

RESEARCH ARTICLE

Propagule availability drives post-wildfire recovery of peatland plant communities

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Abstract

Question: Northern peatlands are increasingly threatened by wildfire. Severe peatland wildfires can provide opportunities for new non-peatland species to colonise post fire. Changes in plant colonisation could lead to longer-term shifts in community composition, compromising recovery of peatland structure and function. Understanding the process of post-fire recovery can thus inform restoration action and help restore peatland vascular plant communities. In this study, we ask: what drives initial vascular plant recovery following a peatland wildfire?

Location: Stalybridge moors, England (commonly referred to as the Saddleworth moors).

Methods: We used a series of vegetation surveys and seed germination experiments to identify the composition of vascular plant community one-year post fire, along with potential propagule sources. We combined this with plant trait data and, using a series of null models, compared observed community trait values against random species assemblages.

Results: Our data suggests that plant species are able to arrive at the burned site through multiple non-exclusive recolonisation pathways. This includes colonisation through the soil seed bank, along with dispersal from surrounding unburned peatland and non-peatland vegetation. The composition and structure of the recolonised communities was largely determined by the ability of species to reach the post-fire site from these donor communities. This resulted in a post-fire community composed of species possessing lower seed masses relative to the wider pool of potential colonisers.

Conclusions: Our results highlight propagule availability as a driver of post-wildfire vascular plant recovery. This provides opportunities for new non-peatland species to colonise, potentially driving changes in the direction of vegetation recovery. Ensuring the availability of peatland species following a wildfire could therefore be key to the immediate recovery of these systems.

KEYWORDS

blanket bog, community assembly, dispersal, moorland, peatland, seed bank, species recolonisation, vascular plants, wildfire

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1 | INTRODUCTION

Northern peatlands represent significant terrestrial carbon stores, holding an estimated 265–600 Pg of carbon (Yu, 2012; Hugelius et al., 2020). This is equivalent to 80% of the carbon held within the atmosphere (Page & Baird, 2016). However, peatlands are at increasing risk from severe wildfires (Turetsky et al., 2015). This is driven by widespread reductions in water table depths (Turetsky et al., 2011; Swindles et al., 2019) that can result in shifts towards highly flammable shrub-dominated plant communities deprived of their characteristic, water-holding peat moss layer (Talbot et al., 2010; Baird et al., 2019). When severe wildfires occur, they can provide opportunities for non-peatland species that were not present pre-fire to colonise. Kettridge et al. (2015) have, for example, reported the post-fire colonisation of non-peatland species to increase vegetation flammability, inducing positive feedback loops that lead to a further increase in wildfire regularity. If left unrestored, this could eventually shift a peatland from a carbon sink to a carbon source (Kettridge et al., 2015). The restoration of peatland plant community composition could therefore be essential to the post-fire recovery of peatlands, with an overall aim of the preservation of peatland carbon stores.

Following a disturbance such as a peatland wildfire, initial vascular plant assembly is thought to be driven by propagule availability, abiotic conditions and interactions with resident biota (Belyea & Lancaster, 1999; Kraft et al., 2015). To examine the strength of these factors, community assembly is often conceptualised to constitute a series of filters, sequentially excluding species from the wider species pool and leading

to the composition of the local community (e.g., Figure 1a). The strength of each filter can be inferred through the traits of established communities (de Bello et al., 2013; Dawson et al., 2017). For example, strong dispersal and abiotic filters could result in trait convergence through the removal of species from the wider species pool with trait values that do not allow them to overcome one or more of these filters (Götzenberger et al., 2012). This results in trait values that allow a species to establish becoming highly abundant in the post-disturbance community. However, recovery also depends on the composition of donor communities that supply species to the disturbed site (Figure 1b).

In order to colonise post disturbance, a species may have to overcome a different set of ecological filters depending on the pathway it uses to arrive at a disturbed site (Figure 1b). This could result in species with different trait values colonising through alternative pathways. For example, following a peatland wildfire, species that colonise through the seed bank must have been able to withstand the harsh abiotic conditions created by the fire (Rein, 2013; Figure 1b). Species that disperse in from surrounding vegetation will not face this abiotic filter but may have to overcome stronger dispersal filters as a result. The pathways in which species recolonise will consequently affect the composition of the post-disturbance community. Therefore, integrating both a classical ecological filter framework (Figure 1a) and a disturbance-colonisation framework (Figure 1b) can provide insight into the drivers of peatland post-fire recovery. Using the insights from these frameworks can then inform restoration by manipulating the recovery of the post-fire community.

