* plugs planted on three *Molinia*-dominated sites in the South Pennines, an initial rapid increase in cover of plug-derived *Sphagnum* (PDS) suggested an advantage over that of naturally occurring *Sphagnum* colonies, the latter remaining below 1% cover throughout; subsequent plateauing of PDS cover in areas of moderate *Molinia* cover (<80%) was linked with drought stress, whereas declining cover in *Molinia*-dense areas (>80%) suggested additional competition for light.
3. The cover of *Molinia* was only weakly reduced by, and then completely recovered from, a baseline flailing treatment. Increasing cover of PDS in all of the treatments had no clear effect on the cover of *Molinia*.
4. The cover of naturally occurring indicator species was strongly reduced by the baseline flailing treatment; subsequent recovery was not complete, even with contributions by PDS. There was a negative linear relationship between *Molinia* cover and indicator species cover, over all ranges of *Molinia* cover.
5. Water table depths were lowered by PDS during the first 3 years of the trial, perhaps due to facilitated capillary conduction of water through the buried plug tissues.
6. It was concluded that PDS can establish rapidly amongst *Molinia*, boosting the diversity and cover of indicator species, but that establishment is slower in areas of dense *Molinia* and also likely to be hampered by periods of severe drought stress. Prior flailing had no clear benefit on the growth of PDS but reduced the cover of naturally occurring indicator species. Further investigations should include the role of water stress, shading and phosphorus limitation in restricting the growth of PDS within *Molinia*-dominated swards.

KEYWORDS
blanket bogs, competition between Sphagnum and Molinia, diversification, Molinia dominance, Molinia management, peatland plant communities, Sphagnum

1 | INTRODUCTION

1.1 | European and UK trends in *Molinia dominance*

During the past few decades, increasing dominance of *Molinia caerulea* (purple moor grass) has become a major threat to diversity and conservation on western European heathlands (e.g. Berendse, 1998; Marrs et al., 2004). On English moorlands and blanket bogs, there is evidence of *Molinia* dominance dating from the beginning of the Industrial Revolution in the late eighteenth century (Chambers & McCarroll, 2015), and it is now particularly prevalent on the South Pennine Moors, where 21% of a total of 620 samples had more than 50% cover of *Molinia* (N. Critchley, 2011; reviewed in Glaves, 2015). On Berry Greave, a South Pennine blanket bog site on the Marsden Moor Estate, an area dominated by *Molinia* doubled in size over a period of 17 years, from 1988 to 2015 (Meade, 2015).

1.2 | Concerns about *Molinia* dominance on UK blanket bogs

Blanket bogs are globally rare and a nationally protected UK Biodiversity Action Plan (BAP) priority habitat; increasing levels of domination by *Molinia* on these sites is a growing concern for conservationists because it can displace or exclude species, especially but not exclusively *Sphagnum* species, which are indicative of bog in 'favourable' and actively peat-building condition (Defra, 2007; JNCC, 2009). Globally, peatlands are the largest natural terrestrial carbon store (International Union for Conservation of Nature [IUCN], 2020) and in upland England, the majority of blanket bogs are already losing carbon (NE, 2010) – losses that an increasing domination by *Molinia* is likely to exacerbate (Berendse, 1998; Jepson, 2015). Wildfire risk and occurrence in the United Kingdom is strongly linked with the dominance of flammable species such as *Calluna vulgaris* (heather) and *Molinia* (Jacquemyn et al., 2005), and escaped management burning and arson can be major causes of ignition, especially in *Molinia* and during hot dry weather (Glaves et al., 2020). However, evidence for the influence of *Molinia on* wildfire risk and occurrence and wider ecosystem services, such as water flow regulation and water quality, is currently lacking (Shepherd et al., 2013).

1.3 | *Molinia* and its rise to dominance in upland vegetation communities

Molinia is an integral, sometimes diagnostic member of the main blanket bog vegetation communities (Table 1), including the heather–hare's tail cotton grass mire community (NVC: M19) typically found throughout the South Pennines (Rodwell et al., 1991). Although typically restricted in these communities (Rodwell et al., 1991), probably due to waterlogging (Meade, 2015) and lack of nutrient supply, *Molinia* has tendencies towards competitive dominance (Anderson et al., 2006) due to its deep and extensive roots, dense tussock formation, robust overwintering strategies, and rapid spring growth (Anderson, 2015; Taylor et al., 2001). Increasing abundance and domination by *Molinia* is most likely the result of decreasing waterlogged conditions due to climate change and anthropogenic drainage, together with an increased supply of atmospherically deposited nutrients over the past few decades, particularly nitrogen (e.g. Anderson, 2015; Bobbink et al., 1998; Caporn et al., 2015; Marrs, 1993; Rodwell et al., 1991). Both *Molinia* and *Sphagnum* mosses are limited in their growth by nitrogen availability, but *Sphagnum* mosses are generally adapted to efficiently absorb and metabolize relatively low levels of atmospherically deposited nitrogen and can act like a filter, preventing access by vascular plant roots and maintaining a competitive advantage (Berendse et al., 2001; Lamers et al., 2000; Limpens et al., 2003; Malmer et al., 2003). However, if N is deposited or added in any of the following ways then vascular species generally, and especially *Molinia* (Limpens et al., 2003) can retain competitive advantage at the expense of *Sphagnum*, if not by direct toxicity, then by shading (Limpens et al., 2003):

- At rates above the productivity rate of *Sphagnum* (Berendse et al., 2001; Lamers et al., 2000; Limpens et al., 2003),
- At levels that cause toxicity to *Sphagnum* (Limpens et al., 2003; Press et al, 1986),
- At sustained high levels (Heil & Diemont, 1983; Lee, 1998; Lamers et al., 2000; Rosenburgh, 2015),
- From fire-related ash (suggested from Noble et al., 2017) and
- Delivered beneath the surface of the moss in addition to experiments or in soligenous peats (Malmer et al., 2003).

Nutrient enrichment is likely to have promoted the overwhelming dominance of *Molinia* in the purple moor grass – tormentil mire community (NVC: M25), which is typically found in cool western lowland areas of Britain, but which can nevertheless extend its range up to the margins of upland blanket bogs (Rodwell et al., 1991). In this community, areas of extreme *Molinia* dominance are accompanied by a significant absence of other species and are likely to have been promoted by some form of enrichment or management such as burning, grazing and drainage, but always on moist, well-aerated peats which have a degree of slope or flushing to remove stagnant water (Godwin & Conway, 1939; Rodwell et al., 1991). Repeated management burning in blanket bogs of the South Pennines, particularly in late winter, may also lead to a loss of specialized bog species and a shift towards the more fire-adapted *Molinia* (Defra, 2007; Rodwell et al., 1991; Glaves,

TABLE 1 Comparison of selected NVC mire communities with European EUNIS classification and EU Habitats Directive Annex 1 list

UK National Vegetation Classification (NVC)	*Molinia* frequency (abundance)	European EUNIS Classification	European EU Habitats Directive Annex 1
M17 *Scirpus cespitosus – Eriophorum vaginatum* blanket mire, particularly of cool, oceanic, wet conditions, below 500 m	**IV (1–8)**	**D1.21** Hyperoceanic low-altitude blanket bog (contained by M17)	**H7150** Depressions on peat substrates **H7130** Blanket bog (overlapping with M17)
M18 *Erica tetralix – Sphagnum papillosum* raised and blanket mire, replacing M17 on raised bogs in moderately wet oceanic conditions	II (1–4)	**D1.111** Raised bog hummocks, ridges and lawns (overlapping with M18)	**H7110** Active raised bogs **H7150** Depressions on peat substrates **H7130** Blanket bog **H7120** Degraded raised bog (0verlapping with M18)
M19 *Calluna vulgaris – E. vaginatum* blanket mire, typical of uplands in the South Pennines, with harsh/freezing winters and cool summers	I (1–7)	**D1.221** Hiberno-Britannic *Eriophorum-Calluna* blanket bog (contained by M19)	**H7110** Active raised bogs **H7130** Blanket bog (overlapping with M19)
M20 *E. vaginatum* blanket and raised mire.	Not denoted, but can be major presence, especially on margins	**D1.222** Britannic *E. vaginatum* blanket bogs (equal to M20)	**H7130** Blanket bog
A species-poor version of M19 (due to over-grazing, burning, draining, pollution)			**H7120** Degraded raised bog (overlapping with M20)
M25 *Molinia caerulea – Potentilla erecta* mire, of cool, wet western lowlands, but extending to upland blanket bog margins, especially with nutrient enrichment	**V (2–10)**	**D1.12** Degraded raised bogs still capable of natural regeneration **D1.21** Hyperoceanic low-altitude blanket bog **E3.512** Acidocline purple moorgrass meadows **F4.13** *Molinia caerulea* wet heaths, on shallow peats/mineral soils (contained by M25)	**H7130** Blanket bog **H7120** Degraded raised bog (overlapping with M25)

Notes: *Molinia* frequency refers to the percentage occurrence of *Molinia* amongst different samples and is denoted by the Roman numerals I–V (I = 1–20%; II = 21–40%, etc.). *Molinia* abundance refers to the average cover of *Molinia* present in samples and summarized as bracketed ranges using the DOMIN scale (Rodwell et al, 1991). Red font indicates major presence of *Molinia*.
The EUNIS classification system is still under development, especially at the more detailed levels, where there appear to be some overlaps. At the broadest level 1 category, blanket bogs are denoted by "D1" while wet grassland types are denoted by "E3" and wet heaths are denoted by "F4.1" (Strachan, 2017). The UK interpretation above is simplified and adapted from the JNCC website (JNCC, 2008) with additional details from Strachan (2017). The list of EU Annex 1 habitats has undergone complex development with different interpretations amongst different member states (Strachan, 2017). The UK interpretation above is simplified and adapted from the JNCC website (JNCC, 2008), but also see Strachan (2017) for more details.

