

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

Kelly, R., Boston, E., Montgomery, W., & Reid, N. (2016). The role of the seed bank in recovery of temperate heath and blanket bog following wildfires. *Applied Vegetation Science*. Advance online publication. https://doi.org/10.1111/avsc.12242

#### Published in:

**Applied Vegetation Science** 

#### **Document Version:** Peer reviewed version

# Queen's University Belfast - Research Portal:

Link to publication record in Queen's University Belfast Research Portal

#### **Publisher rights**

#### © 2016 International Association for Vegetation Science

This is the peer reviewed version of the following article: Kelly, R., Boston, E., Montgomery, W. I., Reid, N. (2016), The role of the seed bank in recovery of temperate heath and blanket bog following wildfires. Applied Vegetation Science, which has been published in final form at [http://onlinelibrary\_wiley.com/doi/10.1111/avsc.12242/abstract. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.

#### General rights

Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

#### **Open Access**

This research has been made openly available by Queen's academics and its Open Research team. We would love to hear how access to this research benefits you. - Share your feedback with us: http://go.qub.ac.uk/oa-feedback

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

Ruth Kelly<sup>1</sup>, Emma Boston<sup>1</sup>, W. Ian Montgomery <sup>1,2</sup>, Neil Reid <sup>1,2</sup>

<sup>1</sup> Quercus, School of Biological Sciences, Queen's University Belfast, Belfast, Northern Ireland (UK) <sup>2</sup> Institute for Global Food Security (IGFS), Queen's University Belfast, Belfast, Northern Ireland (UK)

Running title:	Impact of wildfires on seed-banks					
Correspondence author:	Dr Ruth Kelly					
	Quercus,					
	School of Biological Sciences					
	Queen's University Belfast					
	97 Lisburn Road					
	Belfast BT9 7BL					
	Email: ruth.kelly@qub.ac.uk					
	Tel: +44 77 07627488					
Email addresses of other a	uthors: Boston, E. (emma.boston@qub.ac.uk);					
	Montgomery, W.I. (i.montgomery@qub.ac.uk);					
	Reid, N. (neil.reid@qub.ac.uk)					
Printed journal page estim	ate: Text 6,870 words (8.5 pages), references 1,728 (2 pages), 3					
tables (0.8 pages), 3 figures	(0.7 page), total (12 pages)					
<b>x</b> z <b>x</b> 1 · · ·						

**Key words:** burning, germination, mire, moorland, peatlands, seedbank, recovery, RDA, upland

**Nomenclature:** Rose & O'Reilly (2006) for non-graminoid species; Poland & Clement (2009) for rushes and grasses; Jermy et al. (2007) for sedges; Council of the European Commission (1992) for habitats.

Abbreviations: Akaike Information Criterion adjusted for small sample size (AICc); Area of Special Scientific Interest (ASSI); European Forest Fire Information System (EFFIS); Generalised Linear Mixed Model (GLMM); partial Redundancy Analysis (pRDA); Northern Ireland Environment Agency (NIEA)

#### 1 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 seedbanks differ between heathlands and blanket bog?

5 Location: Northern Ireland, United Kingdom

Methods: Vegetation surveys and seed-bank sampling were conducted in 2012 at burnt and
unburnt areas within six upland sites where large wildfires had occurred during spring 2011.
Differences in seedling abundance, species richness and Jaccard Similarity Indices between
burnt and unburnt areas were compared using Generalised Linear Mixed Models (GLMMs).
Differences in the community composition were examined using partial Redundancy

11 Analysis (pRDA).

12 **Results:** 24 of the 51 species in the vegetation were detected in the germinable seed-bank.

13 Species richness and the abundance of seedlings other than *Calluna vulgaris* were lower in

14 areas where wildfires had occurred. Species composition of both germinable seed-banks and

15 vegetation differed between burnt and unburnt areas within sites; with negative associations

16 between burnt areas and some key indicator species including Drosera rotundifolia,

17 Eriophorum vaginatum and Empetrum nigrum, Narthecium ossifragum and Trichophorum

18 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 habitatin which they occurred.