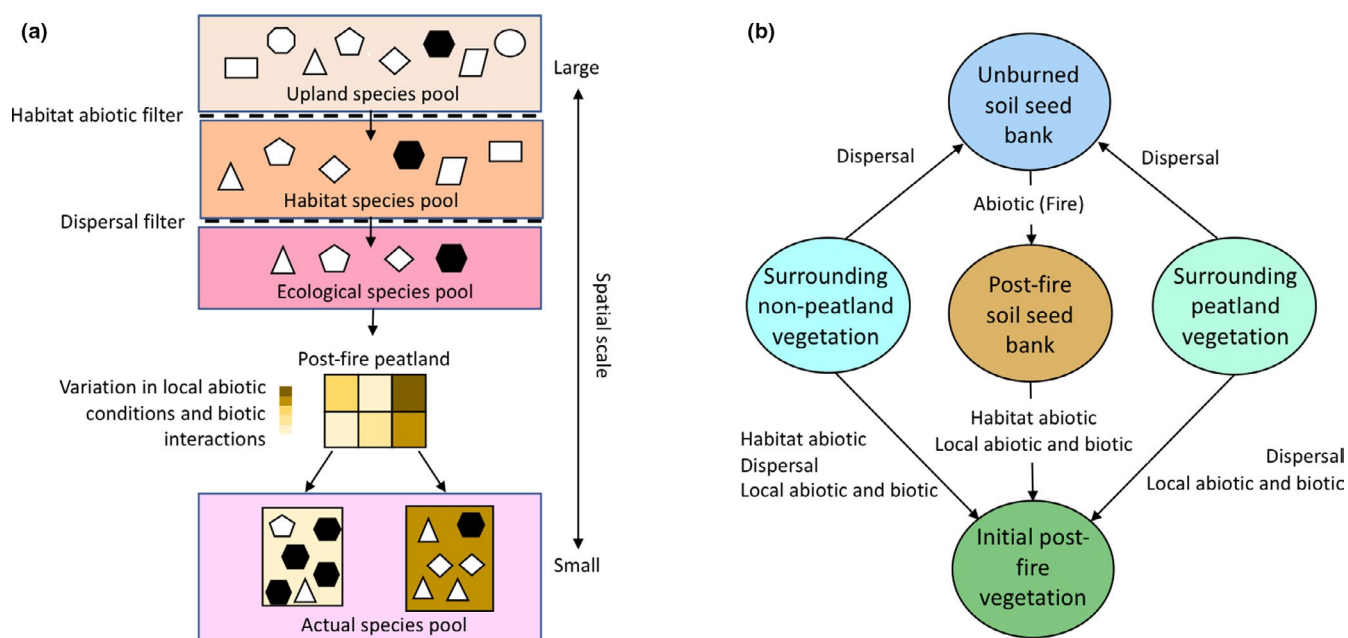


FIGURE 1 Two conceptual figures for the process of species recolonisation following a peatland wildfire. (a) Classical ecological theory depicting the steps controlling the composition and structure of the recovering community. Black-filled shape represents a species not usually found within the undisturbed habitat that is able to colonize following the disturbance and, under certain post-fire conditions, dominate the established community. In this example new species are able to dominate the post-fire community when the strength of local abiotic and biotic interactions is weak. (b) The multiple potential colonisation pathways from potential donor communities for a species to establish following a wildfire. The ecological filters that each species must overcome to progress to the next community are labelled. Definitions and figures adapted from Belyea and Lancaster (1999), Kraft et al. (2015) and Dawson et al. (2017); colours match the communities represented in Figures 2–5

Peatlands in the UK, which cover approximately 10% of the terrestrial area (Bain et al., 2011), are becoming increasingly vulnerable to wildfire (Bonn et al., 2008). UK peatlands therefore provide opportunities to examine the recovery of temperate peatland vegetation communities after wildfire. Maltby, Legg, and Proctor (1990) found that drought and a subsequent severe wildfire in a UK peatland resulted in large areas devoid of vegetation over a decade later. Recently, studies have focused on certain aspects of vascular plant recovery, such as soil seed banks (Kelly et al., 2016), the recolonization success of individual target species (Legg et al., 1992; Davies et al., 2010), or the relationship between vegetation restoration and ecosystem functional recovery (Worrall et al., 2011). However, studies that simultaneously examine factors affecting the recovery of temperate peatland vegetation following wildfire are currently rare.

In this study, we examine the key factors of post-wildfire vascular plant recovery. Working in a temperate peatland that has recently experienced a severe wildfire — the Stalybridge Estate, part of the Stalybridge moors, UK — we aim to determine factors limiting vascular plant recovery one year after the fire. We test three hypotheses:

Hypothesis 1 *Wildfire will reduce the species richness and abundance of seeds that are able to successfully germinate from the soil seed bank (Kelly et al., 2016; Maltby et al., 1990; Figure 1b).*

Hypothesis 2 *The post-fire community will consist of species colonising through both the post-fire seed bank and surrounding peatland (or non-peatland) vegetation (Figure 1b).*

Hypothesis 3 *The composition of vegetation one year after burning will depend on the ability of species to reach the site in sufficient numbers and on local abiotic conditions that remain post-fire (Figure 1a).*

We assume that competition among vascular plant species will be negligible due to the complete removal of established vegetation following the fire. We therefore do not explicitly test the role of competition in the initial recovery. To test the hypotheses, we performed a series of vegetation surveys to establish the taxonomic compositions of the different vascular plant communities in Figure 1b (Hypothesis 1, 2). We then combined taxonomic compositions with plant trait data and constructed a series of null models using the species pools in Figure 1a to detect trait filtering within our sampled communities (Hypothesis 3). In doing so, our work will provide insights into the drivers of initial temperate peatland wildfire recovery.

