The role of the seed bank in recovery of temperate heath and blanket bog following wildfires

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Abstract

Questions: Are the germinable seed banks of upland heath and blanket bog reduced following wildfires? Are some species at particular risk? Do the impacts of wildfires on seed banks differ between heathlands and blanket bog?

Location: Northern Ireland, United Kingdom.

Methods: Vegetation surveys and seed bank sampling were conducted in 2012 at burned and unburned areas within six upland sites where large wildfires had occurred during spring 2011. Differences in seedling abundance, species richness and Jaccard similarity indices between burned and unburned areas were compared using GLMMs. Differences in the community composition were examined using pRDA.

Results: In total, 24 of the 51 species in the vegetation were detected in the germinable seed bank. Species richness and the abundance of seedlings other than *Calluna vulgaris* were lower in areas where wildfires had occurred. Species composition of both germinable seed banks and vegetation differed between burned and unburned areas within sites; with negative associations between burned areas and some key indicator species including *Drosera rotundifolia*, *Eriophorum vaginatum*, *Empetrum nigrum*, *Narthecium ossifragum* and *Trichophorum germanicum*. We did not find any evidence of significant interactions between burning and habitat, suggesting that wildfires had similar impacts on each species regardless of the habitat in which they occurred.

Conclusions: This study differs from other UK studies in that it examines impacts of wildfires at sites that have not been previously intensively managed by burning. In particular, we highlight potential impacts on *N. ossifragum* and *D. rotundifolia*, which are key components of the upland flora and, to our knowledge, were not present in previous UK studies.

Introduction

Wildfires play a major role in shaping ecosystems globally and are likely to become increasingly common in temperate regions less accustomed to this source of environmental stress as a result of climate change and increasing anthropogenic pressures (Krawchuk et al. 2009). Whilst climate change is predicted to increase precipitation and humidity overall in Northwest Europe, seasonal variation in temperature and precipitation is likely to increase (Alcamo et al. 2007). In particular, increased temperatures and decreased precipitation in summer months in the UK and Ireland (Blenkinsop & Fowler 2007; Murphy & Fealy 2010) may

contribute to a higher frequency and intensity of uncontrolled fires (Albertson et al. 2011). European and UK wildfires are predominantly anthropogenic in origin, with more than 95% of wildfires started by people (Birot et al. 2009; McMorrow et al. 2009). Thus, wildfires in the UK and Ireland represent an interaction between people, landscape and climate, which may be mitigated by management actions.

Peatlands may be particularly vulnerable to changes in wildfire regimes, especially where management practices such as drainage, agriculture and peat-cutting have changed them from naturally fire-resistant to fire-prone ecosystems (Turetsky et al. 2014). Heathland and blanket bog are

key upland habitats in Northern Europe and support a unique flora and fauna of conservation interest (Thompson et al. 1995). Prescribed burning has been used to maintain open heathland habitats in Europe since Neolithic times, and has become increasingly common in the UK over the last 150–200 yr, where it is used to improve grazing for *Ovis aries*, *Cervus elaphus* and *Lagopus lagopus scoticus* (Thompson et al. 1995). Despite this, burning for conservation purposes remains controversial (Bradshaw et al. 2011), particularly on blanket bog, where there is not enough evidence to predict its impacts on species of conservation concern (Stewart et al. 2005; Worrall et al. 2010). Specifically, some authors suggest that burning is likely to shift peatland habitats towards a drier state, and lead to the decline of peat-forming species such as *Sphagnum* and *Eriophorum* spp., whilst favouring the establishment of *Calluna vulgaris* (Stewart et al. 2005; Littlewood et al. 2010; Bain et al. 2011). Contrary to these predictions, recent studies of prescribed burning have shown that a 10-yr burning rotation favours peat-forming species when compared to reference plots that had not been burned for >87 yr (Lee et al. 2013a), and that prescribed burning can reduce the dominance of *C. vulgaris* and maximize species diversity on managed moorlands (Harris et al. 2011).

Seed banks play a key role in secondary succession, and represent an important refuge for plant species and source of future vegetation (Vandvik et al. 2016). However, some authors suggest that seed banks usually contain only a subset of the species present in vegetation, and may be biased towards early successional species. Therefore, there is debate about the degree to which seed banks can be useful in the restoration of plant communities following disturbance (Måren & Vandvik 2009). The similarity between seed banks and vegetation depends on the frequency of disturbance events, with plants in disturbed habitats (e.g. anthropogenic heathland) investing more in sexual reproduction than in clonal growth, resulting in a higher similarity between seed banks and vegetation. Conversely, plants in less disturbed habitats invest more in clonal growth and have greater disparity between vegetation and seed bank composition (Bossuyt & Honnay 2008; Klimešová & Herben 2015). Previous studies of managed Northern European heathlands have conformed to this expectation and shown a strong correspondence between species in the vegetation and the seed bank, with 65% of species in the vegetation detected in the seed bank (Måren & Vandvik 2009). However, studies of montane vegetation in Scotland found that, on average, only between 14% and 29% of species from the vegetation were detected in the seed bank, suggesting that the seed bank particularly in high-altitude sites may be less suitable for habitat restoration (Miller & Cummins 2003). However, similarity between seed banks and vegetation in terms of species

overlap is highly dependent on seed bank sampling area, with overlap increasing as sampling effort increases, making it difficult to compare results from different studies (Vandvik et al. 2016).

Studies of the response of seed banks and vegetation to prescribed burning in Northwest European uplands have focused mainly on heathland rather than blanket bog sites (e.g. Måren & Vandvik 2009), while others have been conducted on highly disturbed sites with a previously reduced plant community (e.g. Harris et al. 2011; Lee et al. 2013a, b). Whilst these studies provide useful information for the management of these sites, further studies that examine a wider range of plant species are still needed (Bargmann et al. 2014). This is particularly relevant in ecosystems that have not been subjected to frequent burning in the past and where fire frequency may increase in the future through a combination of climate change and anthropogenic influences.

Wildfires differ from prescribed burns in terms of their intensity and size, and few studies have examined their impacts on temperate seed banks. Experimental studies have found minimal changes in temperature at depths >1–2 cm below the soil surface in prescribed fires (Davies et al. 2010; Ruprecht et al. 2013), but temperature changes during wildfires may be larger (Turetsky et al. 2014). The aim of a prescribed burn is to remove shrub vegetation whilst leaving moss, litter and soil layers intact and causing little change to soil chemistry (Rosenburgh et al. 2013). In practice loss varies from *ca.* 30–100% vegetation, depending on a variety of factors including weather, topography and management practice (Worrall et al. 2010). Conversely, uncontrolled wildfires frequently remove almost all surface vegetation and alter soil structure and topography. Hence, they may cause greater damage to both vegetation and seed banks, particularly on blanket bog sites where smouldering fires penetrate deeper into the soil (Turetsky et al. 2014).

In this study we focused on the impact of wildfires on the viability of seed banks sampled at six upland sites that have a broad plant flora representative of wet and dry heathlands and blanket bog sites. Standing vegetation and seed bank data were collected from burned and unburned areas within each site, in order to examine the impacts of wildfires on germinable seed banks and the role of seed banks in the recovery of vegetation. Specifically, we hypothesised that: (1) abundance and richness of the germinable seed bank would be significantly lower 1.0–1.5 yr post-wildfire; (2) wildfires would have different effects on different species leading to changes in community composition of both the vegetation and germinable seed bank; (3) the community composition of vegetation and the germinable seed bank would be more similar post-wildfire due to the germina-

tion of gap-dependent and fire-adapted species from the seed bank; and, (4) impacts on blanket bog seed banks would be more severe than on the seed banks of either dry or wet heath habitats.