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

## 26 Introduction

Wildfires play a major role in shaping ecosystems globally and are likely to become 27 increasingly common in temperate regions less accustomed to this source of environmental 28 29 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 30 North-western Europe, seasonal variation in temperature and precipitation is likely to 31 increase (Alcamo 2007). In particular, increased temperatures and decreased precipitation in 32 summer months in the UK and Ireland (Blenkinsop & Fowler 2007; Murphy & Fealy 2010) 33 34 may contribute to a greater frequency and intensity of uncontrolled fires (Albertson et al. 2011). European and UK wildfires are predominantly anthropogenic in origin with more than 35 95% of wildfires started by people (Birot et al. 2009; McMorrow et al. 2009). Thus, wildfires 36 37 in the UK and Ireland represent an interaction between people, landscape and climate which may be mitigated by management actions. 38

Peatlands may be particularly vulnerable to changes in wildfire regimes, especially where 39 40 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 41 bog are key upland habitats in northern Europe and support a unique flora and fauna of 42 conservation interest (Thompson et al. 1995). Prescribed burning has been used to maintain 43 open heathland habitats in Europe since Neolithic times, and has become increasingly 44 common in the UK over the last 150-200 years where it is used to improve grazing for Ovis 45 aries, Cervus elaphus and Lagopus lagopus scoticus (Thompson et al. 1995). Despite this, 46 burning for conservation purposes remains controversial (Bradshaw et al. 2011), particularly 47 on blanket bog where there is not enough evidence to predict its impacts on species of 48 conservation concern (Stewart et al. 2005; Worrall et al. 2010). Specifically, some authors 49 suggest that burning is likely to shift peatland habitats towards a drier state, and lead to the 50

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 year burning rotation favours peat-forming species when compared to reference plots which had not been burnt for >87 years (Lee et al. 2013a) and that prescribed burning can reduce the dominance of *C. vulgaris* and maximise species diversity on managed moorlands (Harris et al. 2011).

Seed-banks play a key role in secondary succession and represent an important refuge for 58 59 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 60 may be biased towards early successional species. Therefore, there is debate about the degree 61 62 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 63 depends on the frequency of disturbance events, with plants in disturbed habitats (e.g. 64 65 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 66 disturbed habitats invest more in clonal growth and have greater disparity between vegetation 67 and seed-bank composition (Bossuyt & Honnay 2008; Klimešová & Herben 2015). Previous 68 studies of managed northern European heathlands have conformed to this expectation and 69 70 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). 71 However, studies of montane vegetation in Scotland found that, on average, only between 14 72 and 29% of species from the vegetation were detected in the seed-bank suggesting that the 73 seed-bank particularly in high altitude sites may be less suitable for habitat restoration (Miller 74 & Cummins 2003). However, similarity between seed-banks and vegetation in terms of 75

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 (see
Vandvik et al. 2016).

79 Studies of the response of seed-banks and vegetation to prescribed burning in northwestern European uplands have focused mainly on heathland rather than blanket bog sites 80 (e.g. Måren & Vandvik 2009), while others have been conducted on highly disturbed sites 81 with a previously reduced plant community (e.g. Lee et al. 2013a, b; Harris et al. 2011). 82 Whilst these studies provide useful information for the management of these sites, further 83 84 studies which examine a wider range of plant species are still needed (Bargmann et al. 2014). This is particularly relevant in ecosystems which have not been subjected to frequent burning 85 in the past and where fire frequency may increase in the future through a combination of 86 87 climate change and anthropogenic influences.