2015). Combined with heavy grazing pressure, the removal of vegetation can become so severe that bare peat is exposed, and erosion gullies formed. The subsequent lowering of water tables can ultimately promote *Molinia* dominance because it grows more vigorously in aerated peaty soils (Anderson, 2015); this same train of events was suggested by Jepson (2015) as being responsible for a transition from *Sphagnum*-rich M18 community (NVC: M18, cross-leaved heath – *Sphagnum papillosum* raised and blanket mire; Rodwell et al., 1991) in the Forest of Bowland towards an M25 variant, dominated by *Molinia*. The effect of drainage per se in lowering water tables has been shown to cause irreversible damage to the upper layers of peat and replacement of *Sphagnum* mosses with *Molinia* (Schouwenaars, 1993).

1.4 | Reducing dominance of *Molinia*

On heather moorlands, efforts to reduce the dominance of *Molinia* have been driven by a desire for the re-establishment of *Calluna*, where a more equal balance between the two species can provide fodder for year-round stock grazing (e.g. Milligan et al., 2004; Fraser et al., 2011; Martin et al., 2013). However, the methods employed for this purpose often involve expensive, time-consuming and high-disturbance activities including various combinations and repetitions of burning, flailing, grazing, spraying with herbicide and seeding with *Calluna* (e.g. Chambers et al., 1999; Smith & Bird, 2005; Shepherd et al., 2013), with the risk of pollutant run-off to adjacent reservoirs, as well as highly variable and unpredictable longer term outcomes (C. N. R. Critchley et al., 2008; Marrs et al., 2004). The introduction of scarce or absent mire species, such as *Sphagnum*, is a viable alternative management tool (Shepherd et al., 2013), and there is mounting evidence for an increase in diversity along with a wide range of other benefits resulting from land management activities that focus on re-wetting and raising water tables on upland blanket bogs (Alderson et al., 2019; Anderson, 2015; Buckler et al., 2013; Regensburg et al., 2021; Shuttleworth et al., 2019). These activities include revegetation, blocking gullies, ditches, bunds and pipes and inoculating with *Sphagnum* propagules.

While these activities are primarily aimed at highly degraded blanket bog with depleted vegetation and bare peat, trials on areas dominated by vascular species such as *Molinia* are ongoing (MFFP, 2021). These techniques are likely to weaken dominance by *Molinia*, particularly if stagnant, waterlogged conditions can be achieved.

1.5 | Growing *Sphagnum* in blanket bogs

Recolonizing degraded blanket bog with *Sphagnum* has the potential for strengthening ecosystem service benefits and is an integral part of the process for restoring 'active' blanket bog functioning (Caporn et al., 2015; Defra, 2007; C. D. Evans et al., 2014; Caporn et al., 2015). The presence of *Sphagnum* has been shown to increase carbon sequestration and peat formation (van Breemen, 1995; JNCC, 2011), improve water quality (Ritson et al. et al., 2016) and is likely also to reduce flood and fire risk.

Current levels of nitrogen and sulphur deposition are unlikely to cause direct damage to *Sphagnum* (Carroll et al., 2009), and there is evidence for the successful transplantation of *Sphagnum* on damaged lowland bogs (Money, 1995) and on degraded blanket bogs in the Dark Peak (Caporn et al., 2006). While there is also evidence for some natural recolonization of *Sphagnum* species across the Peak District (Carroll et al., 2009); nevertheless, both abundance and diversity remain low in most of these areas and may be related to a legacy of acidity and metal pollution resident in the substrate (Caporn et al., 2015), ongoing nitrogen deposition (Rosenburgh, 2015), poor surface water conditions (Rogers, 2014), drier peat generally following the disappearance of *Sphagnum* (Anderson, 2015), low frequency of *Sphagnum* refugia (Wheeler & Shaw, 1995) or increased frequency of desiccating events due to climate change (Weltzin et al., 2000).

With regard to the latter concern, peat core studies mainly by Conway (1954), Tallis (1964, 1994), Tallis and Livett (1994) suggested that in shallow peats of the Southern Pennines, *Sphagnum* remains are poorly represented, in some cases having been largely replaced by those of *Eriophorum vaginatum* and coinciding with erosional dissection and subsequent drying of blanket peat 1000 years ago, followed by drier climatic conditions between c. AD 1150 and 1300 and then modifications associated with human interference beginning after the fourteenth century (Tallis, 1994). The scarcity of visible *Sphagnum* macrofossils in the top 50 cm and also at greater depth of cores from Marsden Moor (NTV, 2021) supports the studies of Conway and Tallis et al. These findings may have implications for the current programme of widespread planting of *Sphagnum* plugs. Ideally, implantation would be focused on the deeper peats with evidence of former blanket mire and where the topography and hydrology are most supportive of *Sphagnum* growth (R. Meade, 2021, pers comms).

Above all, re-wetting is regarded as an essential primary action for encouraging re-establishment of *Sphagnum* on bogs, especially the raising and stabilization of fluctuating water tables (Defra, 2007; Wheeler & Shaw, 1995). In this regard, Jepson (2015) observed that widespread recolonization by *Sphagnum* amongst dominant *Molinia* will only be a feasible option if there is sufficient re-wetting together with a cessation of management burning.

1.6 | *Sphagnum* propagules

Various types of commercially available *Sphagnum* propagules have been developed to accelerate recolonization, including fragments encased in protective beads, floating in a viscous gel, or grown on in greenhouses to form plugs (Micropropagation Services, Leicestershire, UK). Experimental trials on a severely degraded, and recently re-vegetated blanket bog habitat showed that the plug-type propagule provided the best cover of *Sphagnum*, closely followed by translocated clumps (Crouch, 2018).

The presence of taller and more abundant dwarf shrubs was suggested to be the reason for greater success of introduced *Sphagnum* propagules at a blanket bog site in the Peak District (Noble et al., 2019), presumably through the same mechanisms proposed by Wheeler and Shaw (1995) for *Sphagnum* growing either in *Molinia*, *E. vaginatum* or *Juncus effusus* and which involved physical support, shelter from winds and maintenance of humidity. Jepson (2015) also concluded a microclimatic effect when *Sphagnum papillosum* hummocks were observed flourishing to such an extent that *Molinia* was actively outcompeted amongst relatively dense *Molinia* in blanket mires of the West Pennine Moors and in the presence of high and stable water tables.

1.7 | Hypothesis, aims and objectives of this trial

This study proposes that the planting of *Sphagnum* propagules will lead to the successful establishment of a wide diversity of *Sphagnum* species, which will reduce the dominance of *Molinia*. The specific aims and objectives of the trial were to find if there is a difference in growth of *Sphagnum* plugs:

1. At different sites with different *Molinia* cover and water table depths
2. With a single pre-flailing treatment, with and without windrowing
3. When planted in gullies.

2 | MATERIALS AND METHODS

2.1 | Site locations

The three *Molinia*-dominated blanket bog study sites were all located in the South Pennines Moors SSSI/SAC (Figure 1 and Table 2). Two of the sites were owned by Yorkshire Water (Green Withens and Linsgreave Clough) and the third by The National Trust (Burne Moss). The main criteria involved in their selection included their presence on blanket bog habitat maps supplied by Natural England, a peat depth greater than 1 m, the presence of gullied areas relatively proximal to flatter areas and general slope less than 10°. All of the sites were noted by

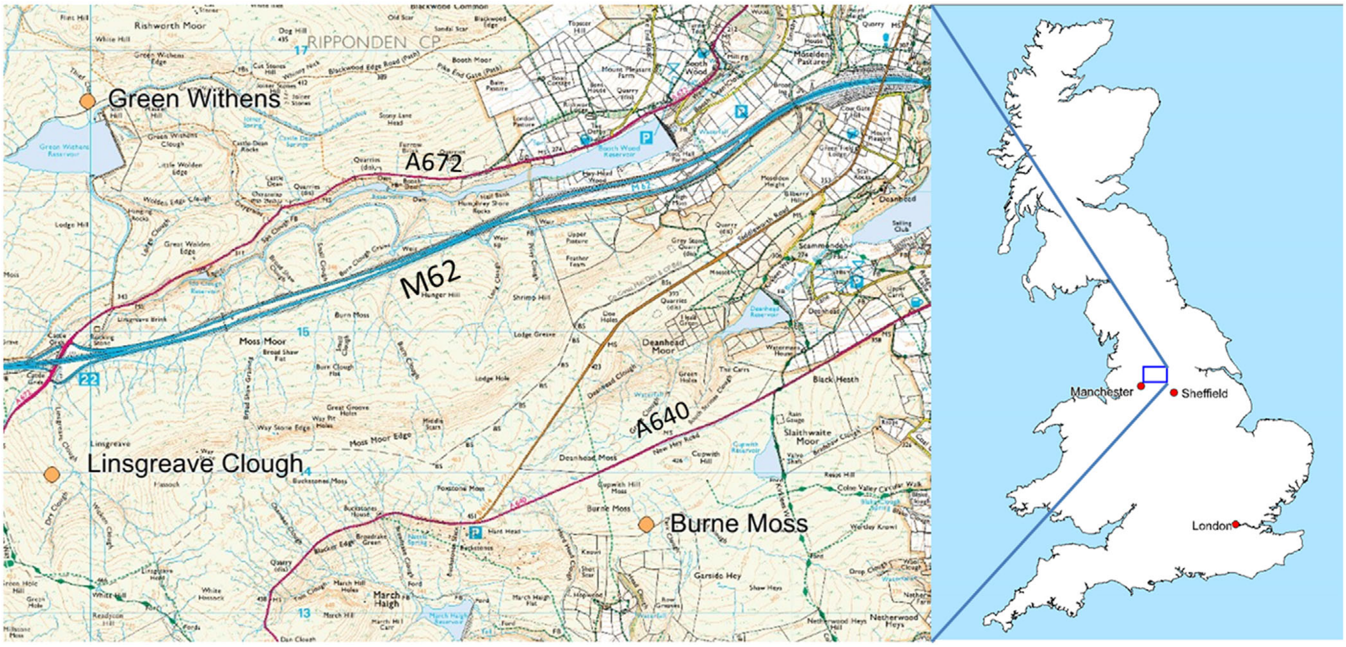

FIGURE 1 Map showing the three replicate trial sites (left) in relation to GB outline (right). The three replicate trial sites (Green Withens, Linsgreave Clough and Burne Moss) are shown on either side of the M62 motorway (blue line). © Crown Copyright and database rights 2020. 100005734

TABLE 2 Characteristics of the three blanket bog sites

			Cover (%)		
Site	Altitude (m)	Aspect	*Sphagnum*	*Molinia*	Indicator species
Green Withens	370	Southerly	0.2	97	2
Linsgreave Clough	400	Easterly	0.6	64	23
Burne Moss	405	Southerly	0.1	81	13

Notes: Cover (%) of vegetation types was measured in the baseline survey of 2014 and does not include non-indicator species except Molinia. Altitude is measured as metres above sea-level. 'Indicator species' are defined in Section 2.5.