2 | METHODS

2.1 | Study site

Blanket bogs are treeless peatlands that are limited to the higher latitudes (Moore, 2002). The Stalybridge Estate, part of the Stalybridge Moor (often referred to as Saddleworth Moor), is a blanket bog near

Manchester, UK (53°54'33" N, −01°95'58" E). Mean annual temperature is 8.2°C and mean annual rainfall for the area is 1,160 mm yr^{−1} (Fick & Hijmans, 2017). The vegetation is dominated by *Calluna vulgaris* (L.) Hull, *Eriophorum vaginatum* L. and *Eriophorum angustifolium* Honck. Moss cover is scarce on the site, consisting mainly of *Sphagnum* spp., *Pleurozium schreberi* (Brid.) Mitt. and *Hypnum jutlandicum* Holmen & Warncke. On 24 June 2018, during a drought, a wildfire broke out on Stalybridge Moor. The fire burned approximately 10 km² of peatland until it was extinguished on 18 July 2018, 24 days later.

2.2 | Experimental design

We established ten 10 m × 10 m plots on the burned area of the Stalybridge Estate in October 2018. We selected plot locations where above-ground vegetation was removed by the fire but peat soil was still remaining. The plots were split into two groups ($n = 5$; Appendix S1). Group 1 plots were situated at lower elevations, had steeper slopes and were northwest facing, as compared to Group 2 which was southwest facing (Appendix S1). Differences in local topography could alter burn severity (Davies et al., 2008) which can impact species recolonisation (Grau-Andrés et al., 2019). Using these plots along with the surrounding unburned peatland, we performed above-ground vegetation surveys and extracted soil for off-site seed germination experiments to determine the composition of the vascular plant communities outlined in Figure 1b (excluding the surrounding non-peatland vegetation). The taxonomic identification of vascular plants followed Fitter and Peat (1994).

2.3 | Soil seed-bank surveys

To determine the post-fire viable soil seed-bank composition, in October 2018 we collected and aggregated three soil samples (25 cm², 5 cm deep) in each of the ten burned plots. We repeated the methodology at five plots at an adjacent unburned site in order to determine the unburned soil seed bank. The unburned site was adjacent (<1 km) to the burn site, and had a similar vegetation composition to the site pre-burn. All samples were transported to the University of Southampton where they were subjected to a stratification treatment consisting of sequential storage of the soils at c. 5°C for 21 days and at −20°C for 48 h. Soil samples were then weighed, mixed with approximately 1 L of nutrient-enriched sand and compost, and spread on germination trays in a greenhouse. Each tray had a soil layer of approximately 3 cm in depth. The soil was not sterilised before use. We added five extra trays consisting solely of the sand-compost mixture to test for between-tray propagule transfer or sand-compost mixture seed contamination. The soil samples were watered twice daily to ensure the seeds were exposed to optimal abiotic conditions for seed germination in peatlands.

TABLE 1 The chosen indicator traits, the ecological filter they indicate and the justification for their inclusion

Trait	Indicated filter	Justification	References
Seed mass	Dispersal	Smaller seed mass correlates with greater seed number and dispersal radius, increasing chance of post-disturbance colonisation and propagule availability	Greene and Johnson (1993); Weiher et al. (1999); Kirmer et al. (2008); Tamme et al. (2014)
Specific leaf area (SLA)	Abiotic (Habitat and Local)	Increased nutrient availability post-disturbance favours fast-growing species (high SLA). Stressful abiotic conditions favour slow-growing species (low SLA)	Grime et al. (1997); Weiher et al. (1999); Reich (2014)
Ellenberg moisture value	Abiotic (Habitat and Local)	Moisture content is a strong abiotic driver of vascular plant community assembly in temperate peatlands. Fire can decrease soil moisture content altering abiotic conditions	Chambers et al. (2007); Sherwood et al. (2013); Gafka et al. (2015)

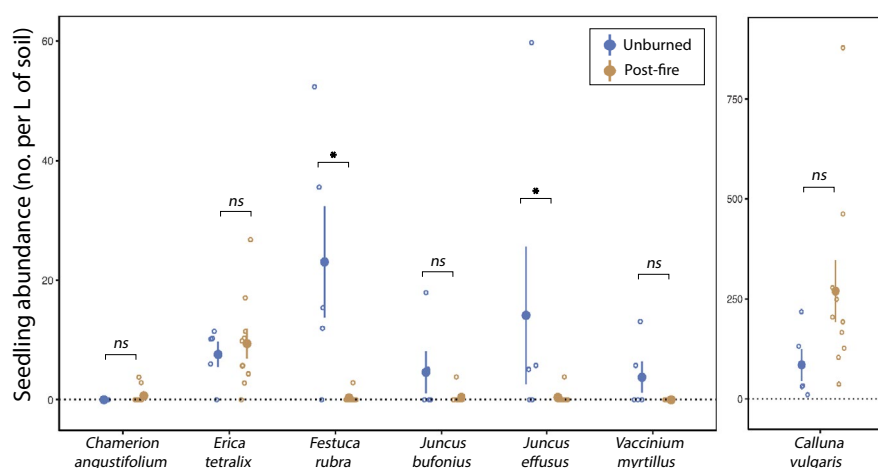


FIGURE 2 The effect of wildfire on the abundance of seedlings emerging from a temperate peatland soil seed bank. The density of seedlings per L of soil taken from a temperate peatland, part of which had experienced a wildfire approximately three months prior; full circles represent mean abundance values, open circles represent individual plot abundances, and error bars represent ± 1 standard error. The results of bootstrapped two-sample Kolmogorov–Smirnov tests are shown. ns, $p > 0.05$; *, $p < 0.05$. Colours represent communities in Figure 1b. Note the y-axis scale for *Calluna vulgaris* is an order of magnitude larger