Wildfires differ from prescribed burns in terms of their intensity and size, and few studies 88 have examined their impacts on temperate seed-banks. Experimental studies have found 89 90 minimal changes in temperature at depths of more than 1-2 cm below the soil surface in prescribed fires (Davies et al. 2010; Ruprecht et al. 2013) but temperature changes during 91 wildfires may be greater (Turetsky et al. 2014). The aim of a prescribed burn is to remove 92 shrub vegetation whilst leaving moss, litter and soil layers intact and causing little change to 93 soil chemistry (Rosenburgh et al. 2013); although in practice loss varies from ca. 30-100% 94 vegetation, depending on a variety of factors including weather, topography and management 95 practice (Worrall et al. 2010). Conversely, uncontrolled wildfires frequently remove almost 96 all surface vegetation and alter soil structure and topography. Hence, they may cause greater 97 damage to both vegetation and seed-banks, particularly on blanket bog sites where 98 smouldering fires penetrate deeper into the soil (Turetsky et al. 2014). 99

100 In this study we focused on the impact of wildfires on the viability of seed-banks sampled at six upland sites which have a broad plant flora representative of wet and dry heathlands 101 and blanket bog sites. Standing vegetation and seed-bank data were collected from burnt and 102 103 unburnt 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 104 hypothesised that: i) abundance and richness of the germinable seed-bank would be 105 significantly lower 1.0 - 1.5 years post-wildfire; ii) that wildfires would have different effects 106 on different species leading to changes in community composition of both the vegetation and 107 108 germinable seed-bank; iii) that the community composition of vegetation and the germinable seed-bank would be more similar post-wildfire due to the germination of gap dependent and 109 fire adapted species from the seed-bank; and, iv) that impacts on blanket bog seed-banks 110 would be more severe than on the seed-banks of either dry or wet heath habitats. 111

#### 112 Methods

113

#### 114 Study sites

Samples were collected from burnt and unburnt areas within six upland sites in Northern 115 Ireland where large wildfires occurred in April 2011 (Fig. 1). The location and size of these 116 fires was derived from satellite data using the European Forest Fire Information System 117 (EFFIS, http://effis.jrc.ec.europa.eu). GIS mapping was used to identify six Areas of Special 118 Scientific Interest (ASSIs) within which large wildfires had occurred for inclusion in this 119 120 study. Information from pre-fire condition assessments, conducted by the Northern Ireland Environment Agency (NIEA), Department of Environment (DOE) was used to classify 121 quadrats into three EU Annex I habitat classes using the Joint Nature Conservation 122 123 Committee (JNCC) National Vegetation Classification (NVC) system for UK habitats (following Averis et al. 2004). Annex I habitats included were "blanket bog" (n=75), 124 "Northern Atlantic wet heaths with *Erica tetralix*" (*n*=25) and "European dry heaths" (*n*=22). 125 A total of 122 guadrats (2 x 2 m) were selected randomly from the guadrats which had been 126 previously surveyed by the NIEA for inclusion in this study. 71 quadrats were in areas burnt 127 during 2011 and 51 in nearby unburnt areas, such that burnt and unburnt areas were sampled 128 within each site. The unequal number of burnt and unburnt sites resulted from a discrepancy 129 between satellite images of burnt areas and actual field conditions. However, this sampling 130 design is adequate for the Generalised Linear Mixed Modelling approach taken in our 131 statistical analyses. The number of quadrats within each habitat was determined in proportion 132 to the occurrence of that habitat at each site. The mean distance between quadrats within sites 133 was 1.77 km (min = 0.07 km, max = 6.07 km). Details of site locations, habitats, fire size and 134 dates of burning are shown in supplementary material, Appendix 1. 135

136

#### 137 Seed-banks and vegetation

Vegetation surveys and seed-bank sampling were conducted between 23<sup>rd</sup> June 2012 and 138 12<sup>th</sup> October 2012 (i.e. 14-18 months post-fire). The percentage cover of all vascular plant 139 140 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 141 (5 cm in depth and 6 cm in diameter) at three locations 1 m apart within each quadrat. This 142 sampling regime accounted for potential aggregation of seeds on small spatial scales by 143 taking multiple samples within quadrats and optimised efficiency by only sampling the top 144 5 cm of soil where most viable seeds occur (Putwain & Gillham 1990; Pywell et al. 1997). 145 Soil samples were refrigerated between (2-5 °C) over-winter until the following April. 146 147 Individual soil samples for seed-bank germination were not aggregated within quadrats.