Methods

Study sites

Samples were collected from burned and unburned areas within six upland sites in Northern Ireland where large wildfires occurred in April 2011 (Fig. 1). The location and size of these fires was derived from satellite data using the European Forest Fire Information System (EFFIS; http://effis.jrc.ec.europa.eu). GIS mapping was used to identify six Areas of Special Scientific Interest (ASSIs) within which large wildfires had occurred for inclusion in this study. Information from pre-fire condition assessments, conducted by the Northern Ireland Environment Agency (NIEA), Department of Environment (DOE), was used to classify quadrats into three EU Annex I habitat classes using the Joint Nature Conservation Committee (JNCC) National Vegetation Classification (NVC) system for UK habitats (following Averis et al. 2004). Annex I habitats included were 'blanket bog' ($n = 75$), 'Northern Atlantic wet heaths with *Erica tetralix*' ($n = 25$) and 'European dry heaths' ($n = 22$). A total of 122 quadrats (2×2 m) were selected randomly from the quadrats that had been previously surveyed by the NIEA for inclusion in this study. A total of 71 quadrats were in areas burned during 2011 and 51 in nearby unburned areas, such that burned and unburned areas were sampled within each site. The unequal number of burned and unburned quadrats resulted from a discrepancy between satellite images of burned areas and actual field conditions. However, this sampling design is adequate for the GLMM approach taken in our statistical analyses. The number of quadrats within each habitat was determined in proportion to the occurrence of that habitat at each site. The mean distance between quadrats within sites was 1.77 km (min = 0.07 km, max = 6.07 km). Details of site locations, habitats, fire size and dates of burning are shown in Appendix S1.

Seed banks and vegetation

Vegetation surveys and seed bank sampling were conducted between 23 Jun 2012 and 12 Oct 2012 (i.e. 14–18 mo post-fire). The percentage cover of all vascular plant species was assessed in each quadrat. All quadrats were surveyed by the same botanist for consistency of evaluation. Seed bank samples were taken using a cylindrical soil sampler (5-cm depth and 6-cm diameter) at three locations 1-m apart within each quadrat. This sampling regime accounted for potential aggregation of seeds on small spatial scales by taking multiple samples within quadrats and optimized efficiency by only sampling the top 5 cm of soil where most viable seeds occur (Putwain & Gillham 1990; Pywell et al. 1997). Soil samples were refrigerated (2–5 °C) over winter until the following April.
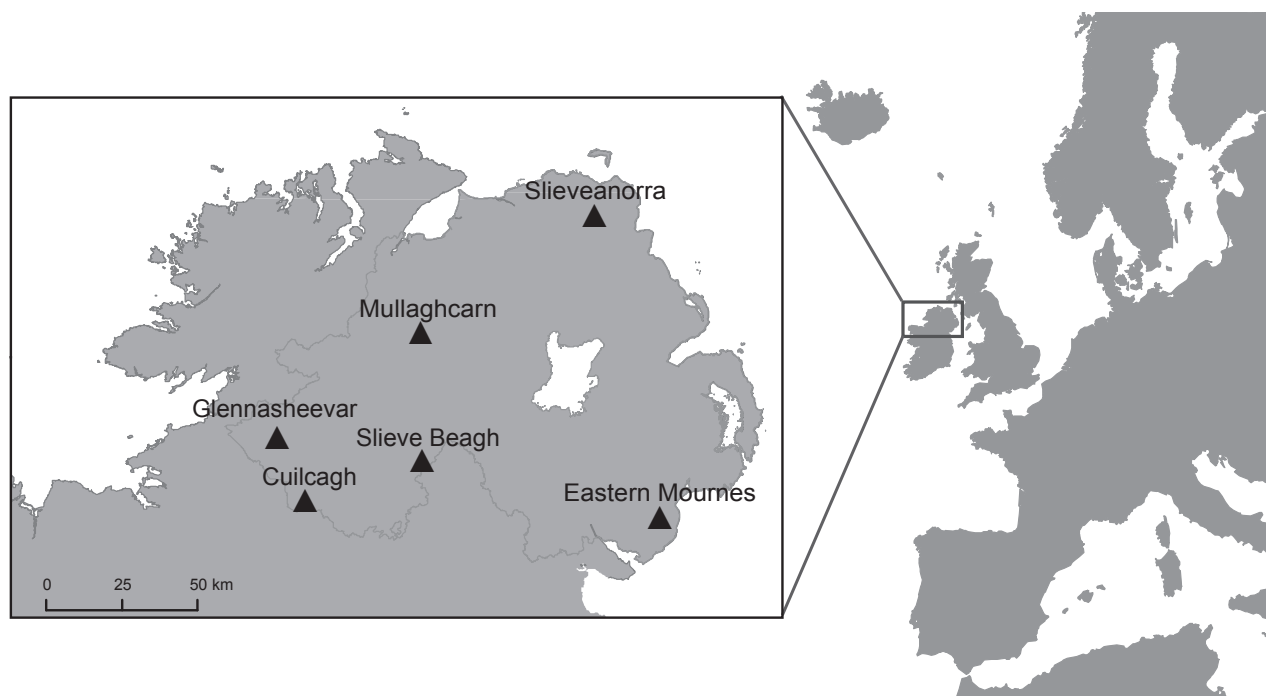

Fig. 1. Locations of field sites.

Individual soil samples for seed bank germination were not aggregated within quadrats.

To maximize germination, seed bank samples were concentrated by passing soil through 4.0-mm and 0.250-mm mesh sieves to remove large material and fine particulate matter (following Ter Heerdt et al. 1996). Seedling germination trials were initiated between 8 and 16 Apr 2013 by spreading individual soil samples on top of ericaceous compost (70% peat). An additional 60 control samples of pure compost were potted, making a total of 426 samples (i.e. 60 control samples + 366 experimental samples; three samples from each of 122 quadrats). Sample pots were 7.5 cm in depth, and sufficient compost was used such that the soil samples were level with the top of the pots. Pots were placed in trays with 1-cm depth of water to maintain adequate water supply, these were checked daily and manually watered from above as required. The positions of burned, unburned and control samples were randomly mixed, and changed twice weekly to reduce potentially confounding position effects on germination. Seed bank samples were germinated and grown under ambient light conditions in an unheated greenhouse for a period of 15 wk, after which all seedlings were identified, enumerated and removed. Soil samples were then vernalized by freezing at −20 °C for 7 d and returned to the greenhouse for germination. Seedlings that emerged following vernalization were identified and enumerated after a further 10-wk growing period. A total of three seeds germinated in the 60 control pots (horticultural compost only) indicating that contamination of the seed bank samples was likely to be very low. Therefore, data from the control pots were excluded from further analysis and no further adjustments were made to the data set to control for contamination. Nomenclature follows Rose & O'Reilly (2006) for non-graminoid species; Poland & Clement (2009) for rushes and grasses, and Jermy et al. (2007) for sedges. Hence *Trichophorum germanicum* is used for the common species 'deergrass', which is often referred to by earlier authors as *Trichophorum cespitosum*.

Soil chemistry

Five soil samples were taken at a minimum distance of 1-m apart for soil chemistry analysis within the same quadrats sampled for vegetation and the seed bank between 3 Oct 2012 and 5 Nov 2012. Soil samples for chemical analysis were combined to provide one soil sample for each quadrat, which were analysed for pH, total N (%) and available P (mg·l^{-1}) by the Agri-Food and Biosciences Institute (AFBI), Northern Ireland. pH was measured using a Skalar SP10 Robotic analyser, total N using a TruMac CN analyser and available P using a Skalar San Plus auto analyser (Skalar Analytical, Breda, NL).