The trays were examined at weekly intervals for germinating seeds after which their position in the greenhouse was re-arranged. Seedlings identified to the species level were then removed. The trays were left for twelve weeks, after which no new vascular plants were recorded, and the experiment was discontinued. Moss and liverwort cover were removed from the trays so as to not hinder the germination of remaining propagules. We did not disturb the soil to avoid damaging the seedlings and preventing species identification. We did not repeat the stratification period in order to best represent the conditions experienced by the seeds within the field at the point of this study (one year post-fire).

We recorded nine vascular plant species. Singletons (*Holcus lanatus* L. and *Betula pubescens* Ehrh.) were removed before analysis to reduce the overrepresentation of rare species. To account for differences in initial soil weight the seedling abundance in each plot was multiplied as follows:

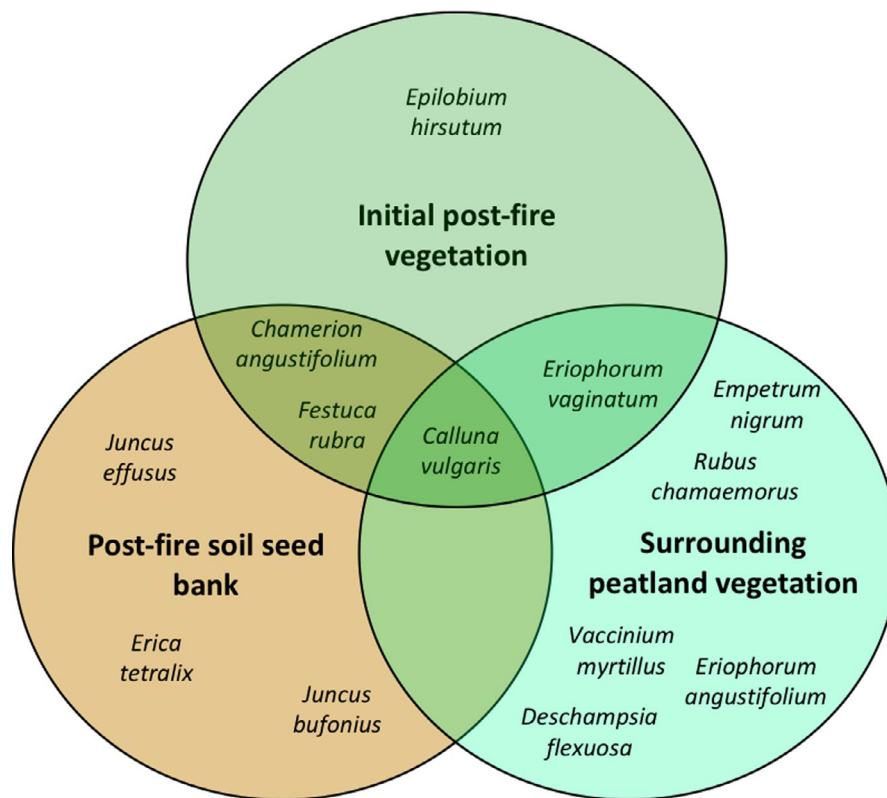
to make each soil sample equivalent to 1 kg of soil. We observed minimal transfer of propagules between trays (Appendix S2). All species found in the control trays were species common to the site and likely to have contaminated the trays through lateral transfer from other trays and not from contamination in the sand–compost mixture or other experiments within the greenhouse.

2.4 | Initial post-fire vegetation survey

We performed vegetation surveys in each of the ten burned plots in May 2019 to assess the vascular plant community that successfully re-colonised the site. We used a 1 m \times 1 m pinpoint quadrat with 10-cm intervals to record species presence and abundance at two randomly placed points within each of the burned plots.

$$\text{Seedling abundance} = \text{Number of recorded seedlings} \times 1,000 / \text{Original Soil Weight (g)},$$

FIGURE 3 The shared species between the initial post-fire vegetation of a temperate peatland following a wildfire and two possible donor communities: the post-fire soil seed bank and surrounding peatland vegetation. Species that overlap multiple communities were present in both; colours represent communities in Figure 1b



2.5 | Surrounding peatland vegetation survey

To determine the community composition of surrounding peatland vegetation we obtained publicly available data (source: Natural England) from surveys performed at Dark Peak in summer 2018, a neighbouring site approximately 1 km from the burn site which has similar environmental conditions (Nisbet et al., 2017). In summary, the data were collected by surveying 50 plots of 2 m × 2 m, each split into 25 equally-sized cells. The vegetation within each cell was recorded to the species level.