To maximise germination, seed-bank samples were concentrated by passing soil through 148 4 mm and 0.250 mm mesh width sieves to remove large material and fine particulate matter 149 (following Ter Heerdt et al. 1996). Seedling germination trials were initiated between the 8<sup>th</sup> 150 and 16<sup>th</sup> of April 2013 by spreading individual soil samples on top of ericaceous compost 151 152 (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; 3 samples from each of 153 122 quadrats). Sample pots were 7.5 cm in depth and sufficient compost was used such that 154 the soil samples were level with the top of the pots. Pots were placed in trays with 1 cm 155 depth of water to maintain adequate water supply, these were checked daily and manually 156 watered from above as required. The positions of burnt, unburnt and control samples was 157 randomly mixed, and changed twice weekly to reduce potentially confounding position 158 effects on germination. Seed-bank samples were germinated and grown under ambient light 159 conditions in an unheated greenhouse for a period of 15 weeks after which all seedlings were 160 identified, enumerated and removed. Soil samples were then vernalized by freezing at -20 °C 161

for 7 days and returned to the greenhouse for germination. Seedlings which emerged 162 following vernalisation were identified and enumerated after a further 10 week growing 163 period. A total of three seeds germinated in the 60 control pots (horticultural compost only) 164 indicating that contamination of the seed-bank samples was likely to be very low. Therefore, 165 data from the control pots were excluded from further analysis and no further adjustments 166 were made to the dataset to control for contamination. Nomenclature follows Rose & 167 O'Reilly (2006) for non-graminoid species; Poland & Clement (2009) for rushes and grasses; 168 and Jermy et al. (2007) for sedges. Hence Trichophorum germanicum is used for the common 169 species "deergrass" which is often referred to by earlier authors as Trichophorum cespitosum. 170

171

## 172 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<sup>rd</sup> October 2012 and 5<sup>th</sup> November 2012. Soil samples for chemical analysis were combined to provide one soil sample for each quadrat which was analysed for pH, total nitrogen (%) and available phosphorus (mg/l) by the Agri-Food and Biosciences Institute (AFBI), Northern Ireland. pH was measured using a Skalar SP10 Robotic Analyser, total nitrogen using a TruMac® CN analyser and available phosphorus using a Skalar San Plus Auto Analyser.

180

#### 181 Statistical analysis

182

183 Seed-banks

184

185 Differences in total seedling abundance, abundance of seedlings other than *C. vulgaris* and 186 seedling species richness between samples from burnt and unburnt plots were assessed using

Generalised Linear Mixed Models (GLMMs). This approach was chosen as most appropriate 187 due to the non-normal distribution of the data and the spatially nested survey design (Bolker 188 et al. 2009; Grueber et al. 2011). An Information Theoretic modelling approach was used to 189 190 compare competing models. All possible variable subsets of the global model were fitted and compared based on Akaike Information Criterion adjusted for small sample size (AICc). 191 Model averaging was used to estimate the relative importance and estimated effect size of 192 predictor variables from models within 2  $\Delta$ AICc of the model with the lowest AICc value 193 (hereafter, referred to as the 'best model'). Model-averaging was used as it is more reliable 194 195 than model selection procedures which rely on a single best model (e.g. stepwise selection and minimum adequate model approaches) in cases where models have similar levels of 196 support as indicated by model Akaike weights (Burnham & Anderson, 2004; Johnson & 197 198 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. 199 2011). This situation can arise as a result of inherent collinearity between environmental 200 201 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 202 overestimating the effect of individual variables when compared to other model selection 203 procedures (Freckleton et al. 2011). Effect sizes of averaged models were estimated using the 204 zero method of model averaging; meaning that effect sizes were averaged across all models 205 206 with a value of zero in models in which they did not occur. This provides a conservative estimate of the effect sizes of variables which occur in only a small proportion of models 207 within the best model set (Burnham & Anderson 2002). 208