Natural England as being in 'unfavourable recovering' condition due to *Molinia* dominance at the time of their most recent SSSI condition assessment (NE, 2021which was attributed to previous overgrazing (at Burne Moss, reported in 2009), overgrazing and management burning and wildfire (at Green Withens, reported in 2014) or repeated wildfire events and over grazing (at Linsgreave Clough, reported in 2015). All of the sites now have reduced grazing rates resulting from management schemes designed to enhance the environment, for example Higher Level Stewardship and Environmentally Sensitive Area agreements on Green Withens and Burne Moss, respectively, whilst Linsgreave Clough is described as having reduced grazing by sheep to help facilitate recovery from *Molinia* dominance (NE, 2021).

2.2 | Experimental design

The basic experimental unit consisted of a random block design with six treatment areas: four square treatment areas on relatively flat terrain accessible by farm machinery; and two elongated treatment areas located in, and following the natural course of, two gullies considered inaccessible by farm machinery. All six treatment areas were replicated over three geographically separated sites (blocks) in the South Pennines (Figure 2).

2.3 | Treatments

Each square treatment area had sides of 20 m, with each area separated by a 5 m boundary. The treatments consisted of control (C); *Sphagnum* plugs in *Molinia* (CP); *Sphagnum* plugs in pre-flailed *Molinia* (FP); and *Sphagnum* plugs in pre-flailed + windrowed *Molinia* (FWP). The gully treatment areas consisted of a gully control (GC) and *Sphagnum* plugs in gully *Molinia* (GP). Ten permanent square quadrats of side 2 m, marked using two stakes at diagonal corners, were placed at random within each treatment area. Water table was measured using a single dipwell in each of the quadrats.

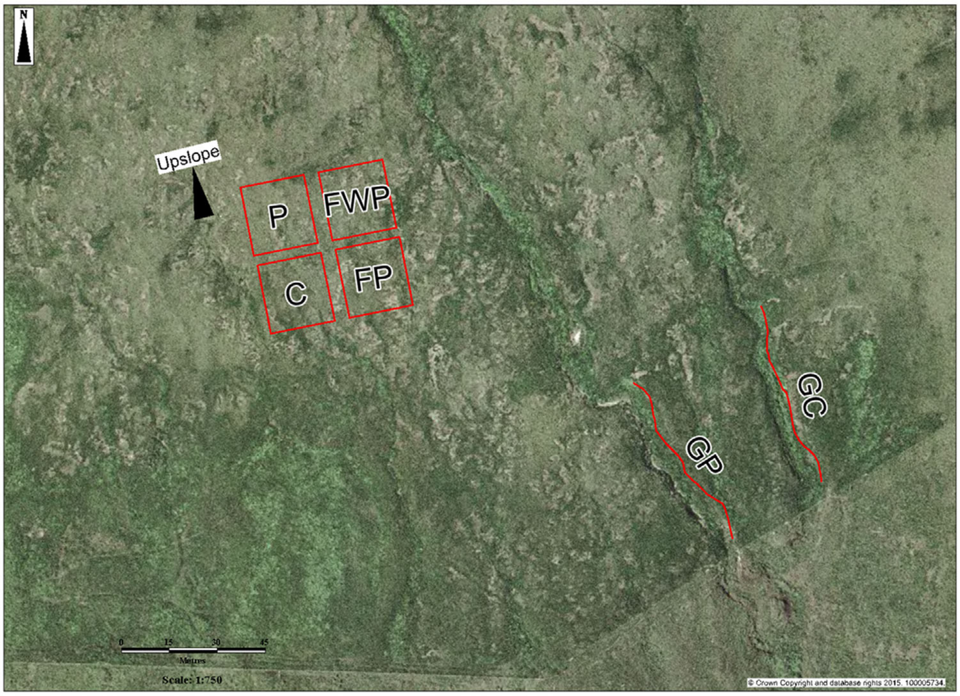

FIGURE 2 Aerial photograph of Burne Moss site with experimental design. This annotated map of the Burne Moss site shows the basic experimental design unit, which consists of four treatment areas (20 m × 20 m) and two elongated treatments of the same area but following the line of gullies. The treatments involved planting *Sphagnum* plugs, as follows: C (control), P (plugs only), FP (flailed with plugs), FWP (flailed and windrowed with plugs), GC (gully control) and GP (gully plugs)

2.3.1 | Flailing and windrowing

The flailing treatment and the flailing + windrowing treatment were applied to two of the four treatment areas in the accessible, relatively flat, non-gully areas. Flailing was achieved using a mechanically powered and rapidly rotating system of metal scallops which was set low enough to cut the vegetation as well as the surface rooting structure. The flailing machine in this trial was powered using a small alpine tractor (Figure 3, left). Windrowing was achieved by hand-raking the flailed material (mulch) into lines about 5 m apart, immediately after flailing (Figure 3, right). Both of these processes were carried out by horticultural contractors.

2.3.2 | Plug-derived *Sphagnum*

Sphagnum propagules in the form of plugs (supplied by Micropropagation Services, Leicestershire, UK) were used as the basis for establishing *Sphagnum* colonies. These plugs consisted of 12 different *Sphagnum* species present in varying proportions (Table 3). *Sphagnum* plugs were planted in the centre of each quadrat, in a square of side 1 m, using a 6 × 6 grid pattern to give a total of 36 plugs per quadrat (Figure 4). The plugs were planted by hand in July 2015 in the treatment areas CP, FP, FWP and in the gully treatment area GP. Each plug was planted using a long-handled dibber to make a hole which was subsequently closed around the plug – this ensured each plug was anchored and in contact with moist peat (Figure 5, left). Many of the treatment areas which had been pre-flailed in autumn the previous year, presented a relatively bare surface through which the shoots of *Molinia* were already beginning to grow (Figure 5, right). By 2018, the PDS had mostly coalesced together in a solid mass but were barely visible under a canopy of *Molinia*.

2.3.3 | Gully locations

An unmarked treatment area of approx. 400 m^2 was set-up in gully areas by measuring a distance of 200 m along the length of the gully and extending 1 m on either side of the semi-permanent central water course. Quadrats were placed randomly in this area, along the bed of the usually mineral-based gullies at intervals of approximately 20 m. Similar to non-gully areas, the *Sphagnum* propagules (plugs) were planted into the central 1 m^2 of a 4-m^2 quadrat in gully locations. Due to the relatively large size of *Molinia* tussocks in the gullies and the deep, water-filled inter-tussock troughs, some of the gully plugs were planted into the sides of the tussocks.

2.4 | Naturally occurring *Sphagnum*

Naturally occurring *Sphagnum* was initially defined as the *Sphagnum* colonies observed during the baseline survey (2014); later, after plug planting in the central 1 m^2 of each 4-m^2 quadrat, naturally occurring

FIGURE 3 Flailing (left) and windrowing (right) at the Green Withens site prior to planting *Sphagnum* plugs. Flailing consists of a cut using rotating metal scallops that can penetrate to the *Molinia* roots; windrowing consists of raking the cut material into parallel rows approximately 5 m apart

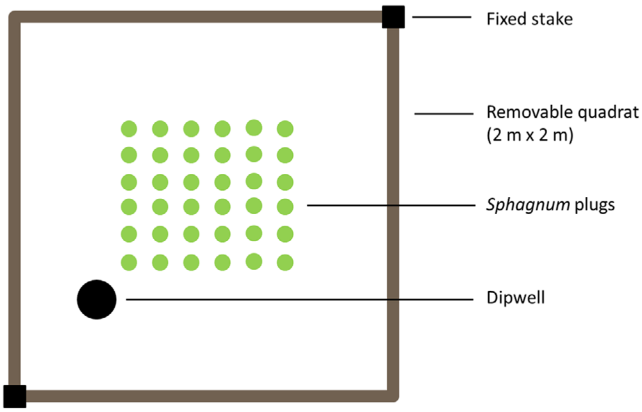

FIGURE 4 Diagram of a quadrat with a dipwell and *Sphagnum* plugs. The *Sphagnum* plugs were arranged in a 6 × 6 grid and occupied a 1 m × 1 m square in the centre of the 2 m × 2 m quadrat. A dipwell was located close to the plugs on a diagonal of the quadrat

TABLE 3 Proportions of *Sphagnum* species in the plugs

Sphagnum species	Proportion	*Sphagnum* species	Proportion
S. fallax	30–50%	*S. subnitens*	5–10%
S. palustre	20–40%	*S. denticulatum*	~1%
S. papillosum	20–40%	*S. squarrosum*	~1%
S. capillifolium	10%	*S. tenellum*	~1%
S. cuspidatum	10%	*S. magellanicum**	~1%
S. fimbriatum	5–10%	*S. russowi*	~1%

Notes: The proportions of species in the table are given as bulk estimates – in any single *Sphagnum* plug, these proportions may differ substantially from those stated. * Now known as S. medium, according to revised classification (Hassel et al., 2018).