Statistical analysis

Seed banks

Differences in total seedling abundance, abundance of seedlings other than *C. vulgaris* and seedling species richness between samples from burned and unburned plots were assessed using GLMMs. This approach was chosen as most appropriate due to the non-normal distribution of the data and the spatially nested survey design (Bolker et al. 2009; Grueber et al. 2011). An information theoretic modelling approach was used to compare competing models. All possible variable subsets of the global model were fitted and compared based on the Akaike information criterion adjusted for small sample size (AICc). Model averaging was used to estimate the relative importance and estimated effect size of predictor variables from models within 2 ΔAICc of the model with the lowest AICc value (hereafter, referred to as the 'best model'). Model-averaging was used as it is more reliable than model selection procedures that rely on a single best model (e.g. step-wise selection and minimum adequate model approaches) in cases where models have similar levels of support as indicated by model Akaike weights (Burnham & Anderson 2004; Johnson & Omland 2004). Specifically, model averaging is strongly advocated in cases where support for the best model is <0.90, which was the case for all of our best models (Grueber et al. 2011). This situation can arise as a result of inherent collinearity between environmental variables, as is common in ecological field studies. Model averaging approaches are robust to moderate levels of collinearity in explanatory variables and reduce the likelihood of overestimating the effect of individual variables when compared to other model selection procedures (Freckleton 2011). Effect sizes of averaged models were estimated using the zero method of model averaging; meaning that effect sizes were averaged across all models with a value of zero in models in which they did not occur. This provides a conservative estimate of the effect sizes of variables that occur in only a small proportion of models within the best model set (Burnham & Anderson 2002).

Explanatory variables were chosen for inclusion in the initial global model based on their importance in determining upland vegetation patterns, and therefore their expected usefulness in explaining the abundance and richness of germinable seed bank species in this study (Thompson et al. 1995; De Graaf et al. 2009). Topographical variables (i.e. altitude and slope) were extracted from GIS raster files at a 25-m resolution. Heat load was a measure of local temperature resulting from solar radiation, slope and aspect specifically designed for use in vegetation science (McCune & Dylan 2002). Here, the heat load index was calculated according to Equation 3 in McCune &

Dylan (2002) based on raster data at a 25-m resolution. This equation was chosen as it was most suitable for areas with slopes of <60° and latitudes of between 30–60°. Whilst this metric does not account for small-scale variation in temperature (e.g. caused by local shading or surface reflectance), it provides a useful measure of differences in thermal environments at a landscape scale (e.g. between north- and south-facing, or shallow and steep slopes). Soil variables (i.e. available P, pH and total N) were checked for multicollinearity prior to inclusion in models. These three soil variables showed low levels of correlation (Spearman's Rho > −0.5 and <0.5 in all cases) and, therefore, all three were included in the analysis. Grazing intensity levels were assessed at each quadrat based on the quantity of dung present in each quadrat and ranked on a five-level ordinal factor scale of None < Rare < Occasional < Frequent < Abundant. Specifically, Rare = 1–2 droppings, Occasional = 3–10, Frequent = 11–20, Abundant > 20.

Initially, a global model was constructed including the explanatory variables 'Burning' (burned or unburned), 'Habitat' (blanket bog, dry heath or wet heath), 'Altitude' (m), 'Slope' (° from horizontal), 'Heat load index', 'Julian day', 'pH', 'Available P' (mg^{-1}), 'Total N' (mg^{-1}) and 'Grazing'. The interactions between Burning × Grazing, Burning × Habitat and Burning × Slope were also fitted to account for potentially different impacts of burning in different contexts. Three level interactions were not included, due to insufficient sample sizes within some three-way interaction groupings. All explanatory variables were rescaled to units of SD prior to model fitting. Quadrat nested within Site were fitted as random factors to account for variation explained by replication within quadrats and of quadrats within sites. Models were initially fitted using a Gaussian response distribution. Where model residuals were not normally distributed (based on a Shapiro-Wilk test), models were refitted by Laplace estimation with a Poisson and a negative binomial distribution (both with log link functions) and the optimal distribution was chosen based on the lowest AICc.

Similarity between germinable seed banks and vegetation

Jaccard's similarity index was used to assess the similarity between seed banks and vegetation in burned and unburned plots. The Jaccard similarity represents the proportion of shared species relative to the total number of species, and ranges from 0 (no shared species) to 1 (all species shared). It was chosen because it is based only on the presence/absence of species and not species abundances, hence, avoiding the conceptual issues that arise from comparing percentage cover in the vegetation and frequency in the germinable seed bank. Prior to the calculation of Jaccard similarity indices between vegeta-

tion and the germinable seed bank, seed bank samples within each quadrat were combined so that they were on the same spatial scale as the vegetation. However, it should be noted that due to the different sample sizes within each quadrat (i.e. 4 m^2 for vegetation vs 0.01 m^2 for the seed bank), species present in the seed bank at low abundances may not have been sampled. Nevertheless, the total volume of soil sampled for seed bank analysis across sites (51 170 cm^3) should have been sufficient to estimate the relative frequency of most taxa in the seed bank based on previous estimates of minimum sample volume for seed bank studies, which has varied from *ca.* 500 cm^3 in transient grasslands to *ca.* 50 000 cm^3 in late successional forests (Csontos 2007). Factors affecting the Jaccard similarity between the vegetation and the seed bank were assessed using the same fixed factors, variables, GLMM approach and model averaging as described above. 'Site' was fitted as a random factor.

Species composition of seed banks and vegetation

Differences in plant community composition of seed banks and vegetation were each assessed separately using partial redundancy analysis (pRDA). The species matrices were transformed using a Hellinger transformation prior to analysis. This transformation is appropriate for both percentage cover (i.e. vegetation data) and frequency data (i.e. seed bank; Legendre & Gallagher 2001). Pre-transformation of species data followed by Euclidean-based RDA is a powerful statistical method for testing the relationship between environmental variables and species community data, which is robust to the presence of rare species and long environment gradients (Legendre & Gallagher 2001). Partial RDA was used to account for differences between sites, hence allowing for the interpretation of other environmental influences whilst the effect of Site was held constant (Borcard et al. 2011). Species matrices for seed bank species were the number of seedlings of each species per quadrat. Species matrices for vegetation were the percentage cover of each species per quadrat and percentage other, representing space not occupied by vascular plants (i.e. cover of non-vascular plants and bare ground). Explanatory variables in the global model pRDAs were the same as those described above in GLMM modelling. Explanatory variables were rescaled to units of SD prior to model fitting. Model selection was conducted by forward step-wise selection from a null model containing only Site as a conditional variable. In each step, the variable from the global model that most significantly improved the model fit was added to the model based on pseudo-*F* statistics resulting from Monte Carlo permutations of the data set (*n* permutations = 999). This process continued until no further vari-

ables improved the model fit significantly at a cut-off of $P = 0.05$. This is the most commonly used method of model selection in RDA (Borcard et al. 2011). Significance of pRDA models and explanatory variables were calculated by Monte Carlo permutation with residuals of the species matrix permuted after accounting for variation within sites by pRDA (i.e. 'reduced' method). This was computed using the function anova.cca in the package vegan in R where n permutations = 999. Significance of individual variables is given as marginal terms (i.e. each term was evaluated as the last term added to the model).

Mean values and confidence intervals in results and figures were calculated by non-parametric bootstrapping of the raw data values, 95% confidence intervals are calculated by the bias-corrected accelerated percentile method (BCa) suitable for non-parametric data (Crawley 2013). All analyses were conducted using R 3.1.1 (R Foundation for Statistical Computing, Vienna, AT). GLMMs were fitted using the R packages glmmADMB (v 0.7.7) and MuMIn (v 1.9.11). Bootstrapping was conducted using the R package boot (v 1.3-11). Jaccard's similarity and pRDA were calculated in the R package vegan (v 2.0-9).

Results

A total of 53 vascular plant species were present in the vegetation and 26 germinated from the seed bank. Only two species in the germinable seed bank were not present in the vegetation, *Juncus bufonius* and *Sagina procumbens*. Twenty-four species were common to both the germinable seed bank and vegetation.