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

11

study (Thompson et al. 1995; De Graaf et al. 2009). Topographical variables (i.e. Altitude 212 and Slope) were extracted from GIS raster files at a 25m resolution. Heat Load was a 213 measure of local temperature resulting from solar radiation, slope and aspect specifically 214 designed for use in vegetation science (McCune & Dylan, 2002). Here, the Heat Load Index 215 was calculated according to Equation 3 in McCune & Dylan (2002) based on raster data at a 216 25 m resolution. This equation was chosen as it was most suitable for areas with slopes of 217 less than 60° and latitudes of between 30-60°. Whilst this metric does not account for small-218 scale variation in temperature caused by, for example, local shading or surface reflectance, it 219 220 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 221 phosphorous, pH and total nitrogen) were checked for multicollinearity prior to inclusion in 222 models. These three soil variables showed low levels of correlation (Spearman's Rho > -0.5223 and < 0.5 in all cases), and, therefore, all 3 were included in the analysis. Grazing intensity 224 levels were assessed at each quadrat based on the quantity of dung present in each quadrat 225 and was ranked on a five-level ordinal factor scale of None < Rare < Occasional < Frequent < 226 Abundant. Specifically, Rare = 1-2 droppings, Occasional = 3-10, Frequent = 11-20, 227 Abundant > 20. 228

Initially, a global model was constructed including the explanatory variables "Burning" 229 (burnt or unburnt), "Habitat" (blanket bog, dry heath or wet heath), "Altitude" (m), "Slope" (° 230 from horizontal), "Heat load Index", "Julian day", "pH", "Available phosphorous" (mg<sup>-1</sup>), 231 "Total Nitrogen" (mg<sup>-1</sup>) and "Grazing". The interactions between "Burning\*Grazing", 232 "Burning\*Habitat" and "Burning\*Slope" were also fitted to account for potentially different 233 impacts of burning in different contexts. Three level interactions were not included, due to 234 the insufficient sample sizes within some three-way interaction groupings. All explanatory 235 variables were rescaled to units of standard deviation prior to model fitting. "Quadrat" nested 236

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.

243

## 244 Similarity between germinable seed-banks and vegetation

Jaccard's Similarity Index was used to assess the similarity between seed-banks and 245 vegetation in burnt and unburnt plots. The Jaccard Similarity represents the( proportion of 246 shared species relative to the total number of species, and ranges from 0 (no shared species) 247 248 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 which arise from 249 comparing percentage cover in the vegetation and frequency in the germinable seed-bank. 250 251 Prior to the calculation of Jaccard Similarity Indices between vegetation and the germinable seed-bank, seed-bank samples within each quadrat were combined so that they were on the 252 same spatial scale as the vegetation. However, it should be noted that due to the different 253 sample sizes within each quadrat (i.e.  $4 \text{ m}^2$  for vegetation vs.  $0.01 \text{ m}^2$  for the seed-bank) 254 species present in the seed-bank at low abundances may not have been sampled. 255 Nevertheless, the total volume of soil sampled for seed-bank analysis across sites 256 (51,170 cm<sup>3</sup>) should have been sufficient to estimate the relative frequency of most taxa in 257 the seed-bank based on previous estimates of minimum sample volume for seed-bank studies 258 which has varied from ca. 500 cm<sup>3</sup> in transient grasslands to ca. 50,000 cm<sup>3</sup> in late 259 successional forests (Csontos 2007). Factors affecting the Jaccard Similarity between the 260

vegetation and the seed-bank were assessed using the same fixed factors, variables, GLMMapproach and model averaging as described above. "Site" was fitted as a random factor.