Sphagnum was defined as the *Sphagnum* colonies growing outside of the central 1 m^2 area. The cover of naturally occurring *Sphagnum* in the treatment areas remained at or below 1% in all surveys throughout the course of the trial.

FIGURE 5 Planting Sphagnum plugs. The plugs were planted using a dibber (left); appearance of plugs immediately after planting in 2015 (middle) and after 3 years growth in 2018 (right), with the plugs coalesced underneath a returning *Molinia* canopy

TABLE 4 Timetable of events

Action	Year	Month
Full survey (all)	2014	August
Flailing/windrowing		September
Plug planting	2015	July
Plug cover survey		August
Vascular species survey		September
Plug cover survey		October
Full survey (all)	2016	November
	2017	
	2018	
Full survey (all)	2019	September

2.5 | Indicator species and favourable condition of blanket bogs

Indicator species are those that are typical of a particular habitat and which provide an indication of diversity and richness. Indicator species are chosen from species that occur with relatively high frequency in randomly distributed samples or quadrats, that is in more than 40–100%, of quadrats, regardless of their cover (abundance) when found. Thus, for blanket bog habitats, indicator species include species of dwarf shrubs, cotton grasses and Sphagna as well as groups such as 'feather mosses' (JNCC, 2009; Rodwell et al., 1991). The names of the most commonly occurring indicator species in these trial sites are provided in Sections 3.1 and 3.5.

For a habitat to be considered in 'favourable condition' by Natural England, minimum targets must be met for a set of characteristics or 'attributes' in at least 90% of quadrats or samples (JNCC, 2009). For example, for blanket bog habitats there are two main attributes concerning indicator species; one of which requires the presence of at least six indicator species; the other requiring that at least 50% of the cover should consist of at least three indicator species. Other attributes include measures that determine the degree of grazing or burning, as well as the cover of certain non-indicator species, especially those that have a tendency to dominate and exclude other species, such as hare's tail cotton grass (JNCC, 2009), although it should be noted that *Molinia* is not listed in this regard.

2.6 | Timetable

The three sites were chosen and marked out for treatment areas and quadrats in early 2014. This was followed by a full baseline vegetation survey (with *Sphagnum* species identification) in August 2014; the flailing and windrowing treatments were applied in September 2014 (Table 4). The *Sphagnum* plugs were planted in July 2015, followed by two surveys in August 2015 and October 2015 to record short-term settling-in and survival – no *Sphagnum* species identification was possible at this early stage of plug development. A survey of vascular plants was also carried out in September 2015. Thereafter, a full vegetation survey (with *Sphagnum* species identification) was carried out in 2016 and 2019.

Dipwells were installed after the flailing treatments in late 2014, and recording starting in January 2015 after a settling-in period.

2.7 | Statistical testing

All statistical testing was carried out using Minitab 14 (Minitab LLC, Pennsylvania). Differences in cover and water table depth between different sites and treatments were analysed using Mann Whitney U tests as the data did not fulfil the ANOVA criteria of a normal distribution. For plug-derived *Sphagnum* (PDS) cover, statistical testing for differences between sites or treatment areas was carried out directly on observed data. Due to naturally occurring variations in the cover of both *Molinia* and indicator species and also in water table depth between sites and treatment areas, statistical testing was performed relative to cover/water table depth in the control and presented as temporal changes from a standardized, common 'zero' baseline.

Trend lines describing the relationship between covers of *Molinia*, PDS and indicator species were fitted using linear/polynomial regression models, with *Molinia* and PDS/indicator species cover as the predicting and responding variables, respectively.

3 | RESULTS

3.1 | Site characterization and species diversity

The lowest cover of *Molinia* was found at the Linsgreave Clough site, where the highest cover of indicator species was also found (Table 2 and Figure 6, top); this pattern was reversed at the Green Withens site. Using the baseline (2014) dataset, there was a strong linear and negative relationship between the covers of *Molinia* and indicator species (Figure 6, middle).

The most abundant indicator species present at Green Withens and Linsgreave Clough were the hare's tail and common cotton grasses, *E. vaginatum* and *E. angustifolium*, whilst at Burne Moss, heather, *Calluna vulgaris* was the most abundant indicator species, with a cover of 9.1% (Figure 6, bottom).

The baseline cover of naturally occurring *Sphagna* was relatively low, with overall mean cover of 0.3%, and a maximum cover of 0.6% at Linsgreave Clough (Figure 6, bottom). The five most frequently encountered naturally occurring *Sphagnum* species in 2016 were, in decreasing order of frequency: *S. cuspidatum*, *S. fallax*, *S. palustre*, *S. squarrosum and S. fimbriatum* (Figure 7, top). Frequencies were much higher in those species arising from plugs in 2016; these were, in decreasing order of frequency: *S. capillifolium S. fimbriatum*, *S. fallax*, *S. palustre and S. squarrosum* (Figure 7, bottom). Frequencies of these and the other less commonly occurring *Sphagnum* species are given in Table 5. By 2019, this pattern was essentially the same, although frequencies throughout had mostly declined.

TABLE 5 Mean frequency (%) of Sphagnum species

	Naturally occurring				Plug derived		
***Sphagnum* species**	**2014**	**2016**	**2019**	**Av**	**2016**	**2019**	**Av**
S. capillifolium	0	5	0	2	82	43	63
S. cuspidatum	0	24	3	9	33	8	21
S. denticulatum	1	0	0	0	38	13	25
S. fallax	3	19	8	10	73	93	83
S. fimbriatum	7	8	4	6	82	28	55
S. magellanicum	0	0	0	0	33	4	18
S. palustre	3	19	13	11	66	97	81
S. papillosum	0	4	0	1	16	32	24
S. squarrosum	0	13	2	5	58	2	30
S. subnitens	15	5	9	10	22	21	21
S. tenellum	0	1	1	1	7	0	3

Notes: The five most commonly occurring species over all surveys are indicated by shaded boxes. Data were taken over all sites and treatment areas, with controls removed (no plugs in controls). Frequency was calculated as mean presence per quadrat and expressed as % (presence = 1, absence = 0), $n = 120$.

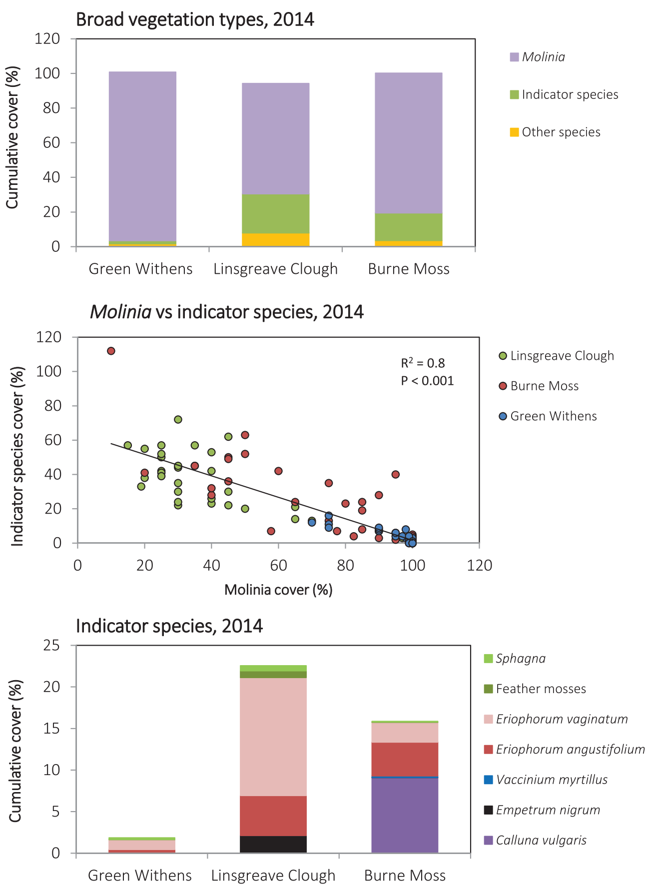

FIGURE 6 Cover of broad vegetation types (top), *Molinia* versus indicator species (middle) and cover of indicator species (bottom). 'Indicator species' are defined in Section 2.5. The fitted line in the middle graph was drawn using linear regression with R^2 = regression coefficient. Note the different *y*-axis scales, $n = 120$ (non-plug control areas excluded)

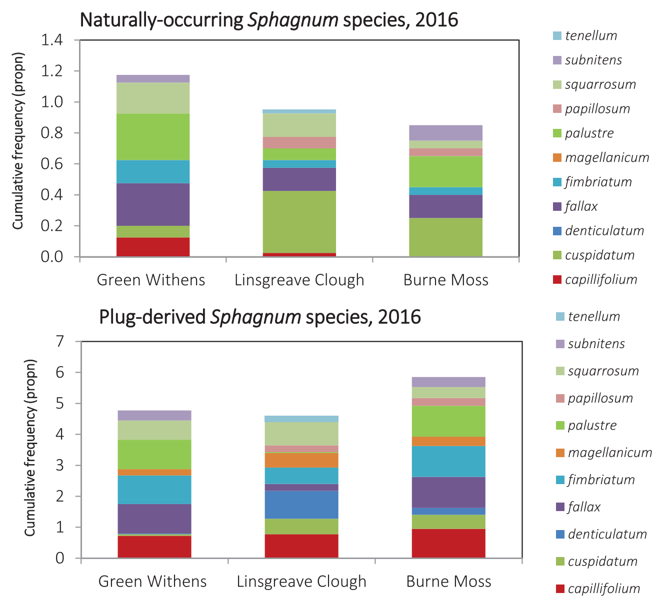

FIGURE 7 Frequency of *Sphagnum* species, naturally occurring (top) and plug-derived (bottom). Note the different *y*-axis scales. In both charts, $n = 120$ (non-plug control areas excluded for comparison with post-treatment data). The mean frequency of each species was scored as the presence or absence in each quadrat and then averaged per quadrat. A maximum score of 100% for a species indicates the presence in all quadrats

3.2 | The growth of plug-derived *Sphagnum*

The use of adjectives such as 'lower' or 'higher' is only used where tests have confirmed a difference in the value of the variables between treatments based on statistical probabilities. Otherwise, variables are considered to be the same, even if the values of the presented variables appear to be different.