All 26 plant species that emerged from seed bank soil samples germinated prior to vernalization by freezing. In total, 6369 seeds geminated. The most commonly occurring species in the seed bank were *C. vulgaris* (present in 98% of quadrats), *Erica tetralix* (62%) and *Erica cinerea* (34%). The most common species in vegetation were
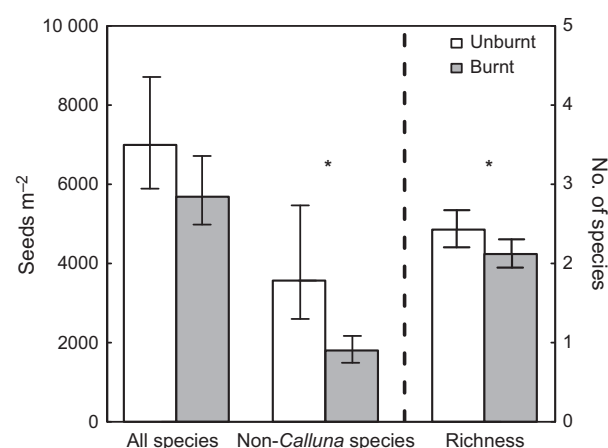

Fig. 2. Mean seed abundance per m² and mean species richness per sample in burnt and unburnt areas. Error bars show bootstrapped 95% confidence intervals on the mean. *'s indicate a significant difference between burnt and unburnt areas based on Generalised Linear Mixed Model outputs.

C. vulgaris (94% of quadrats), *E. tetralix* (61%) and *Eriophorum vaginatum* (57%). Species richness and most commonly occurring species in the vegetation and germinable seed bank in each habitat type are shown in Table 1. For a full list of species occurrences in vegetation and seed bank, see Appendix S2.

Seed banks

Germinable seed abundance in the seed bank was not significantly affected by burning, median seedling density in unburned areas was 5423 m^{-2} (mean = 6994 m^{-2}, 95% confidence = 5889–8710 m^{-2}) compared to burned areas with 5069 m^{-2} (mean = 5662 m^{-2}, 95% confidence = 4981–6714 m^{-2}; Fig. 2). The most important variable associated with total germinable seed abundance

Table 1. Comparison of seed banks and vegetation in each habitat type, showing species richness, percentage of seed bank species found in vegetation and the most commonly occurring species in each habitat type.

Habitat	Species Richness		% of Vegetation Species in Seed Bank	Most Common Species (% of Quadrats in which Species is Detected)	
	Vegetation	Seed Bank		Vegetation	Seed Bank
Blanket Bog	33	21	58	*Calluna vulgaris* (99%)	*Calluna vulgaris* (99%)
				Eriophorum vaginatum (82%)	*Erica tetralix* (68%)
				Erica tetralix (62%)	*Juncus effusus* (21%)
Dry Heath	35	19	40	*Calluna vulgaris* (95%)	*Calluna vulgaris* (100%)
				Erica cinerea (81%)	*Erica cinerea* (86%)
				Potentilla erecta (77%)	*Carex binervis* (55%)
Wet Heath	25	17	44	*Molinia caerulea* (92%)	*Calluna vulgaris* (92%)
				Erica tetralix (84%)	*Erica tetralix* (68%)
				Trichophorum germanicum (80%)	*Erica cinerea* (68%)
				Calluna vulgaris (80%)	

Table 2. Model averaged results of GLMMs for (a) germinable seed abundance, (b) Non-*Calluna vulgaris* germinable seed abundance, (c) germinable seed bank richness and (d) Jaccard similarity of germinable seed banks and vegetation. Explanatory variables are listed in descending order of importance based on their model averaged Akaike (AICc) weights ($\sum\omega_i$). Factorial comparisons of habitat types are given as 'Habitat1/Habitat2' where the habitat after the '/' was the reference condition.

Model (Response Distribution) Explanatory Variables	$\sum\omega_i$	$\beta \pm$ SE	Z-Value	P
(a) Total Germinable Seed Abundance (Negative Binomial)				
Slope	1.00	-0.253 ± 0.100	2.522	0.012
Altitude	0.94	-0.200 ± 0.109	1.838	0.066
Burning	0.49	-0.099 ± 0.145	0.685	0.493
Julian Date	0.37	-0.052 ± 0.091	0.564	0.573
Heat Load	0.27	-0.020 ± 0.053	0.371	0.711
Grazing	0.11	-0.015 ± 0.069	0.219	0.827
Soil N	0.06	-0.003 ± 0.023	0.125	0.901
Burning $\times$ Grazing	0.06	0.015 ± 0.074	0.201	0.841
(b) Non-*Calluna vulgaris* Germinable Seed Abundance (Negative Binomial)				
Altitude	1.00	-0.547 ± 0.131	4.158	<0.001
Burning	1.00	-0.523 ± 0.196	2.653	0.008
pH	0.94	0.217 ± 0.123	1.767	0.077
Slope	0.77	0.250 ± 0.223	1.118	0.264
Heat Load	0.76	-0.142 ± 0.122	1.166	0.243
Julian Date	0.39	0.070 ± 0.123	0.571	0.568
Burning $\times$ Slope	0.29	-0.081 ± 0.166	0.166	0.622
Soil P	0.18	0.017 ± 0.061	0.274	0.784
Soil N	0.12	0.012 ± 0.051	0.230	0.818
Grazing	0.12	-0.009 ± 0.047	0.196	0.845
(c) Germinable Seed Bank Species Richness (Negative Binomial)				
Burning	1.00	-0.163 ± 0.080	2.036	0.042
Slope	1.00	0.199 ± 0.078	2.535	0.011
Burning $\times$ Slope	0.91	-0.127 ± 0.081	1.568	0.117
Heat load	0.86	-0.060 ± 0.042	1.406	0.159
Habitat – Bog/Dry Heath	0.71	-0.196 ± 0.161	1.217	0.224
Habitat – Bog/Wet Heath	0.71	-0.186 ± 0.152	1.219	0.223
Habitat – Dry Heath/Wet Heath	0.71	0.011 ± 0.104	0.104	0.917
Altitude	0.65	-0.066 ± 0.067	0.988	0.323
Julian Date	0.39	0.028 ± 0.045	0.616	0.538
Soil N	0.29	-0.016 ± 0.035	0.457	0.648
Soil P	0.29	0.019 ± 0.039	0.481	0.631
Soil pH	0.11	0.004 ± 0.019	0.234	0.815
Grazing	0.06	-0.001 ± 0.011	0.112	0.911
(d) Jaccard Similarity of Germinable Seed Banks and Vegetation (Gaussian)				
Habitat – Bog/Dry Heath	1.00	-0.003 ± 0.038	0.077	0.938
Habitat – Bog/Wet Heath	1.00	0.114 ± 0.037	3.035	0.002
Habitat – Dry Heath/Wet Heath	1.00	0.117 ± 0.038	3.097	0.002
Julian Date	0.91	-0.025 ± 0.014	1.699	0.089
Burning	0.90	0.002 ± 0.021	0.100	0.921
Slope	0.90	0.054 ± 0.027	1.987	0.047
Burning $\times$ Slope	0.90	-0.059 ± 0.029	2.014	0.044
Soil pH	0.89	-0.023 ± 0.015	0.015	0.113
Altitude	0.44	-0.010 ± 0.015	0.692	0.489
Soil P	0.27	-0.004 ± 0.009	0.448	0.654

was slope, with which it was significantly negatively associated (Table 2a).

Seedling abundance of species other than *C. vulgaris* was negatively associated with burning, with a median seedling density in unburned areas of 1297 m^{-2} (mean = 3567 m^{-2}, 95% confidence = 2598–5466 m^{-2}) and reduced densities in burned areas of 1178 m^{-2} (mean = 1802 m^{-2}, 95% confidence = 1490–2168 m^{-2}; Fig. 2). Non-*C. vulgaris* seedling abundance was significantly negatively associated with altitude (Table 2b).