2.6 | Plant trait data

We compiled trait data for seed mass (mg), specific leaf area (SLA; mm² mg⁻¹), and Ellenberg moisture value (EMV) for all observed species. Seed mass can indicate dispersal capabilities (Weiher et al., 1999), and EMV and SLA can indicate abiotic filtering (Ellenberg et al., 1991; Weiher et al., 1999; Hedberg et al., 2014). We extracted the data from the databases LEDA (Kleyer et al., 2008) and Ecoflora (Fitter & Peat, 1994), only using records measured in the UK. Seed mass was log-transformed and all traits were standardised for analysis. Justification for the inclusion of these traits can be found in Table 1.

2.7 | Null-model construction

We produced a series of null models to test our observed species compositions against random community assemblages. Significant

differences in the trait values of our observed communities compared with random (null) communities can indicate trait convergence (Götzenberger et al., 2012). To construct the null models, we first produced a series of species–abundance matrices based upon the framework in Figure 1a. Species were included within each matrix if they were identified as being able to overcome the preceding filters in the framework. This allowed us to produce random assemblages from pools of species that varied in the filters they had passed. Once each species–abundance matrix was produced we input our observed species abundances into the matrices. The order of the columns (species identities) was then repeatedly randomised to produce 1,000 null community matrices. We repeated this process for each of the sampled communities in Figure 1b (all communities except the surrounding non-peatland vegetation). A full description of the null model constructions can be found in Appendix S3.

2.8 | Statistical analyses

To test Hypothesis 1, we performed bootstrapped two-sample Kolmogorov–Smirnov tests comparing the seedling abundance of each observed species and the overall species richness in the unburned samples to the post-fire seed bank. We considered $p < 0.05$ to indicate a significant change in the seedling abundance of a species between the two seed banks.

To test Hypothesis 2, we used Non-Metric Multidimensional Scaling (NMDS) to visualise differences between the sampled seed bank (unburned and post-fire soil seed bank) and vegetation

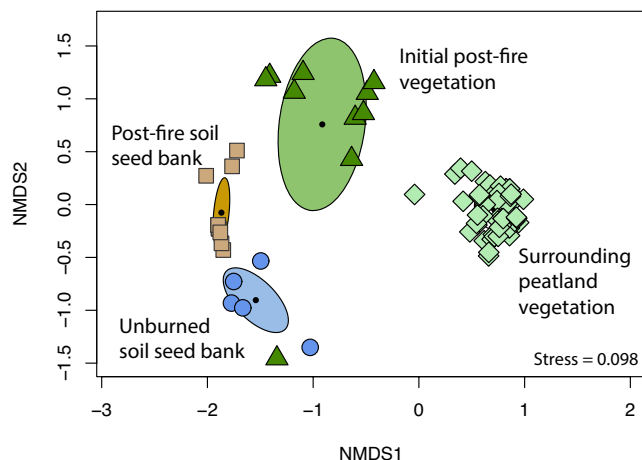


FIGURE 4 The effect of wildfire on the vascular plant community composition of a temperate peatland soil seed bank and intact vegetation. Non-metric Multidimensional Scaling (NMDS) plot of the vascular plant community composition found in the soil seed bank and intact vegetation following a temperate peatland wildfire. These are compared with the composition of the surrounding peatland vegetation and the soil seed bank at unburned neighbouring sites. We did not survey the surrounding non-peatland vegetation so consequently it is not included within this figure. Shapes represent individual plots; black dots indicate centroid points for each community; envelopes = 1 standard error around the centroid point; stress value is given; and colours represent communities in Figure 1b

(surrounding peatland and initial post-fire vegetation) communities (Figure 1b). Stress values were used to test to what extent the NMDS plot explains the multidimensional differences in the community composition. We then used permutational multivariate analysis of variance (PERMANOVA, permutations = 999) to test for variation in centroid position of the four different vascular plant communities using community type (seed bank vs vegetation) and wildfire history (unburned vs post fire) as interacting factors. We additionally included community type and wildfire history as single effects in the model. We consider $p < 0.05$ to indicate a significant effect of an explanatory variable on the vascular plant community composition.

To test Hypothesis 3, we calculated the community-weighted mean (CWM) for the three traits described above for each sampled seed bank and vegetation community and their corresponding null communities. We then calculated standardised effect size (SES) values using Glass's delta ($[(CWM_{\text{observed}} - CWM_{\text{null}}) / SD_{\text{null}}]$; Glass et al., 1981). When interpreting the SES values, we consider a response to be non-random if the 95% confidence limits do not overlap with zero.