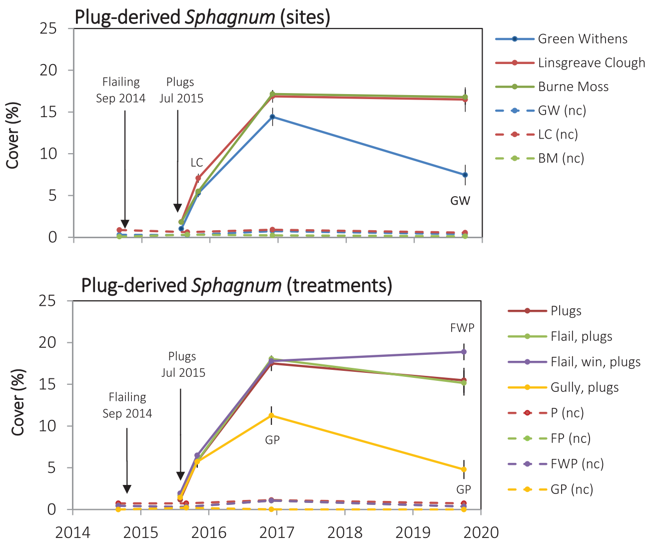

FIGURE 8 Effect of site and treatment on PDS. Sites: GW = Green Withens; LC = Linsgreave Clough; BM = Burne Moss: Treatments: P = plugs; FP = Flail, plugs; FWP = Flail, windrow, plugs; GP = Gully, plugs; nc = naturally occurring. Error bars are ± 1 standard error and *n* = 40 for each site (non-plug control quadrats not included) or 10 for each treatment area. R^2 = regression coefficient. Letters marked on the graph indicate significant differences in cover between the marked site/treatment area and that of the site/treatment area with mean cover values closest to it

Generally: During the first 15 months of growth 2015–2016, the cover of PDS increased rapidly from 2% to 16%, as an average of all sites (Figure 8, top) and all treatment areas (Figure 8, bottom). During this initial period, the rate of increasing cover in the 'Gully, plug' treatment areas (from 1% to 11%) was slower than other treatment areas (Figure 8, bottom). By the time of the 2019 survey, cover had plateaued at the Linsgreave Clough and Burne Moss sites but was lower at the Green Withens site (Figure 8, top). Similarly, growth had plateaued in all of the treatment areas but was lower in the 'Gully, plug' treatment areas (Figure 8, bottom). The cover of naturally occurring *Sphagnum* remained below 1% during this period and throughout the duration of the trial reported here (Figure 8, top and bottom).

Flailing: The flailing treatments, either with or without windrowing ('Flail/Win, plugs' or 'Flail, plugs'), had no additional effect on PDS growth until the time of the 2019 survey, when cover in the 'Flail/Win, plug' treatment area was greater than that of the 'Flail' treatment area. The statistical probabilities of differences in cover between sites and treatment are detailed in Table S1 in the Supporting Information.

3.3 | Effect of treatment on *Molinia* cover

Due to naturally occurring variations in the cover of *Molinia* between sites and treatment areas (Figure 9, top), statistical comparisons were made relative to cover in the control, and presented as temporal changes from a standardized, common 'zero' baseline. The 'Plugs' treatment had no effect on *Molinia* cover (Figure 9, middle), except in gully locations ('Gully, plugs' treatment areas) where a decrease occurred throughout, and by a maximum of 7 percentage points in the 2016 survey, relative to that in the gully control (Figure 9, bottom). In the Flail, plugs (FP) treatment *Molinia* cover initially appeared to decrease (−5 points, 2015 survey, not significant), but then increased (+9 points) by the time of the 2019 survey (Figure 9, middle). In the Flail, win, plugs (FWP) treatment, *Molinia* cover initially decreased (−8 points, 2015 survey) and then recovered by the time of the 2019 survey (−3 points, not significant, Figure 9, middle). The statistical probabilities of differences in the extent of these changes between treatments are detailed in Table S1 in the Supporting Information.

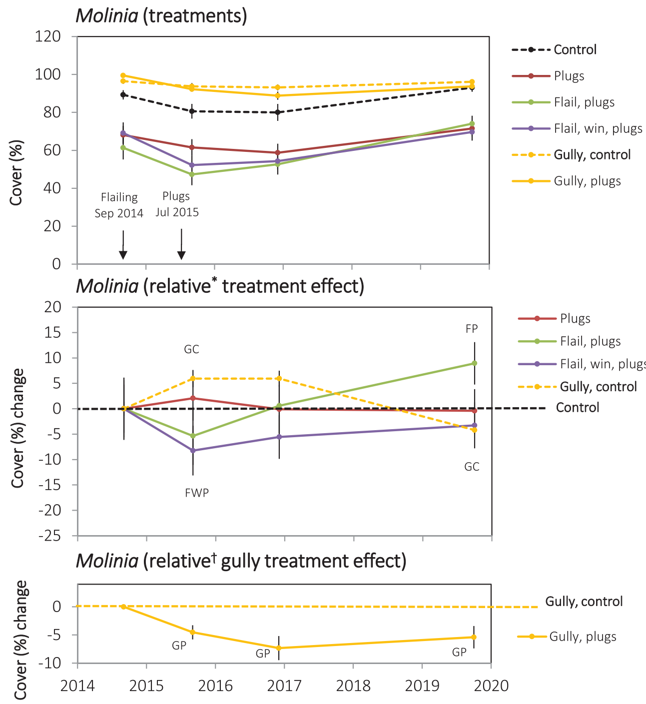

FIGURE 9 Effect of treatment on *Molinia* cover. Mean cover of *Molinia* (top) is shown *relative to the control (middle) and †relative to the gully control (bottom). All relative effects were standardized to zero at the time of the baseline survey. Letters marked on the graph indicate significant differences in cover between the marked site/treatment area and that of the site/treatment area with mean cover values closest to it. Treatment codes, error bars and *n* are as described in Figure 8, with the addition of C = Control; GC = Gully, control

3.4 | Relationships between *Molinia* and plug-derived *Sphagnum*

There was a strong and highly significant relationship between *Molinia* cover and PDS cover in the 2019 survey ($R^2 = 0.6$, $p < 0.001$; Figure 10, top). The relationship suggested that spatial variations of *Molinia* cover between 30% to 80% were not related to spatial variations in PDS cover (which remained around 18%), but that there was a threshold cover of *Molinia* (approximately 80%), above which the relationship

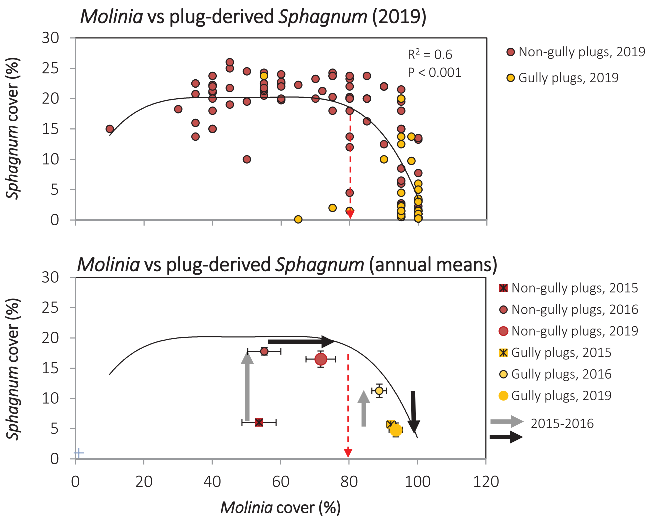

FIGURE 10 Relationships between cover of Molinia and PDS. Top: Data points represent cover in each quadrat of the non-gully plug treatment areas in red (P, FP, FWP) and the gully plug treatment areas in yellow (GP). The red vertical dotted line suggests a threshold mean cover of *Molinia* above which the relationship changes. $n = 120$, R^2 = regression coefficient, trend line fitted using polynomial regression of 2019 dataset. Bottom: The 2019 trend line was superimposed on a **meaned** dataset from the 2015, 2016 and 2019 surveys; data points represent **mean** cover of non-gully plug treatment areas in red ($n = 90$) and gully plug treatment areas in yellow ($n = 30$). Black/grey arrows indicate a significant temporal change in *Molinia* cover (horizontal arrow) and PDS cover (vertical arrow). Error bars = ± 1 standard error, R^2 = regression coefficient

became steeply and negatively linear, reducing the cover of PDS to a cover of less than 5% at a *Molinia* cover of about 95%, as found in the gullies. Almost half (47%) of the 120 quadrats treated with plugs contained *Molinia* at a cover above the threshold. The largest proportion of these *Molinia*-dense quadrats was found at the Green Withens site (54%) and in the 'Gully, plug' (GP) treatment areas across all sites (46%), the latter shown in Figure 10 (top). *Temporal* changes in these spatial relationships between *Molinia* and PDS from 2016 to 2019 also conform to the spatial relationships in 2019 (Figure 10, bottom).

3.5 | Diversity of indicator species

The flailing treatments, applied immediately after the baseline survey of 2014, reduced the cover of baseline, naturally occurring indicator species in the 2015 survey (Table 6). However, during the same inter-survey period of time (2014—2015), the introduction of plugs increased the overall cover of *Sphagna* from 0.4% to 6%, making this group the most abundant, followed by the cotton grasses *E. vaginatum* and *E. angustifolium* (Table 6).

The increase in indicator species cover from 18% to 36% between 2015 and 2016 was mainly due to growth of PDS, although there was also a substantial increase in the cover of *E. angustifolium* during this period (Table 6).