Burning and slope were the most important variables associated with the species richness of the germinable seed

bank (as indicated by their inclusion in all models within 2 ΔAICc units of the best model). However, this result should be interpreted with caution, as P-values were borderline for the effect of burning ($\beta = -0.163 \pm 0.080$, $P = 0.042$). Burning was negatively associated with mean species richness, with a median richness of two species per sample in unburned areas (mean = 2.4, 95% confidence = 2.2–2.6) compared to two species per sample in burned areas (mean = 2.1, 95% confidence = 1.9–2.3; Fig 2). Seedling species richness was significantly positively associated with slope (Table 2c).

Similarity between germinable seed banks and vegetation

In total, 24 of 51 (47%) species present in the vegetation were detected in the germinable seed bank. Notably, some species characteristic of wet heath or blanket bog that were common in the vegetation were absent or rare in the germinable seed bank e.g. *Eriophorum angustifolium, E. nigrum, Narthecium ossifragum, T. germanicum* and *Vaccinium myrtillus. Juncus bulbosus* and *J. effusus* were much more common in the germinable seed bank than in vegetation (Appendix S2).

The Jaccard similarity between germinable species in the seed bank and vegetation differed between habitat types and was significantly higher in dry heath (mean = 0.33, 95% confidence = 0.27–0.39) and blanket bog (mean = 0.33, 95% confidence = 0.30–0.36) than in wet heath (mean = 0.23, 95% confidence = 0.19–0.27) where $\beta = 0.117 \pm 0.038$, $P = 0.002$ and $\beta = 0.114 \pm 0.037$, $P = 0.002$, respectively. Dry heath and blanket bog did not differ in terms of Jaccard similarity ($\beta = 0.003 \pm 0.038$, $P = 0.938$). Areas with steeper slopes had

a higher similarity between vegetation and germinable seed banks, although this association was marginal ($\beta = 0.054 \pm 0.027$, $P = 0.046$). A marginal interaction between burning and slope was also evident such that germinable seed banks were less similar on steeper burned plots ($\beta = -0.059 \pm 0.029$, $P = 0.044$; Table 2d).

Species composition of germinable seed banks and vegetation

The community composition of both the germinable seed bank and vegetation differed significantly between burned and unburned areas (pseudo-$F = 2.004$, $P = 0.010$ and pseudo-$F = 3.485$, $P = 0.005$, respectively) based on pRDA. The best model for germinable seed bank composition included burning, habitat, soil pH and available P and explained 10.6% of the variation in seed bank community composition after accounting for variance between sites (pseudo-$F_{df\ =\ 5,111} = 3.057$, $P = 0.001$; Table 3a, Fig. 3a). The best model for vegetation cover included altitude, burning, habitat, heat load, soil pH and available P and explained 16.2% of variation in the vegetation community after accounting for variance between sites (pseudo-$F_{df\ =\ 7,109} = 3.485$, $P = 0.005$; Table 3b, Fig. 3b).

In the germinable seed bank only *E. tetralix* and *C. vulgaris* showed increased germination in soil samples from burned areas, whilst the majority of other species present in the germinable seed bank, including sedge, rush and grass species, showed a negative association with burned areas (Fig. 3a).

In the vegetation, many species showed a positive association with burned areas, including many sedges, rushes, grasses, herbs (e.g. *Galium saxatile* and *Polygala serpyllifolia*) and shrubs (*E. cinerea* and *V. myrtillus*), suggesting that the

Table 3. Partial redundancy analysis (pRDA) permutation test results of variables in best fitting model for (a) species composition of germinable seed bank and (b) species composition of vegetation. Site was fitted as a conditional factor in all models. Constrained and conditional variances are given as the proportion of the total variance in each species community. 'Variance explained' is shown as the proportion of the total variance in the species community explained when a variable is fitted as the last term in the model (i.e. marginal terms). Explanatory variables are listed in descending order of importance based on the variance explained.

| Model Explanatory Variables	df	Explained Variance (%)	Pseudo-F	P
(a) Germinable Seed Bank (Constrained Variance = 10.6%, Conditional Variance (Site) = 12.1%, Residual df = 111, pseudo-F = 3.057, P = 0.001)				
Soil pH	1	5.1	7.350	0.005
Soil P	1	1.9	2.723	0.010
Burning	1	1.4	2.004	0.010
Habitat	2	2.1	1.510	0.060
(b) Vegetation Cover (Constrained Variance = 16.2%, Conditional Variance (Site) = 11.3%, Residual df = 109, pseudo-F = 3.485, P = 0.005)				
Soil pH	1	5.5	8.341	0.005
Habitat	2	3.6	2.684	0.005
Burning	1	2.5	3.687	0.005
Soil P	1	1.4	2.057	0.010
Altitude	1	1.1	1.713	0.017
Heat Load	1	1.1	1.586	0.033
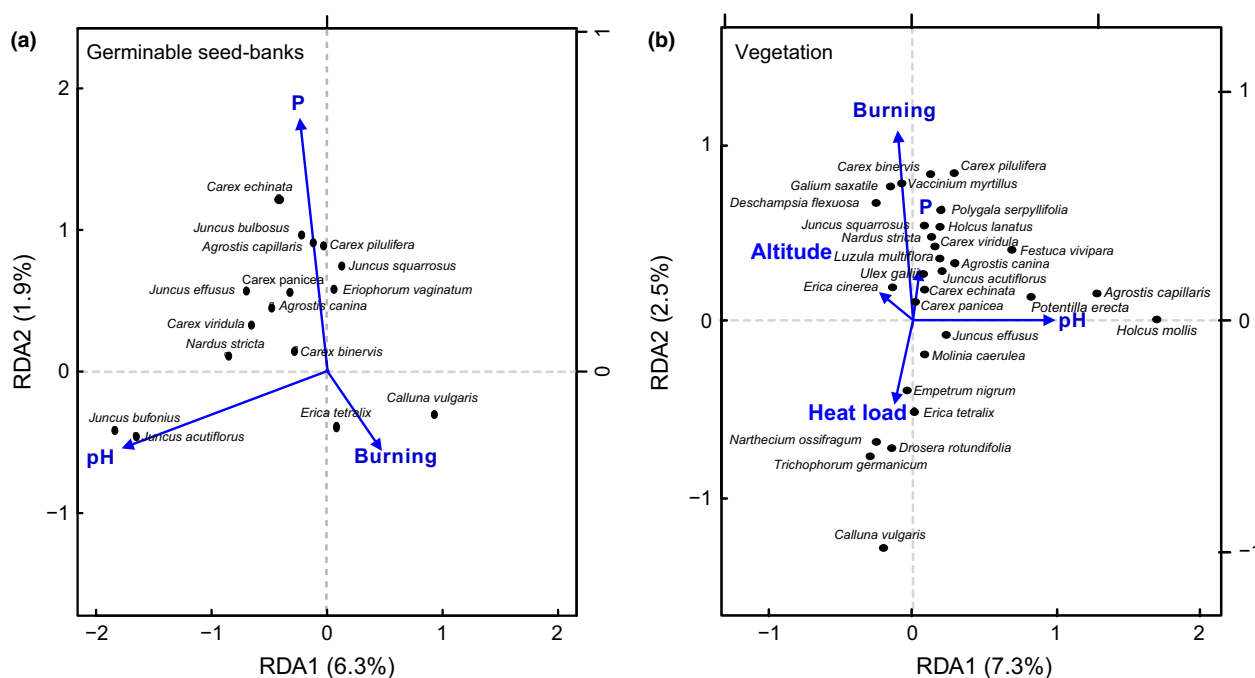
Fig. 3. Biplots showing the association between environmental variables and plant species composition. Species are plotted where they occur in more than 1 quadrat and more than 5% percent of the variation in their abundance is explained by the RDA model after differences between sites are accounted for.

decline of these species in the germinable seed bank may correspond with *in-situ* germination post-fire prior to our sampling. Only three species that were negatively associated with burning in the seed bank did not show a positive association with burning in the vegetation surveys, namely: *J. bulbosus*, *J. effusus* and *E. vaginatum*. Furthermore, some species were reduced in the vegetation post-burning, namely *C. vulgaris, Drosera rotundifolia, T. germanicum, N. ossifragum, E. tetralix, E. nigrum* and *Molinia caerulea* (Fig. 3b). Four of these seven species (*D. rotunifolia, E. nigrum, N. ossifragum* and *T. germanicum*) were rare in the germinable seed bank (i.e. detected in <1% of quadrats; Appendix S2).