As our study design had multiple groups nested within the post-fire site, we ran the analysis twice: once where each group was treated independently ($n = 5$) and once where post-fire sites were combined ($n = 10$). When treated independently, a large majority (86%; 20/24) of the null models tested resulted in the same response between the two groups, with the groups displaying either both a significant or non-significant difference compared with

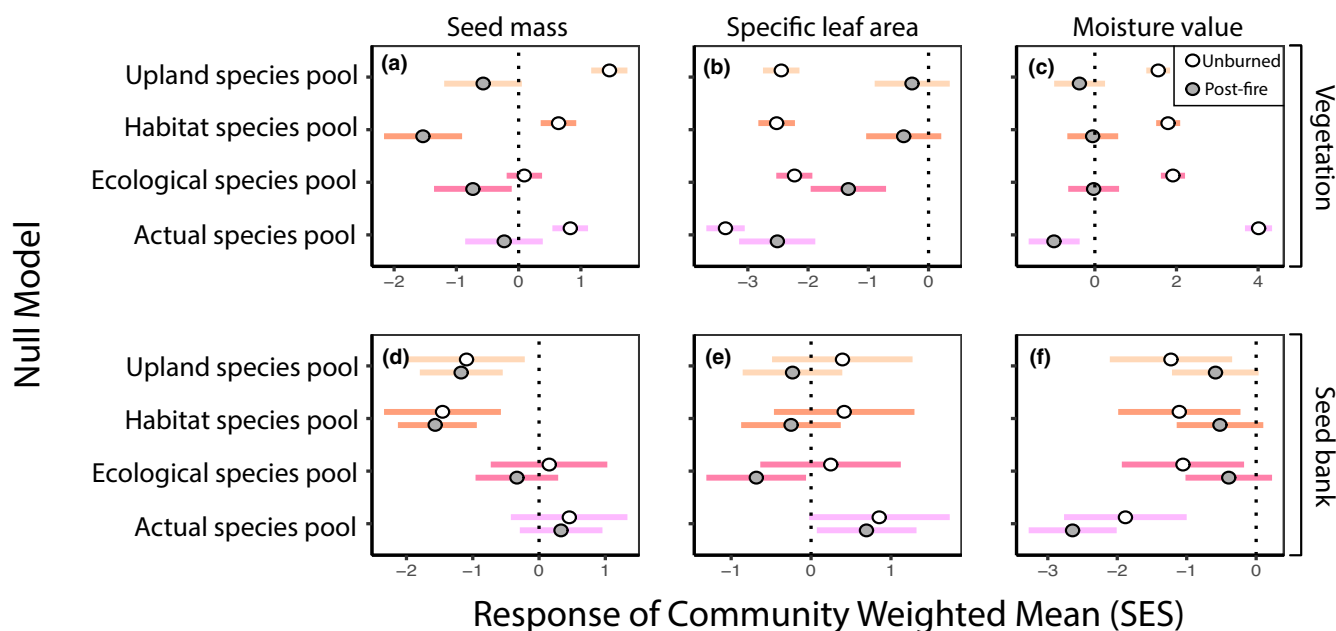


FIGURE 5 The response of trait community weighted means to wildfire in the seed bank and the vegetation vascular plant communities against randomly assembled null models. Response of community-weighted means of seed mass (a, d), specific leaf area (b, e) and Ellenberg moisture index (c, f) of the intact vascular plant vegetation (a, b, c) and soil seed bank of a temperate peatland that has undergone a wildfire compared with surrounding unburned communities. Different null models are representative of varying species pools (Figure 1b). Response represented as standardised effect size (SES) values (Glass's delta). Error bars represent 95% confidence errors

the null mean (Appendix S4). There was also little variation between the abundance of seedlings germinating from unburned and post-fire soil samples across groups (Appendix S5). Additionally, previous research had shown fire severity to increase vascular plant beta diversity following a temperate peatland wildfire (Grau-Andrés et al., 2019). In our study, individual sampling plots were no more taxonomically dissimilar (no change in beta diversity) to plots in the other groups compared with plots within their own group (Appendix S6). Given the largely similar response of the two groups, we present only data where the plots are combined to form one dataset ($n = 10$).

All analyses were conducted in R v. 3.5.1 (R Core Team, 2018). Bootstrapped Kolmogorov–Smirnov tests, conducted using the package *Matching* (Sekhon, 2011). NMDS plots were produced and analysed using the package *vegan*. CWM was calculated using the package *FD* (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). SES calculations and confidence intervals (Cis) were calculated using the package *effsize* (R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

3 | RESULTS

Wildfire had limited effect on the abundance of successfully germinated seedlings in the soil seed bank; only two of seven species had lower seedling abundance in post-fire seed banks as compared with unburnt seed banks (Figure 2). At the community level, the post-fire vegetation composition was distinct from the post-fire seed bank and surrounding peatland vegetation (Figure 4), but shared species with both of these communities (Figure 3). The initial post-fire vegetation was lower in CWM trait values for seed mass, SLA and EMV than predicted from random assemblages; however, this varied depending on the species included within the null models (Figure 5).

3.1 | Soil seed-bank species richness and abundance

In the seed-bank germination surveys, we found seven vascular plant species (Figure 2; Appendix S7), all of which successfully germinated from both unburned and post-fire soil seed banks, except for *Chamerion angustifolium* (L.) Holub. (post-fire seed bank only) and *Vaccinium myrtillus* L. (unburned seed bank only). Species richness decreased from an average of four species per plot in the unburned soil seed bank, to 2.4 species in the post-fire soil seed bank (bootstrapped two-sample Kolmogorov–Smirnov test, $D = 0.8$, $p < 0.05$; Appendix S7), providing support for Hypothesis 1. However, only the abundance of *Festuca rubra* L. and *Juncus effusus* L. seedlings significantly reduced following the wildfire (bootstrapped two-sample Kolmogorov–Smirnov test, *Festuca rubra*: $D = 0.8$, $p < 0.05$; *Juncus effusus*: $D = 0.6$, $p < 0.05$). There were no statistically significant changes in other species' germinated seedling abundances (Figure 2; Appendix S5).