A decrease in indicator species cover 2016–2019 were due mainly to decreases in *E. vaginatum*, *E. angustifolium* and *Sphagna*, although the proportional presence of the latter increased, along with that of *E. nigrum* and feather mosses.

3.6 | Effect of treatment on indicator species cover

Due to naturally occurring variations in the cover of indicator species between sites and treatment areas (Figure 11, top), statistical comparisons were made relative to cover in the control and presented in graphs as temporal changes from a standardized, common 'zero' baseline. There were strong differences in cover of indicator species between treatment areas at the start. The cover of indicator species increased in the 'Plugs' treatment by +8, +16 and +13 percentage points in the surveys of 2015, 2016 and 2019, respectively (Figure 11, middle). Increases in cover of indicator species in the 'Gully, plugs' treatment area followed the same pattern (+7, +13 and +5 points, respectively) (Figure 11, bottom). Relative increases in cover in 'Plugs' were greater than those of 'Gully, plugs' in 2016 and 2019 (Annex).

There were relative decreases in indicator species in both of the 'Flail, plug' treatments (FP and FWP) (−9 and −8 points, respectively, 2015 survey), but by 2016, relative cover in the flailed areas was not different from that of the non-flailed 'Plugs' treatment area. Despite decreases (2016–2019), relative cover in flailed areas remained elevated (+4 in FP and +6 in FWP, in the 2019 survey), but both were lower than that of 'Plugs' (Figure 11, middle). The statistical probabilities of differences in the extent of these changes in response to different treatments are detailed in Table S1 in the Supporting Information.

3.7 | Relationships between *Molinia* and indicator species

There was a strong and highly significant linear and negative relationship between *Molinia* cover and indicator species cover in the 2019 survey ($R^2 = 0.8$, $p < 0.001$; Figure 12, top). The relationship suggested that incremental spatial increases of *Molinia* cover caused proportionately incremental decreases in the cover of indicator species. *Temporal* changes in these spatial relationships between *Molinia* and indicator species from 2016 to 2019 also conform to the spatial relationship in 2019 (Figure 12, bottom).

3.8 | Mean monthly water table depth

Mean monthly water tables in all three sites showed seasonal fluctuations, mainly falling to lowest levels in summer and rising closest to the surface in winter (Figure 13, top). Mean monthly water tables in 2018 were almost twice as low as previous low periods and remained low from July to December 2018.

Water table depths in the 'Gully, plug' treatment area were deeper than those in the 'Plug' treatment area during the four deepest periods

TABLE 6 Cover of individual indicator species in each survey

Indicator species	2014	2015	2016	2019
Eriophorum vaginatum	8 (43)	6 (34)	10 (27)	7 (25)
Eriophorum angustifolium	4 (25)	3 (17)	8 (21)	3 (11)
Calluna vulgaris	4 (22)	2 (10)	2 (4)	2 (7)
Empetrum nigrum	1 (6)	0.2 (1)	0.1 (0.3)	0.2 (1)
All *Sphagna*	0.4 (2)	6 (36)	17 (46)	14 (54)
Feather mosses	0.3 (2)	0.3 (2)	0.4 (1)	0.5 (2)
Vaccinium myrtillus	0.1 (1)	0.1 (0.4)	0.1 (0.2)	0.0 (0.1)
Total indicator species cover (%)	**18 (100)**	**18 (100)**	**36 (100)**	**26 (100)**

Notes: Each cell contains cover (%) as an average of all treatment areas except the controls, followed (in brackets) by its proportion (%) of total indicator species cover (%), $n = 120$. Identical total cover scores in 2014 and 2015 are coincidental.

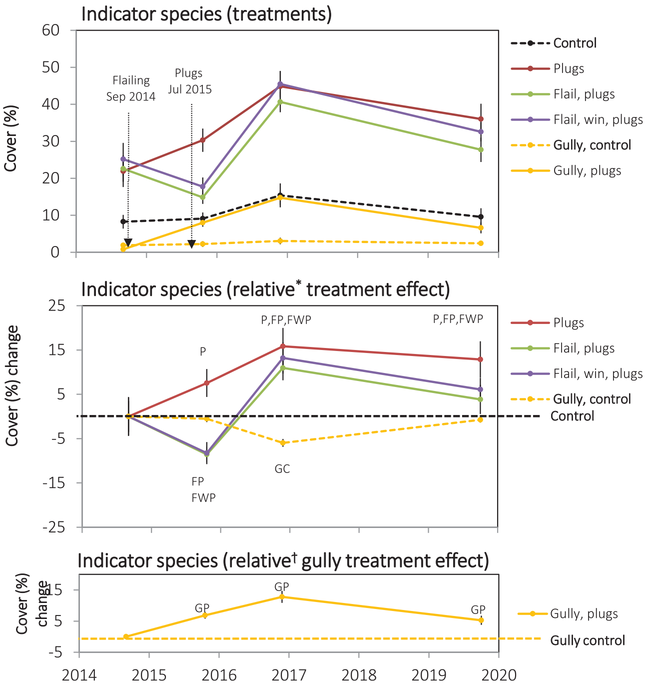

FIGURE 11 Effect of treatment on cover of indicator species. Treatment codes, error bars and *n* are as described in Figure 8, with the addition of C = control; GC = gully, control. Mean cover of indicator species (which included cover of PDS) (top), is shown *relative to the control (middle) and *relative to the gully control (bottom), with all relative effects standardized to zero at the time of the baseline survey

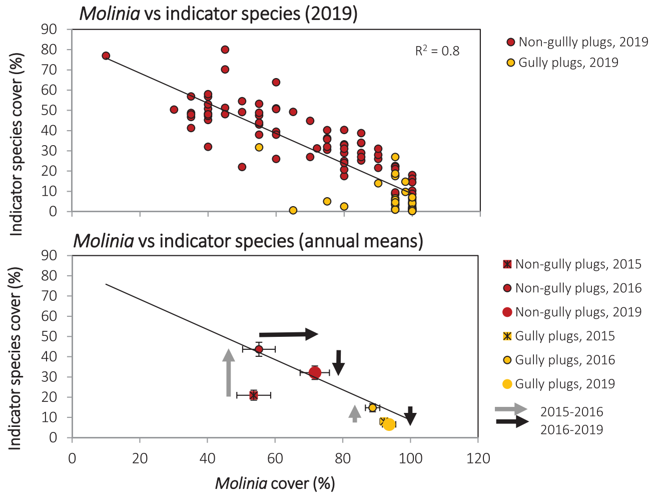

FIGURE 12 Relationships between cover of *Molinia* and indicator species. Top: Data points represent cover in each quadrat of the non-gully plug treatment areas in red (P, FP, FWP) and the gully plug treatment areas in yellow (GP). $n = 120$, R^2 = regression coefficient, trend line fitted using linear regression of 2019 dataset. Bottom: The 2019 trend line was superimposed on a **meaned** dataset from the 2015, 2016 and 2019 surveys; data points represent **mean** cover of non-gully plug treatment areas in red ($n = 90$) and gully plug treatment areas in yellow ($n = 30$). Black/grey arrows indicate a significant temporal change in *Molinia* cover (horizontal arrow) and PDS cover (vertical arrow). Error bars = ± 1 standard error, R^2 = regression coefficient

for each area ($p < 0.001$) and shallower during the four shallowest periods for each area ($p < 0.05$) as an average per year over all surveyed years (Figure 13, bottom and Table 7).

3.9 | Effect of treatment on mean annual water table depth

Due to naturally occurring variations in median annual water table depth between sites and treatment areas (Figure 14, top), statistical comparisons were made relative to depth in the control and presented in graphs as temporal changes from a standardized, common 'zero' baseline. The median annual water table was apparently lowered, inconsistently, in the non-gully treatments (Figure 14, middle); in the 'Flail, plug' areas (−2 cm in 2016), 'Plug' areas (−2 cm in 2017) and 'Flail/win, plug' areas (−2 cm in 2018), but in each case with *p* values between 0.05 and 0.1. Water table depths in the 'Gully control' appeared to come closer to the surface than the 'Control' (+3 cm in 2016 and 2017) and then deeper (−1 cm in 2018) (Figure 14, middle), but the addition of plugs in 'Gully, plug' areas had no effect (Figure 14, bottom). The statistical probabilities of differences in the extent

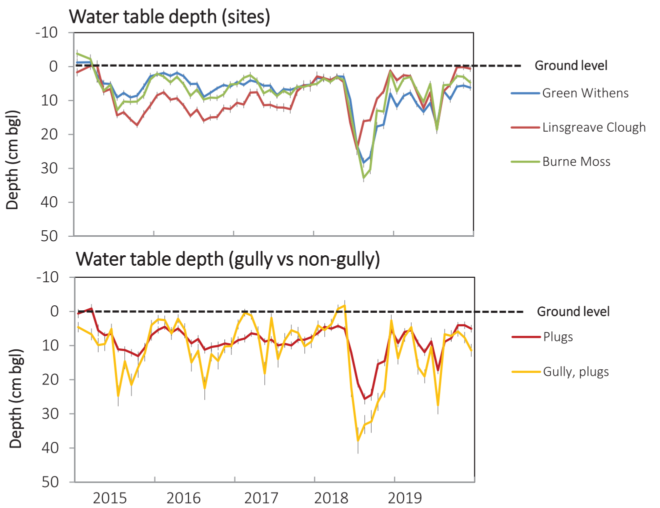

FIGURE 13 Monthly water table depth. Mean monthly water table depth in each of the three sites, $n = 60$ (top) and in the 'Plugs' and 'Gully, plugs' treatment areas $n = 30$ (bottom). Error bars = ± 1 standard error