Discussion

Our findings suggest that seed banks in these sites of conservation concern had a lower abundance of non-*Calluna vulgaris* species and species richness following wildfires. Similar to previous studies, we found that the total abundance of germinating seed was not reduced following recent burning, probably due to the increased germination of the most common species, *C. vulgaris* and *E. tetralix,* which have been previously shown to increase in germination post-fire (Bargmann et al. 2014; Vandvik et al. 2014). The majority of species that declined in the germinable seed bank increased in the post-fire vegetation, suggesting

that these germinated from the seed bank post-fire and prior to our sampling, as would be expected in secondary successional dynamics. Notably, some species did not show this pattern, including *E. vaginatum* (which declined in the seed bank and did not increase in the vegetation) and *D. rotundifolia, E. nigrum, N. ossifragum* and *T. germanicum* (which declined in the vegetation and were very rare in the seed bank). These five species are indicators of 'favourable condition' in blanket bog and wet heath habitats in the UK (JNCC 2006) and, therefore, important in maintaining the status of these habitats under the EU Habitats Directive (Council of the European Commission 1992).

As expected, other environmental factors were also very important in determining germinable seed bank abundance, richness and composition. In particular, steeper slopes had a lower abundance and higher richness of germinable seeds, whilst the abundance of non-*Calluna* species was lower at higher altitudes. Acidity and nutrient levels strongly influence the species composition of Northern European moorlands (De Graaf et al. 2009), and these associations were reflected in our data set with pH and P availability being associated with differences in species composition of both the germinable seed bank and vegetation. As expected, altitude and heat load were also associated with differences in community composition of the vegetation, although these were less important than pH and P. The total amount of variance in plant communities

accounted for by environmental variables, after accounting for differences between sites (10.6% in germinable seed banks and 16.2% in vegetation) were similar to those explained by environmental variables in similar habitat types using multivariate techniques (e.g. Vandvik et al. 2005; Harris et al. 2011) and to that explained in many other ecological studies (Møller & Jennions 2002). High levels of unexplained residual variance in these species communities may indicate a strong role of stochasticity in species assembly and/or the effects of environmental variables not accounted for here.

We hypothesized that impacts on blanket bog would be more severe than those in heathland habitats due to the potential for smouldering burns of longer duration. However, we found no evidence of significant interactions between burning and habitat in any of our models, suggesting that wildfires had similar impacts on each species regardless of the habitat in which the species occurred. Despite this, pRDA highlighted declines in key indicator species of blanket bog and wet heath (*D. rotundifolia, E. nigrum, N. ossifragum* and *T. germanicum*), suggesting that some species in those habitats may be at higher risk.

These results indicate some support for the suggestion of Littlewood et al. (2010) that burning (in this case by wildfires) may reduce the prevalence of peatland specialist species and should be avoided if 'favourable condition' is to be maintained (Stewart et al. 2005). However, our results need to be put in the context of successional dynamics and previous studies. Two of the aforementioned species, *E. vaginatum* and *T. germanicum*, have been suggested to have positive associations with burning management (Preston et al. 2002), and in particular *E. vaginatum* has been shown to have higher abundance in areas with a 10-yr management burning rotation than in areas which have been unburned for >87 yr. Both species have low occurrence in persistent seed banks (Miller & Cummins 2003; Måren & Vandvik 2009) and are capable of clonal regeneration by rhizomes both above and below the ground (Klimešová & de Bello 2009). The observed contrast between the negative associations shown here and previous studies may be due to the higher temperatures and durations of wildfires relative to prescribed burning and/or to differences in the time frame between studies.

Narthecium ossifragum, E. nigrum and *D. rotundifolia* are less common in upland vegetation than *E. vaginatum* and *T. germanicum* (present in 21%, 10%, 4%, 57% and 43% of vegetation quadrats, respectively, in this study). Reproduction of *N. ossifragum* is primarily clonal from both above- and below-ground rhizomes and bud banks (Summerfield 1974; Klimešová & de Bello 2009; Tsaliki & Diekmann 2009). Sensitivity to fires has been previously suggested in *N. ossifragum* at UK sites (Summerfield 1974), although to our knowledge this has not been shown

empirically. *N. ossifragum* is associated with late successional vegetation, *ca.* 20 yr after prescribed fires, in Scandinavian heathlands, indicating the potential for recovery in the later stages of succession (Måren & Vandvik 2009). Populations of this species in the UK appear stable over last 20 yr, but the species is of concern as it shows high habitat specificity and is likely to require stable habitat conditions for population stability (Tsaliki & Diekmann 2009).

Empetrum nigrum is a low-growing shrub species that was similarly rare in other studies of upland seed banks (e.g. Miller & Cummins 2003; Måren & Vandvik 2009). This may be due in part to poor germination, as this species shows deep dormancy and may require multiple cold stratifications and/or higher germination temperatures (Bell & Tallis 1973; Graae et al. 2008). Vegetative reproduction by *E. nigrum* is by rhizomes and resprouting at or above soil level rather than below ground (Klimešová & de Bello 2009), making it more likely for these to be damaged by severe fires. Results from previous UK studies on prescribed burning of blanket bog in the UK have been equivocal, with *E. nigrum* showing complex responses to combinations of grazing and burning (e.g. Lee et al. 2013a). However, two previous studies of shrubland and forest fires found no recovery of *E. nigrum* over periods of 4–5 yr post-burning (Penney et al. 2008; Hekkala et al. 2014).

Drosera rotundifolia may be under-detected in the seed bank in this study due to its low frequency in the vegetation and, therefore, results should be treated with particular caution. *D. rotundifolia* is capable of sexual and asexual reproduction in peatland habitats (Hoyo & Tsuyuzaki 2015), and similar to *E. nigrum*, asexual reproduction is mostly at or above soil level, although in *D. rotundifolia* below-ground bud banks may also be present (Klimešová & de Bello 2009). *Drosera* sp. are particularly dependent on mature rosettes for the maintenance of population sizes due to high mortality rates of seedlings (Nordbakken et al. 2004) and, therefore, may be particularly vulnerable to disturbances such as fire that can destroy large numbers of adult plants. However, given the low occurrence of this species in this study (present in 4% of quadrats) further species-specific research to quantify the effects of fire on its seed banks and secondary succession are required.

In total, 47% of the species in the vegetation were detected in the seed bank (24 of 51), suggesting that many species do not have large persistent seed banks in these habitats. Due to the disparity between the sampling area of seed banks and vegetation in this study (i.e. 4-m^2 quadrats in vegetation and 0.01 m^2 per quadrat in the seed bank) it is likely that the estimated Jaccard similarity indices of germinable seed banks and vegetation would be higher if larger seed bank areas were sampled, since some species with a lower frequency of seeds would probably be detected

(see Vandvik et al. 2016). Furthermore, as these Jaccard similarity indices are calculated per quadrat for the purposes of GLMM analyses, they are lower than would be expected when calculated across all quadrats within each habitat type. For comparison with previous studies, similarity at this broader habitat scale was calculated as the proportion of species in the vegetation that are also present in the seed bank (Table 1). Despite this, as sampling regimes were constant across areas within this study, relative differences in Jaccard similarity (e.g. between habitats) are reliable.