3.2 | Community composition of the soil seed bank and above-ground vegetation

We recorded five vascular plant species in the initial post-fire vegetation (Appendix S7). These were species that overlapped with either the post-fire seed bank (*Chamerion angustifolium*, *Festuca rubra*), surrounding peatland vegetation (*Eriophorum vaginatum*), both of these communities (*Calluna vulgaris*) or neither (*Epilobium hirsutum* L.; Figure 3). Additionally, a number of species were present in the donor communities but failed to recolonise the post-fire site (Figure 3; Appendix S7). At the community level the post-fire vegetation was visually distinct from any other sampled community but had a greater similarity to each donor community (post-fire seed bank and surrounding peatland vegetation) than the donor communities had to each other (Figure 4). Indeed, wildfire and community type (seed bank or vegetation) interacted to produce a different community composition (PERMANOVA, $F_{1,74} = 20.2$, $p = 0.001$). Taken together, these results are consistent with Hypothesis 2.

3.3 | Plant trait responses

We observed a significant reduction in the post-fire vegetation community trait values for all of our chosen traits against one or more of our null models (Figure 5). Depending on the trait, the greatest reductions occurred following different ecological filters (Figure 1a), with seed mass displaying the greatest reduction against the habitat species pool null model (SES = -1.53 , CI = 0.63 , Figure 5a), and SLA and EMV against the actual species pool null model (SLA, SES = -2.51 , CI = 0.63 , Figure 5b; EMV, SES = -1.0 , CI = 0.63 , Figure 5c). Additionally, we did observe similar results in the seed bank for seed mass (habitat species pool: SES = -1.57 , CI = 0.56 , Figure 5d) and EMV (actual species pool: SES = -3.28 , CI = 0.63 , Figure 5f). Whilst SLA trait responses varied considerably between the post-fire seed bank and vegetation, we observed strong convergence for reduced SLA values in the surrounding peatland vegetation (Figure 5e).

4 | DISCUSSION

Using a combination of seed bank analysis and field surveys, we have assessed the drivers of initial post-fire recovery of peatland vegetation. Notably, our work provides insights into the immediate recovery trajectory of peatlands after wildfire and the sources for plant recolonisation. Our study shows that wildfire reduces the overall species richness of the soil seed bank, along with the overall viability of two species (seven species total; Figure 2), providing partial support for Hypothesis 1. This effect was sufficient to cause differences between the composition of the soil seed bank in the burnt and unburnt areas (Figure 4). The composition of standing vegetation one year after fire differed from both the post-fire soil seed bank and the surrounding peatland vegetation (Figure 4). This suggests that vegetation recovery

post-fire depends on colonists from the surviving seed bank and surrounding (but not necessarily peatland) vegetation (Hypothesis 2; Figures 1b and 3). Finally, we identified lighter seed mass and lower SLA and EMV values in the post-fire vegetation compared with randomly assembled communities (Figure 5a–c). However, similar trait responses were observed in the potential donor communities (Figure 5). Combining the trait evidence with taxonomic observations, our results suggest propagule availability largely determines the post-fire vegetation community composition (Hypothesis 3; Figure 1a).

4.1 | Drivers of initial vascular plant recovery

We combined two related frameworks, a classical ecological filter framework (Figure 1a) and a disturbance-colonisation framework (Figure 1b) to determine the drivers of vascular plant recovery one year post fire. Our results suggest mixed evidence for abiotic filtering via wildfire to reduce seedling abundance of individual species within the peat soil seed bank (Figure 2). These findings potentially contradict earlier observations from other temperate peatland wildfire studies which showed post-fire reductions in seedling abundances (Maltby et al., 1990; Kelly et al., 2016); however, these studies largely considered seedling abundance at a community level rather than species level. In line with earlier results, wildfire did result in a reduction in overall species richness and changes to the vegetation composition (Kelly et al., 2016), producing seed-bank communities with a higher relative abundance of ericaceous species (Hypothesis 1; Figure 4; Appendix S7). Notably, Kelly et al. (2016) found only approximately half of the species within their post-fire seed bank established in the recovering vegetation, similar to the results of our study (Figure 3). Taken together, our results indicate species arrival through multiple colonisation pathways drives the composition and structure of the initial post-fire vegetation (Hypothesis 2; Figure 1b). Additionally, wildfire can act as an abiotic filter that influences the overall composition of the soil seed bank.