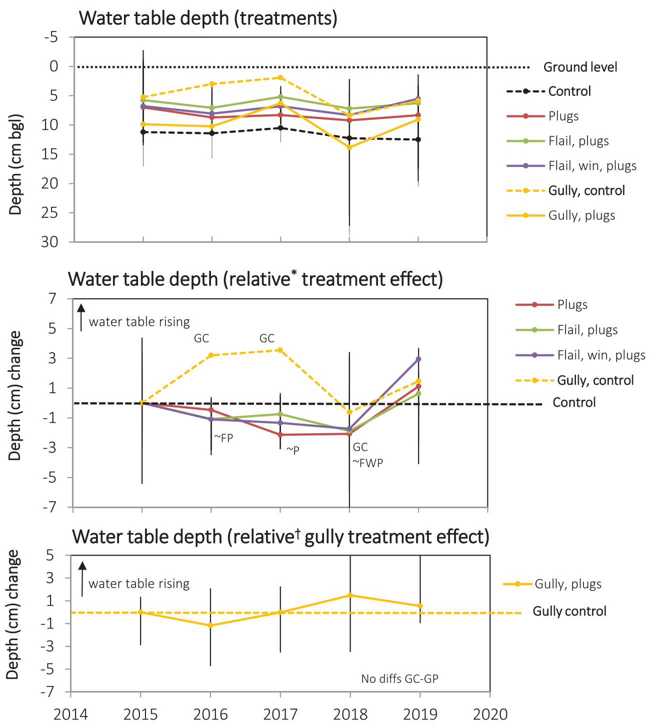

FIGURE 14 Effect of treatment on annual water table depth. Median annual water table depth (top) is shown *relative to the control (middle) and †relative to the gully control (bottom), with the relative data standardized to the median annual 2015 value. Treatment codes and n are as described in Figure 8, with the addition of C = control; GC = gully, control and ~ denotes $0.05 < p < 1.0$, Bgl = below ground level. Error bars are + (max-median) and – (median-min) but omitted for gully, control (beyond axis scale limits)

TABLE 7 Extremes of water table depths in gully versus non-gully treatment areas

	Deepest water table depths (cm bgl)		Shallowest water table depths (cm bgl)	
Year	Plugs	Gully, plugs	Plugs	Gully, plugs
2015	11	15	−1	0
	11	16	0	4
	12	22	1	5
	13	25	6	5
2016	10	13	5	2
	10	15	5	2
	10	15	5	3
	11	23	6	5
2017	9	9	6	0
	10	10	7	1
	10	14	8	2
	10	18	8	4
2018	15	27	4	−2
	21	32	5	−1
	24	33	5	3
	26	38	5	4
2019	9	14	4	5
	9	16	4	6
	12	19	5	7
	17	27	6	7
Average	**13**	**20**	**5**	**3**
p-value	$p < 0.001$		$p < 0.05$	

Notes: Bgl = below ground level. Water table depths in gully locations were deeper than non-gully locations during dry periods ($p < 0.001$) and shallower during wet periods ($p < 0.05$) as an average of the four most extreme cases per year over all years – see Figure 13, $n = 10$.

of these changes between different treatments are detailed in Table S1 in the Supporting Information.

4 | DISCUSSION

4.1 | Diversity of *Sphagnum* species

In 2016, when the PDS had reached its maximum recorded cover, nine species of *Sphagnum* were identified as occurring naturally in the trial sites; and 11 from the plugs. Carroll et al. (2009) also found a good diversity of *Sphagnum* species present throughout the Peak District moorlands, although they mostly occurred infrequently, in isolated patches. In the present study sites too, naturally occurring species were encountered at substantially lower frequencies than those derived from plugs. While acknowledging the improvement in atmospheric deposition of acidifying pollution implicated in the original demise of *Sphagnum* from the Peak District, Caporn et al. (2015) point to a continuing legacy of both acidity and metals in the peat as well as ongoing critical exceedance of nitrogen deposition.

Four of the top five most frequently encountered *Sphagna* at the study sites, from both naturally occurring sources as well as those derived from plugs (*S. fallax*, *S. palustre*, *S. squarrosum and S. fimbriatum*), are typical of nutrient-rich conditions, consistent with ongoing high levels of atmospherically deposited nitrogen pollution (RoTAP, 2012). However, the topmost frequently encountered species from natural sources was *S. cuspidatum* and that derived from plugs was *S. capillifolium*. While the former species is more typical of wet or submerged conditions, which can be a feature of *Molinia* domination, the unexpectedly high frequency of plug-derived *S. capillifolium*, a species typical of lower nutrient conditions and reportedly rare in the Peak District (Caporn et al., 2015), cannot be wholly explained by the plug production process, in which it is included with a proportion of 10%, considerably less than the proportions given to *S. fallax* (30–50%), *S. palustre* (20–40%) *and S. papillosum* (20–40%). Rather its success may be associated with its relative efficiency at transporting water to the growing apex (see Section 4.2).

4.2 | Rapid growth of plug-derived *Sphagnum*

The rapid growth of PDS with cover increasing from 2% shortly after planting in 2015 to 16% in 2016 suggested that environmental conditions were at least initially favourable for *Sphagnum* growth. In the same surveys, the cover of naturally occurring *Sphagnum* never exceeded 1%, suggesting an advantage conferred to PDS. This advantage was unlikely to be genotypic because the plugs were developed from fragments of *Sphagna* taken from the Peak District; rather the physical structure of the plugs (composed entirely from *Sphagnum* stems) and their insertion into the peat perhaps provided a more consistent supply of water, thereby creating greater growth potential during drier periods than was available to naturally occurring colonies. The physical structure of *Sphagnum* stems and leaves allows for the capillary rise of water along stems to the growing apices (capitula) (Malmer et al., 1994), and hummock-forming species of *Sphagnum*, growing at a greater height above water level, have an external physical structure adapted to greater capillary rise than pool species (Hayward and Clymo, 1983). Thus, *S. capillifolium* was observed to grow relatively well in drier niches due to its efficacy at transporting water vertically to the capitulum and so avoiding desiccation of the growing apex (Wheeler & Shaw, 1993).

4.3 | Plateauing growth of plug-derived *Sphagnum*

The plateauing of PDS cover between 2016 and 2019 at Linsgreave Clough and Burne Moss sites and non-gully treatment areas generally may have been a result of water stress. There were two possible causes; firstly, there may have been a gradual deterioration of the 'buried stems' mechanism described above, due to decomposition of the surface stem structures responsible for capillary rise; secondly, the UK experienced what has been termed the 'extreme summer drought of 2018 (Peters et al., 2020). During this period, mean summer temperature across England was around 2°C above average and many UK met stations recorded their hottest June day on record. Large areas of central England experienced 125% or more of average summer sunshine totals at the same time as receiving less than 50% average rainfall (Met Office, 2018), and satellite imagery reported an unprecedented general 'browndown' of the landscape across Europe (Buras et al., 2020). At all three sites of the present trial, water tables were observed falling almost twice as low as in the previous summer periods, and this fall was more extreme in the mineral-based gully areas.

Although *Sphagnum* has evolved to persist during periods of drought (Malmer et al., 1994), permanently wet surroundings are necessary for active growth, and negative effects on *Sphagnum* growth have been attributed to drought stress associated with raised temperatures in controlled experimental conditions (Gunnarsson et al., 2004). Even during shorter dry periods, drying and bleaching of surface *Sphagnum* tissues were commonly observed in these trial sites. In a separate trial on re-vegetated areas of degraded and gullied areas of blanket bog on Kinder Scout (Crouch, 2018), substantially slower growth of PDS was found on hagg-top areas compared to undulating, lower and wetter ground with water table depths closer to the surface. Dry periods may also provide the conditions for increased concentration of residual atmospherically deposited toxins in the soil surface (Rosenburgh, 2015).

In contrast, *Molinia*'s deep-rooting habit, highly efficient photosynthetic capabilities (Taylor et al., 2001) and more developed vascular water-conducting system would have enabled it to draw on deep water reserves and maximize recovery after experiencing water stress (Anderson, 2015).

In the present trial, the cover of *Molinia* increased during this same period, 2016–2019, although these increases were not implicated in the plateauing cover of PDS during the same period. This is because plateauing cover of PDS occurred where the cover of *Molinia* varied between 30% and 80% (at the Linsgreave Clough and Burne Moss sites generally and the non-gully locations of all sites), and within this range there was no correlation, either spatial or temporal, to the cover of PDS. In fact, there is evidence to suggest a facilitating effect afforded to *Sphagnum* by moderate densities of vascular plants in general (Malmer et al., 1994) and *Molinia* in particular (Meade, 1992), in terms of physical support, maintenance of humidity and protection against wind (Malmer et al., 2003; Rochefort, 2000; Wheeler & Shaw, 1995). A similar relationship was shown in the national survey of 2008–2009 by N. Critchley (2011) where mean *Sphagnum* cover was maintained in the range 7–13% up to 70% *Molinia* cover (reviewed in Glaves, 2015).

Dry periods are also likely to increase the supply of limiting nitrogen and phosphorus to deep-rooted vascular plants like *Molinia* due to greater aeration promoting decomposition and mineralization processes (Malmer et al., 1994). However, in the presence of ongoing high deposition of atmospheric nitrogen (RoTAP, 2012), phosphorus limitation on bryophyte growth cannot be dismissed as an alternative explanation to account for restrictions in the growth of PDS in these trials. Growth of mosses generally on an upland moor in the United

Kingdom was substantially boosted by additions of phosphorus, even to the extent of causing reductions in the dominant cover of *Calluna vulgaris* (Pilkington et al., 2007).

4.4 | Declining cover of plug-derived *Sphagnum*

The declining cover of PDS cover 2016–2019 was observed at the Green Withens site generally and from gully treatment areas averaged across all sites. While drought conditions and the potential for phosphorus limitation may have played a part in this decline, it was also likely that intensifying competitive interactions between *Sphagnum* and a particularly dense cover of *Molinia* at these locations also played a major part.