Rapid germination of many species post-fire is likely, due to increased light and nutrient availability, reduced competition and/or fire related cues such as smoke and temperature (Bargmann et al. 2014; Snyman 2015). Therefore, we expected that in areas where wildfires occurred, vegetation and seed banks would be more similar; however, we did not find any evidence to support this hypothesis. Furthermore, we found species such as *V. myrtillus* and *Carex pilulifera* that were uncommon in the seed bank became more common in the vegetation post-fire. These species have clonal traits including below-ground bud banks and rhizomes (Klimešová & de Bello 2009), which may also be important in post-fire recovery. Germinable seed banks and vegetation in steep areas were marginally less similar in burned areas. This may be due to a loss of germinable seed and/or seedlings on steep slopes after wildfires due to altered abiotic conditions, such as increased erosion and extreme weather conditions (Maltby et al. 1990).

All seed bank studies are dependent on the sampling and germination methods employed. Here, mean seed abundances per m^2 were at the lower end of the range of abundances found in similar upland communities (Miller & Cummins 2003; Måren & Vandvik 2009), but were similar to those found in upland bog habitats and European heaths (Bossuyt & Honnay 2008; Lee et al. 2013b). Community composition detected in this study was similar to that found by previous authors, with a dominance of *C. vulgaris* and *E. tetralix*, and an over-representation of *Juncus* spp. in the germinable seed bank relative to the vegetation (Miller & Cummins 2003; Bossuyt & Honnay 2008; Måren & Vandvik 2009). Species that were not detected in germinable seed banks here include those with transient seed banks, which would not be expected due to the timing of the sampling, and species that have shown similarly low seedling abundances in previous studies, such as *Vaccinium* sp. (Miller & Cummins 2003; Måren & Vandvik 2009). Hence, the relative frequencies of species found in this study are comparable with those of other studies in similar habitats and are, therefore, considered by the authors to be suitable for comparing the relative frequencies of major species in germinable seed banks between burned and unburned areas. However, inevitably, some species with low germinable seed abundances and/or clumped distributions may have been overlooked by the sampling regime employed.

Here, we focused on differences between sites over a short time frame (14–18 mo post-fire) and, therefore, it was not possible to determine the long-term impacts of wildfires on species communities. Further research is required to ascertain whether the differences in the germinable seed bank observed here are due to damage to the seed bank or early post-fire succession. This will have important implications for whether management interventions such as reseeding or alterations to the abiotic environment are necessary for the re-establishment of some key species post-wildfire.

The impact of fire on key peatland species may have been overlooked in previous studies due to the overwhelming dominance of *C. vulgaris* in the seed bank, because of a focus on sites with a history of regular burning for management, or on sites where species richness was already low. In particular, we highlight the potential negative impacts on key indicator species such as *N. ossifragum* and *D. rotundifolia*, which are characteristic of wetter sites, and which, to our knowledge, were not present in previous studies of moorland burning in the UK. The absence of a focus on these species in previous studies may relate to shifting baselines, where species composition post-disturbance is being compared to an already reduced or altered species community. In addition, we found negative associations between these wildfires and some key indicator species (T. *germanicum*, *E. vaginatum* and *E. nigrum*), which have been found to be positively associated with prescribed burning in previous UK studies. This may relate to the variable influence of burning at different sites, differences between wildfires and prescribed burning and/or differences in time scales between studies. In conclusion, this study provides evidence of the potential negative impacts of wildfires on key indicator taxa and highlights the need for further studies on a more diverse range of sites in order to quantify potential impacts on key species.

Acknowledgements

References

Albertson, K., Aylen, J., Cavan, G. & McMorrow, J. 2011. Climate change and the future occurrence of moorland wildfires in the Peak District of the UK. *Climate Research* 45: 105–118.

Alcamo, J., Moreno, J.M., Nováky, B., Bindi, M., Corobov, R., Devoy, R.J.N., Giannakopoulos, C., Martin, E., Olesen, J.E. & Shvidenko, A. 2007. Europe. In: Parry, M.L., Canziani, J.P., Palutikof, O.F., van der Linden, P.J. & Hanson, C.E. (eds.) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, pp. 541–580. Cambridge University Press, Cambridge, UK.

Averis, A., Averis, B., Birks, J., Horsfield, D., Thompson, D. & Yeo, M. 2004. *An illustrated guide to British upland vegetation*. Joint Nature Conservation Committee, Peterborough, UK.

Bain, C.G., Bonn, A., Stoneman, R., Chapman, S., Coupar, A., Evans, M., Gearey, B., Howat, M., Joosten, H., (...) & Worrall, F. 2011. *IUCN UK commission of inquiry on peatlands*. IUCN UK Peatland Programme, Edinburgh, UK.

Bargmann, T., Måren, I.E. & Vandvik, V. 2014. Life after fire: smoke and ash as germination cues in ericads, herbs and graminoids of northern heathlands. *Applied Vegetation Science* 17: 670–679.

Bell, J.N.B. & Tallis, J.H. 1973. Biological flora of the British isles: *Empetrum nigrum* L. *Journal of Ecology* 61: 289–305.

Birot, Y., Borgniet, L., Camia, A., Dupuy, J.-L., Fernandes, P., Goldammer, J.G., Gonzalez-Olabarria, J.R., Jappiot, M., Lampin-Maillet, C., (...) & Velez, R. 2009. *Living with Wildfires: What Science Can Tell Us. Discussion Paper 15*. European Forest Institute, Joensuu, FI.

Blenkinsop, S. & Fowler, H.J. 2007. Changes in European drought characteristics projected by the PRUDENCE regional climate models. *International Journal of Climatology* 27: 1595–1610.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24: 127–135.

Borcard, D., Gillet, F. & Legendre, P. 2011. *Numerical ecology with R*. Springer Science & Business Media, New York, NY, US.

Bossuyt, B. & Honnay, O. 2008. Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *Journal of Vegetation Science* 19: 875–884.

Bradshaw, S.D., Dixon, K.W., Hopper, S.D., Lambers, H. & Turner, S.R. 2011. Little evidence for fire-adapted plant traits in Mediterranean climate regions. *Trends in Plant Science* 16: 69–76.

Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. pp. 151–153. Springer, New York, NY, US.

Burnham, K.P. & Anderson, D.R. 2004. Multimodel inference – understanding AIC and BIC in model selection. *Sociological Methods and Research* 33: 261–304.

Council of the European Commission 1992. Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Communities. Series L* 206: 7–49.

Crawley, M.J. 2013. *The R book*, 2nd edn. John Wiley & Sons, Chichester, UK.

Csontos, P. 2007. Seed banks: ecological definitions and sampling considerations. *Community Ecology* 8: 75–85.

Davies, G.M., Smith, A.A., MacDonald, A.J., Bakker, J.D. & Legg, C.J. 2010. Fire intensity, fire severity and ecosystem response in heathlands: factors affecting the regeneration of *Calluna vulgaris*. *Journal of Applied Ecology* 47: 356–365.

De Graaf, M.C.C., Bobbink, R., Smits, N.A.C., Van Diggelen, R. & Roelofs, J.G.M. 2009. Biodiversity, vegetation gradients and key biogeochemical processes in the heathland landscape. *Biological Conservation* 142: 2191–2201.

Freckleton, R. 2011. Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. *Behavioural Ecology and Sociobiology* 65: 91–101.

Graae, B.J., Alsos, I.G. & Ejrnaes, R. 2008. The impact of temperature regimes on development, dormancy breaking and germination of dwarf shrub seeds from arctic, alpine and boreal sites. *Plant Ecology* 198: 275–284.

Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* 24: 699–711.

Harris, M.P., Allen, K.A., McAllister, H.A., Eyre, G., Le Duc, M.G. & Marrs, R.H. 2011. Factors affecting moorland plant communities and component species in relation to prescribed burning. *Journal of Applied Ecology* 48: 1411–1421.