Using our assembly framework (Figure 1), we compiled a series of null models to test for non-random convergence of traits within our initial post-fire vegetation. Our results provide evidence of trait convergence for all three of our indicator traits (Table 1). However, this does not necessarily confirm our earlier predictions (Hypothesis 3) that propagule availability and abiotic conditions will drive the composition of the post-fire vegetation community. If this were true, then trait convergence (i.e. the difference between the trait CWM of the observed community compared with a random assemblage) should be reduced once the species that are unable to overcome the corresponding filter(s) have been removed from the null matrices. Such a response was observed in the case of seed mass with a reduced effect size (i.e. weaker trait convergence), observed when comparing between species pools either side of the dispersal filter. However, the opposite effect was observed for SLA and EMV, with the removal of species unable to overcome the local abiotic conditions resulting in increased trait convergence. This unexpected result could instead be driven by the composition of the donor communities (Figure 1b),

which displayed similar trait patterns to the post-fire vegetation. Trait convergence within these communities could therefore skew the availability of species that are able to colonise the post-fire site. Consequently, our study only provides evidence for propagule availability, and not post-fire abiotic conditions, driving the initial post-fire composition of a temperate peatland vascular plant community.

4.2 | Implications for temperate peatlands

Initial species colonisation can drive the trajectory of taxonomic and functional recovery in a wildfire-damaged peatland (Kettridge et al., 2015). Following the wildfire, we observed species that were not found within the surrounding peatland vegetation. These were non-peatland species known for their abilities to exploit disturbances such as fire (e.g., *Chamerion angustifolium*; Moss, 1936). Additionally, their establishment success has previously been shown to increase with the removal of bryophyte layers (e.g., *Festuca rubra*; Otsus & Zobel, 2004), a widespread feature of this site. Given the short time-frame of this study, it is unclear whether these species will disappear during natural succession, and become replaced by a community that is more representative for peatlands. Nevertheless, in the short term the early colonisation of new non-peatland species increases the risk of inducing novel fire regimes (Kettridge et al., 2015), altering nutrient cycles (Gogo et al., 2011) and reductions in water table levels (Ohlson et al., 2003) that could compromise the recovery of this system.

Ecological restoration can target drivers of plant community assembly, manipulating them in order to produce a composition that meets their restoration aims (Temperton et al., 2004; Catford, 2016; Johnson et al., 2018). Our results show that the initial natural recovery of temperate peatlands following a wildfire is driven by the availability of propagules. The importance of propagule availability for the restoration of pre-disturbance plant communities has previously been observed in grasslands (Johnson et al., 2018) and wetlands (Kettenring & Galatowitsch, 2011). Conventional peatland restoration methods that target this driver (e.g., seeding; Quinty & Rochefort, 2003; Schumann & Joosten, 2008; Mitchell et al., 2009) may therefore be effective in manipulating the recovery of temperate peatlands post fire by ensuring that desirable species are able to reach the post-fire site. Additionally, the presence of non-peatland species may require further actions such as the manual removal of individuals (Quinty & Rochefort, 2003), reducing the availability of undesirable species on site. Our results do not mean that restoration techniques targeting alternate drivers will be ineffective. However, they do suggest that propagule availability should be considered when planning the potential restoration of a wildfire-damaged peatland.

4.3 | Study considerations

This study combines classical community assembly theory with an additional disturbance-colonisation framework (Figure 1) to

determine the drivers of peatland wildfire recovery. By using a single time point, our study represents a snapshot of the drivers of recolonisation one-year post fire. However, drivers of plant community assembly can vary throughout succession (Chu et al., 2007; Maire et al., 2012) and become more complex and interlinked as communities re-establish (Tilman, 2004). Stochastic elements, including initial species arrival times (e.g., priority effects; Fukami, 2015; Weidlich et al., 2017), along with soil microbial compositions (Wubs et al., 2016), can alter the direction of post-disturbance plant community composition adding temporal and spatial variability to the recovery process. In peatlands, this could drive observed patterns of species turnover and compositional changes to the vegetation community in the decade following a fire (Maltby et al., 1990; Noble et al., 2019). Future work could therefore focus on the relative role of ecological community assembly drivers across a fire recovery gradient, in order to maximise the effectiveness of restoration action given the time point and direction of post-fire recovery.

5 | CONCLUSIONS

Severe peatland wildfires threaten the taxonomic composition and functioning of peatlands (Maltby et al., 1990; Kettridge et al., 2015). Consistent with findings from others ecosystems (Morzaria-Luna & Zedler, 2007; Kettenring & Garatowitsch, 2011; Johnson et al., 2018), our study highlights that propagule availability drives the initial recovery of temperate peatlands post fire. Additionally, we show that species are able to colonise through multiple colonisation pathways. This in turn provides opportunities for new non-peatland species to colonise, which could compromise the recovery of these systems (Kettridge et al., 2015). Taken together, these results suggest ensuring the availability of peatland species following a wildfire could be key to the immediate recovery of these systems.

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AUTHOR CONTRIBUTIONS

BJMR, PH, MGD and RTEM designed and established the experiment; HERS, BJMR and JAC conceived the idea for this work, with contributions from MNS; HERS and MNS collected the data, with contributions from BJMR, MGD and RTEM; HERS analysed the data, with contributions from BJMR and JAC; HERS wrote the first draft of the paper with contributions from BJMR and JAC; all authors contributed to revisions and subsequent drafts.

DATA AVAILABILITY STATEMENT

Primary data from this study are available at: <https://doi.org/10.5258/SOTON/D1767>. Plant trait and surrounding peatland vegetation data are publicly available from the associated references (see *Methods*) and can be provided by the corresponding author on request along with code used for analysis.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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