In the present trial, correlations showed that increasing spatial and temporal cover of *Molinia*, taking place above a threshold of approximately 80%, such as was found at the Green Withens site and in the gully areas overall, was strongly linked with negatively linear decreases in the spatial and temporal cover of PDS. Suppressed growth of *Sphagnum* as a result of shading was found when photosynthetically active radiation (amount of light available for photosynthesis) was reduced below 50% (Clymo & Hayward, 1982) and specifically by *Molinia* (Limpens et al., 2003). Increased shading from a cover of *E. angustifolium* above at least 60% reduced *Sphagnum* growth (Heijmans et al., 2002). In the national survey of 2008–2009 by N. Critchley (2011), mean *Sphagnum* cover declined from 7% to 13% amongst 70% *Molinia* cover, to only 0.5% at 91–100% *Molinia* cover (reviewed in Glaves, 2015). In the gully locations of the present trial, shading and a reduction in Photosynthetically Active Radiation (PAR) caused by dense *Molinia* growth together with annual die-back of *Molinia* leaves forming thick enveloping mats was strongly likely to outweigh the advantages of microhabitat humidity or physical support (see Malmer et al., 1994), resulting in etiolation and reduced biomass production (Gunnarsson et al., 2004), which was clearly observed, along with the reduction in cover.

Particularly dense *Molinia* cover associated with the gully areas of the present study were commensurate with its special ability to benefit from areas with a combination of flowing, oxygenated groundwater together with an enriched nutrient supply (Anderson, 2015; Rodwell et al., 1991); these conditions are associated with water tracks of valley mires where *Molinia* grows in particular abundance (Meade, 2015), but also in seepage areas and gully systems of blanket bogs (JNCC, 2009). *Molinia* forms tussocks as a survival adaptation to high or fluctuating water tables (Meade, 2015) and water table in the gullies of the present trial sites fluctuated over a substantially greater range of depths than those in non-gully locations, being generally closer to the surface but falling substantially and significantly deeper during the summer months, usually July, August and sometimes also September. It is likely that these extremes contributed to the relatively large and robust tussocks and dense cover of *Molinia* found in the gully treatment areas. Tussock formation can provide a niche for a variety of vascular plants and mosses to escape waterlogged conditions (Meade, 2015), but inter-tussock spaces in the gully area of the present trials were often deep, shaded and water-filled. With no option but to mainly plant the *Sphagnum* plugs directly into the tussocks, the plugs were wholly dependent on atmospheric humidity and rain water and particularly vulnerable to dry periods. It is assumed that the higher cover and more tussocky nature of *Molinia* generally at the Green Withens site is also attributable to these same features.

4.5 | Molinia

There were few effects of treatment on *Molinia* cover. A decrease in cover in the flailing treatment was short-lived, followed by a rapid recovery consistent with *Molinia*'s deep roots, efficient photosynthetic capabilities and annual growth habit (Anderson, 2015). There was a relative increase in *Molinia* cover in one of the flailed treatment areas, but this effect was found only in 2019 and only in one of the flailed treatment areas (mulch left lying) and may have been an artefact. In this flailed area, the cover of *Molinia* had started from a relatively low level in 2014, thus contributing to a large relative increase between 2014 and 2019. However, actual cover of *Molinia* in 2019 did not differ from actual *Molinia* cover in the other flailed treatment area or even the plug-only treatment area. Finally, the reduction in the cover of *Molinia* in the 'Gully, plugs' treatment was also considered unlikely to be a real effect, given the weak and wispy growth forms of PDS growing in these *Molinia*-dense areas. More likely, the decrease in *Molinia* cover was an artefact due to inevitable surveyor disturbance while searching through these dense *Molinia* areas, an action not required in the gully control areas.

4.6 | Indicator species

Changes to the cover of indicator species, a group including individual *Sphagnum* species, were similar to and influenced by changes brought about by the addition and growth of PDS. Thus there was an increase in cover when plugs were added between 2014 and 2015, followed by a period of rapid growth reaching a peak in 2016. There were two main differences in the growth pattern of indicator species, compared to that of PDS: firstly, there were decreases in indicator species cover 2016–2019 in all treatment areas, not just gullies, which was consistent with a strong and uniformly linear negative relationship between *Molinia* and indicator species cover over space as well as time. Unlike the case for PDS, the vascular elements of the indicator species group (i.e. mainly cotton grasses and dwarf shrubs) appeared to contribute a more continuous susceptibility to the increasing shade imposed by areas of dense *Molinia* over space as well as time – there were general increases in cover of *Molinia* from 2016 to 2019. N. Critchley (2011), also found what appeared to be a similar linear-type spatial relationship, in a national survey of English blanket bog sites (reviewed in Glaves, 2015).

The second way in which changes in the cover of indicator species differed from those of PDS involved their response to the 2014 flailing treatments. Naturally occurring indicator species, which made up 18% of plant cover overall in 2014 experienced the full effects of

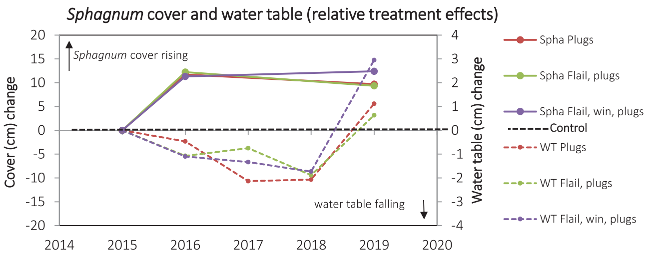

FIGURE 15 Changes in PDS and water table depth. Mean PDS cover and median water table depth is shown relative to the control and standardized to the 2015 value. Water table depths appear to have been weakly lowered by the growth of PDS cover possibly through drawing up water by capillary action of buried stems. Error bars have been removed for clarity, $n = 30$

flailing, while PDS planted in 2015 after the flailing action, did not. In spite of the uplift in cover of total indicator species provided by the introduction and growth of PDS, severe flailing-related reductions in total cover remained evident at the time of the 2015 survey, a year after the flailing treatment was imposed, and particularly affecting the most abundant components of the group, that is the cotton grasses (*E. vaginatum* and *E. angustifolium*) at the Linsgreave Clough site, but also heather (*C. vulgaris*) at the Burne Moss site. Although strong recovery of indicator species was evident in the 2016 survey, flailing-related reductions in cover were again evident in the 2019 survey, and particularly at Linsgreave Clough. Rodwell et al. (1991) and Anderson (2015) suggested that the removal of competitors following burning or grazing can benefit *Molinia*, but in the present trial there was no strong evidence of this, rather there were general increases in *Molinia* cover at all sites and in all treatment areas between 2016 and 2019, regardless of whether they had been flailed or not.

4.7 | Water table depth

As already mentioned, the summer drought of 2018 was likely to have played some part in the plateauing or declining cover of PDS between the surveys in 2016 and 2019. Although the presence of surface water (rather than water table depth) has been directly implicated in the establishment and success of *Sphagnum* colonies (Rogers, 2014), nevertheless periods of unusually low water table depths observed in the present trial, reaching maxima during August and September 2018, provided an indication of relative environmental stress and, by implication, the lack of available surface moisture necessary for the growth of *Sphagnum* (Malmer, 1994).

Increasing cover of PDS was associated with a fall in water table depth by up to approximately 2 cm relative to the control, over a 3-year period (Figure 15). This was in contrast to Shuttleworth et al. (2019) who reported that re-vegetation of mainly bare peat surfaces (mainly using seeds of both native and amenity grasses (listed in Buckler et al., 2013) caused a 3.5-cm rise in water tables over a 3-year period. However, as mentioned in Section 4.2, the structure of the plugs and their burial in the peat is likely to have facilitated capillary conduction of water through tissues, increasing evapotranspiration rates and thus causing the observed drawdown of water tables. Secondly, mean annual water table depths in the more deeply eroded and gullied blanket bog sites of Shuttleworth et al. (2019) typically varied between 20 and 50 cm, thus providing sufficient peat depth in which to accommodate a rise towards the surface. In the present trial, however, with relatively high water table depths mostly between 2 and 15 cm (more comparable to intact peatlands; see M. G. Evans et al., 1999), there was less available peat depth within which to accommodate a substantial and significant rise.

5 | CONCLUSIONS

The initial rapid growth phase by the PDS suggested an advantage associated with more efficient hydration of tissues during dry spells – an advantage possibly arising from facilitated capillary conduction of water through the buried stems of the *Sphagnum* plugs. This was associated with water tables trending slightly downwards in these plug-planted areas during the same period. Subsequent plateauing of cover suggested the gradual decay of this water-conducting mechanism, or a reduction of available 'edge' for increasing cover after plugs coalesced, and/or water stress associated with severe drought during the summer of 2018. Subsequent decline in cover suggested additional competition for light by dense covering of *Molinia*.

There was no clear indication that pre-flailing treatments benefitted the growth of PDS, or that it discouraged *Molinia* beyond a temporary setback; rather its effect was a severe temporary reduction in and signs of lasting damage to the cover of the desired indicator species.

In summary, we conclude that there was an early and highly successful establishment of PDS colonies, which boosted the cover and diversity of indicator species. However, there are also indications of a vulnerability to dry spells and drought stress and to negative competition from shading and lack of space in dense, tussocky *Molinia*.

Further trials are needed to find if the physical structure of the *Sphagnum* plugs and their depth of implantation influence establishment. These trials should also investigate the specific roles of water stress, shading and phosphorus limitation on the growth of naturally occurring and PDS and whether there is a minimum depth and cover of *Sphagnum* that can preserve competitive superiority over aggressive vascular plants like *Molinia* in areas of exceedance of N critical loads and increasing frequency of drought periods.

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CONFLICT OF INTEREST

The *Sphagnum* plugs used in this trial were supplied by Micropropagation Services, Leicestershire, UK, which is a contracted supplier to Moors for the Future Partnership for wider restoration work on degraded blanket bogs.

AUTHORS' CONTRIBUTIONS

TK and EF conceived the ideas, and JW, CF and MP designed the methodology; PE, RM, NP, TR, TH, EF and MP collected the data: MP analysed the data and wrote the manuscript. DC, RM and PE contributed critically to the drafts, and all authors gave final approval for publication.

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SUPPORTING INFORMATION

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