Hekkala, A.M., Tarvainen, O. & Tolvanen, A. 2014. Dynamics of understory vegetation after restoration of natural characteristics in the boreal forests in Finland. *Forest Ecology and Management* 330: 55–66.

Hoyo, Y. & Tsuyuzaki, S. 2015. Sexual and vegetative reproduction of the sympatric congeners *Drosera anglica* and *Drosera rotundifolia*. *Flora* 210: 60–65.

Jermy, A.C., Simpson, D.A., Foley, M.J.Y. & Porter, M.S. 2007. *Sedges of the British Isles, B.S.B.I. Handbook No. 1*, 3rd edn. Botanical Society of the British Isles, London, UK.

J.N.C.C. 2006. *Common standards monitoring guidance for upland habitats*. Joint Nature Conservation Committee, London, UK.

Johnson, J.B. & Omland, K.S. 2004. Model selection in ecology and evolution. *Trends in Ecology & Evolution* 19: 101–108.

Klimešová, J. & de Bello, F. 2009. CLO-PLA: the database of clonal and bud bank traits of Central European flora. *Journal of Vegetation Science* 20: 511–516.

Klimešová, J. & Herben, T. 2015. Clonal and bud bank traits: patterns across temperate plant communities. *Journal of Vegetation Science* 26: 243–253.

Krawchuk, M.A., Moritz, M.A., Parisien, M.-A., Van Dorn, J. & Hayhoe, K. 2009. Global pyrogeography: the current and future distribution of wildfire. *PLoS ONE* 4: e5102.

Lee, H., Alday, J.G., Rose, R.J., O'Reilly, J. & Marrs, R.H. 2013a. Long-term effects of rotational prescribed burning and low-intensity sheep grazing on blanket-bog plant communities. *Journal of Applied Ecology* 50: 625–635.

Lee, H., Alday, J.G., Rosenburgh, A., Harris, M., McAllister, H. & Marrs, R.H. 2013b. Change in propagule banks during prescribed burning: a tale of two contrasting moorlands. *Biological Conservation* 165: 187–197.

Legendre, P. & Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271–280.

Littlewood, N., Anderson, P., Artz, R., Bragg, O., Lunt, P. & Marrs, R. 2010. *Peatland biodiversity. Scientific review.* IUCN UK Peatland Programme, Edinburgh, UK.

Maltby, E., Legg, C.J. & Proctor, M.C.F. 1990. The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation development. *Journal of Ecology* 78: 490–518.

Måren, I.E. & Vandvik, V. 2009. Fire and regeneration: the role of seed banks in the dynamics of northern heathlands. *Journal of Vegetation Science* 20: 871–888.

McCune, B. & Dylan, K. 2002. Equations for potential annual direct radiation and heat load. *Journal of Vegetation Science* 13: 603–606.

McMorrow, J., Lindley, S., Aylen, J., Cavan, G., Albertson, K. & Boys, D. 2009. Moorland wildfire risk, visitors and climate change: patterns, prevention and policy. In: Bonn, A., Allott, T., Hubacek, K. & Stewart, J. (eds.) *Drivers of change in upland environments*. Routledge, Abingdon, UK.

Miller, G.R. & Cummins, R.P. 2003. Soil seed-banks of woodland, heathland, grassland, mire and montane communities, Cairngorm Mountains, Scotland. *Plant Ecology* 168: 255–266.

Møller, A. & Jennions, M.D. 2002. How much variance can be explained by ecologists and evolutionary biologists? *Oecologia* 132: 492–500.

Murphy, C. & Fealy, R. 2010. Climate change impacts for Ireland. Part 2: changes in key climatic variables. *Geographical Viewpoint* 38: 29–43.

Nordbakken, J.F., Rydgren, K. & Økland, R.H. 2004. Demography and population dynamics of *Drosera anglica* and *D. rotundifolia*. *Journal of Ecology* 92: 110–121.

Penney, B.G., McRae, K.B. & Rayment, A.F. 2008. Effect of long-term burn-pruning on the flora in a lowbush blueberry (*Vaccinium angustifolium* Ait.) stand. *Canadian Journal of Plant Science* 88: 351–362.

Poland, J. & Clement, E.J. 2009. *The vegetative key to the British Flora*. John Poland, Southampton, UK.

Preston, C.D., Pearman, D.A. & Dines, T.D. 2002. *New atlas of the British and Irish flora. An atlas of the vascular plants of Britain, Ireland, the Isle of Man and the Channel Islands*. Oxford University Press, Oxford, UK.

Putwain, P.D. & Gillham, D.A. 1990. The significance of the dormant viable seed bank in the restoration of heathlands. *Biological Conservation* 62: 1–16.

Pywell, R.F., Putwain, P.D. & Webb, N.R. 1997. The decline of heathland seed populations following the conversion to agriculture. *Journal of Applied Ecology* 34: 949–960.

Rose, F. & O'Reilly, C. 2006. *The Wild Flower Key - How to identify wild plants, trees and shrubs in Britain and Ireland*. Penguin Group, London, UK.

Rosenburgh, A., Alday, J.G., Harris, M.P.K., Allen, K.A., Connor, L., Blackbird, S., Eyre, G. & Marrs, R.H. 2013. Changes in peat chemical properties during post-fire succession on blanket bog moorland. *Geoderma* 211–212: 98–106.

Ruprecht, E., Fenesi, A., Fodor, E.I. & Kuhn, T. 2013. Prescribed burning as an alternative management in grasslands of temperate Europe: the impact on seeds. *Basic and Applied Ecology* 14: 642–650.

Snyman, H.A. 2015. Short-term responses of southern African semi-arid rangelands to fire: a review of impacts on soils. *Arid Land Research and Management* 29: 222–236.

Stewart, G.B., Coles, C.F. & Pulin, A.S. 2005. Applying evidence-based practice in conservation management: lessons from the first systematic review and dissemination projects. *Biological Conservation* 126: 270–278.

Summerfield, R.J. 1974. *Narthecium Ossifragum* (L.) Huds. *Journal of Ecology* 62: 325–339.

Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M. & Bakker, J.P. 1996. An improved method for seed bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology* 10: 144–151.

Thompson, D.B.A., Macdonald, A.J., Marsden, J.H. & Galbraith, C.A. 1995. Upland heather moorland in Great Britain: a review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation* 71: 163–178.

Tsaliki, M. & Diekmann, M. 2009. Fitness and survival in fragmented populations of *Narthecium ossifragum* at the species' range margin. *Acta Oecologica* 35: 415–421.

Turetsky, M.R., Benscoter, B., Page, S., Rein, G., van der Werf, G.R. & Watts, A. 2014. Global vulnerability of peatlands to fire and carbon loss. *Nature Geoscience* 8: 11–14.

Vandvik, V., Heegaard, E., Måren, I.E. & Aarestad, P.A. 2005. Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. *Journal of Applied Ecology* 42: 139–149.

Vandvik, V., Töpper, J.P., Cook, Z., Daws, M.I., Heegaard, E., Måren, I.E. & Velle, L.G. 2014. Management-driven evolution in a domesticated ecosystem. *Biology Letters* 10: 20131082.

Vandvik, V., Klanderud, K., Meineri, E., Måren, I.E. & Töpper, J. 2016. Seed banks are biodiversity reservoirs: species–area relationships above versus below ground. *Oikos* 125: 218–228.

Worrall, F., Clay, G.D., Marrs, R. & Reed, M.S. 2010. *Impacts of Burning Management on Peatlands Report IUCN UK Peatland Programme*. IUCN UK Peatland Programme, Edinburgh, UK.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Table S1. Details of study site locations, characteristics and management.
Appendix S2. Table S2. Relative frequency of species in vegetation and germinable seed bank.
Appendix S3. Germinable seed bank data set summarized at quadrat level.