263

## 264 Species composition of seed-banks and vegetation

Differences in plant community composition of seed-banks and vegetation were each 265 assessed separately using partial Redundancy Analysis (pRDA). The species matrices were 266 transformed using a Hellinger transformation prior to analysis. This transformation is 267 appropriate for both percentage cover (i.e. vegetation data) and frequency data (i.e. seed-268 bank) (Legendre & Gallagher, 2001). Pre-transformation of species data followed by 269 Euclidean-based RDA is a powerful statistical method for testing the relationship between 270 environmental variables and species community data, which is robust to the presence of rare 271 272 species and long environment gradients (Legendre & Gallagher, 2001). Partial RDA analysis was used to account for differences between sites, hence allowing for the interpretation of 273 other environmental influences whilst the effect of "Site" was held constant (Bocard et al. 274 2011). Species matrices for seed-bank species were the number of seedlings of each species 275 per quadrat. Species matrices for vegetation were the % cover of each species per quadrat and 276 % other representing space not occupied by vascular plants (i.e. cover of non-vascular plants 277 and bare ground). Explanatory variables in the global model pRDAs were the same as those 278 279 described above in GLMM modelling. Explanatory variables were rescaled to units of 280 standard deviation prior to model fitting. Model selection was conducted by forward stepwise selection from a null model containing only "Site" as a conditional variable. In each 281 step, the variable from the global model which most significantly improved the model fit was 282 added to the model based on pseudo-F statistics resulting from Monte Carlo permutations of 283 the dataset (*n* permutations = 999). This process continued until no further variables 284 improved the model fit significantly at a cut-off of p = 0.05. This is the most commonly used 285

method of model selection in RDA analyses (Bocard 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 (Legendre et al. 2011). 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 293 parametric bootstrapping of the raw data values, 95% confidence intervals are calculated by 294 the bias corrected accelerated percentile method (BCa) suitable for non-parametric data 295 (Crawley, 2013). All analyses were conducted using R 3.1.1. GLMMs were fitted using the 296 packages "glmmabmb" (Fournier et al. 2012, vr. 0.7.7) and "MuMIn" (Barton 2013, vr. 297 1.9.11). Bootstrapping was conducted using the package "boot" (Canty & Ripley 2014, vr. 298 1.3-11). Jaccard's Similarity and pRDA were calculated in the package "vegan" (Oksanen et 299 300 al. 2013, vr. 2.0-9).

#### 301 **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 306 vernalisation by freezing. In total, 6,369 seeds geminated. The most commonly occurring 307 species in the seed-bank were C. vulgaris (present in 98% of quadrats), Erica tetralix (62.3%) 308 309 and Erica cinerea (34%). The most common species in vegetation were C. vulgaris (94% of quadrats), E. tetralix (61%) and Eriophorum vaginatum (57%). Species richness and most 310 commonly occurring species in the vegetation and germinable seed-bank in each habitat type 311 312 are shown in Table 1. For full list of species occurrences in vegetation and seed-bank (see supplementary material, appendix 3). 313

314

## 315 Seed-banks

Germinable seed abundance in the seed-bank was not significantly affected by burning, median seedling density in unburnt areas was  $5,423 \text{ m}^{-2}$  (mean =  $6,994 \text{ m}^{-2}$ , 95% confidence  $= 5,889 - 8,710 \text{ m}^{-2}$ ) compared to burnt areas with  $5,069 \text{ m}^{-2}$  (mean =  $5,662 \text{ m}^{-2}$ , 95% confidence =  $4,981 - 6,714 \text{ m}^{-2}$ ; Fig. 2). The most important variable associated with total germinable seed abundance 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 unburnt areas of 1,297 m<sup>-2</sup> (mean = 3,567 m<sup>-2</sup>, 95% confidence = 2,598 - 5466 m<sup>-2</sup>) and substantially reduced densities in burnt areas of 1,178m<sup>-2</sup> 325 (mean = 1,802 m<sup>-2</sup>, 95% confidence = 1,490 – 2,168 m<sup>-2</sup>; Fig. 2). Non-*C. vulgaris* seedling 326 abundance was significantly negatively associated with altitude (Table 2b).

Burning and slope were the most important variables associated with the species richness 327 of the germinable seed-bank (as indicated by their inclusion in all models within 2  $\Delta$ AICc 328 units of the best model). However, this result should be interpreted with caution as *p*-values 329 were borderline for the effect of burning ( $\beta = -0.163 \pm 0.080$ , p = 0.042). Burning was 330 negatively associated with mean species richness, with a median richness of 2 species/sample 331 in unburnt areas (mean = 2.4, 95% confidence = 2.2 - 2.6) compared to 2 species/sample in 332 burnt areas (mean = 2.1, 95% confidence = 1.9 - 2.3; Fig 2.). Seedling species richness was 333 significantly positively associated with slope (Table 2c). 334

335

## 336 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 which 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*.
Whilst *Juncus bulbosus* and *Juncus effusus* were much more common in the germinable seedbank than vegetation (Appendix 3).

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 greater 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 burnt plots ( $\beta = -0.059 \pm 0.029$ , p = 0.044; Table 2d).

353

## 354 Species composition of germinable seed-banks and vegetation

The community composition of both the germinable seed-bank and vegetation differed 355 significantly between burnt and unburnt areas (pseudo-F = 2.004, p = 0.010 and pseudo-F =356 3.485, p = 0.005 respectively) based on pRDA analyses. The best model for germinable seed-357 bank composition included burning, habitat, soil pH and available phosphorus and explained 358 explained 10.6% of the variation in seed-bank community composition after accounting for 359 variance between sites (pseudo- $F_{df} = 5,111 = 3.057$ , p = 0.001; Table 3a and Fig 3a). The best 360 model for vegetation cover included altitude, burning, habitat, heat load, soil pH and 361 available phosphorus and explained 16.2% of the variation in the vegetation community after 362 accounting for variance between sites (pseudo- $F_{df=7,109} = 3.485$ , p = 0.005, Table 3b, Fig 3b). 363 In the germinable seed-bank only E. tetralix and C. vulgaris showed increased 364 germination in soil samples from burnt areas, whilst the majority of other species present in 365 the germinable seed-bank including sedge, rush and grass species showed a negative 366 association with burnt areas (Fig. 3a). 367

In the vegetation, many species showed a positive association with burnt areas, including many sedges, rushes, grasses, herbs e.g. *Galium saxatile* and *Polygala serpyllifolia* and shrub species (*E. cinerea* and *V. myrtillus*), suggesting that the decline of these species in the germinable seed-bank may correspond with *in-situ* germination post-fire prior to our sampling. Only 3 species which 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*. Conversely, some species were reduced in the vegetation postburning, 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 seedbank (i.e. detected in <1% of quadrats; Appendix 3).</li>

379

## 380 Discussion

Our findings suggest that seed-banks in these sites of conservation concern had a lower 381 abundance of non-Calluna vulgaris species and species richness following wildfires. Similar 382 383 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 384 species, C. vulgaris and E. tetralix, which have been previously shown to increase in 385 386 germination post-fire (Bargmann et al. 2014; Vandvik et al. 2014). The majority of species which declined in the germinable seed-bank increased in the post-fire vegetation, suggesting 387 that these germinated from the seed-bank post-fire and prior to our sampling as would be 388 expected in secondary successional dynamics. Notably, some species did not show this 389 pattern including E. vaginatum (which declined in the seed-bank and did not increase in the 390 vegetation) and D. rotundifolia, E. nigrum, N. ossifragum and T. germanicum (which 391 declined in the vegetation and were very rare in the seed-bank). These five species are 392 indicators of "favourable condition" in blanket bog and wet heath habitats in the UK (JNCC, 393 394 2006) and, therefore, important in maintaining the status of these habitats under the EU Habitats Directive (Council of the European Commission, 1992). 395

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

19

400 the species composition of Northern European moorlands (De Graaf et al. 2009) and these associations were reflected in our dataset with pH and phosphorus availability being 401 associated with differences in species composition of both the germinable seed-bank and 402 403 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 404 phosphorus. The total amount of variance in plant communities accounted for by 405 environmental variables, after accounting for differences between sites (10.6% in germinable 406 seed-banks and 16.2% in vegetation) were similar to those explained by environmental 407 408 variables in similar habitat types using multivariate techniques (e.g. Vandvik et al. 2005; Harris et al. 2011) and to that which can be explained by many other ecological studies 409 (Møller & Jennions 2002). High levels of unexplained residual variance in these species 410 411 communities may indicate a strong role of stochasticity in species assembly and/or the effects of environmental variables not accounted for here. 412

We hypothesised 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 analysis 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 by 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 425 particular E. vaginatum has been shown to have higher abundance in areas with a 10 year 426 management burning rotation than in areas which have been unburnt for >87 years. Both 427 428 species have low occurrence in persistent seed-banks (Miller and Cummins 2003; Måren & Vandvik 2009) and are capable of clonal regeneration by rhizomes both above and below 429 ground (Klimešová & de Bello 2009). The observed contrast between the negative 430 associations shown here and previous studies may be due to the higher temperatures and 431 durations of wildfires relative to prescribed burning and/or to differences in the time-frame 432 433 between studies.

N. ossifragum, E. nigrum and D. rotundifolia are less common in upland vegetation than 434 E. vaginatum and T. germanicum (present in 21%, 10%, 4%, 57% and 43% of vegetation 435 436 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 437 Bello 2009; Tsaliki & Diekmann 2009). Sensitivity to fires has been previously suggested in 438 *N. ossifragum* at UK sites (Summerfield, 1974), although to our knowledge this has not been 439 shown empirically. N. ossifragum is associated with late successional vegetation, ca. 20 years 440 after prescribed fires, in Scandinavian heathlands indicating the potential for recovery in the 441 later stages of succession (Måren & Vandvik, 2009). Populations of this species in the UK 442 appear stable over last 20 years but the species is of concern as it shows high habitat 443 444 specificity and is likely to require stable habitat conditions for population stability (Tsaliki & Diekmann, 2009). 445

*E. nigrum* is a low growing shrub species which was similarly rare in other studies of upland seed-banks (eg. 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. 450 2008). Vegetative reproduction by *E. nigrum* is by rhizomes and resprouting at or above soil 451 level rather than below-ground (Klimešová & de Bello, 2009) making it more likely for these 452 to be damaged by severe fires. Results from previous UK studies on prescribed burning of 453 blanket bog in the UK have been equivocal with *E. nigrum* showing complex responses to 454 combinations of grazing and burning (e.g. Lee et al. 2013a). However, two previous studies 455 of shrubland and forest fires found no recovery of *E. nigrum* over periods of 4-5 years post-456 burning (Penney et al. 2007; Hekkala et al. 2014).

D. rotundifolia may be under-detected in the seed-bank in this study due to its low 457 458 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 (Hovo & 459 Tsuyuzaki 2015), and similarly to E. nigrum asexual reproduction is mostly at or above soil 460 461 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 462 maintanence of population sizes due to high mortality rates of seedlings (Nordbakken et al. 463 464 2004), and, therefore, may be particularly vulnerable to disturbances such as fire which can destroy large numbers of adult plants. However, given the low occurrence of this species in 465 this study (present in 4% of quadrats) further species-specific research to quantify the effects 466 of fire on its seed-banks and secondary succession are required. 467

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. 4m<sup>2</sup> quadrats in vegetation and 0.01m<sup>2</sup> 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 which 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 481 availability, reduced competition and/or fire related cues such as smoke and temperature 482 483 (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 484 evidence to support this hypothesis. Furthermore, we found species such as V. myrtillus and 485 486 Carex pilulifera which 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 487 rhizomes (Klimešová & de Bello, 2009), which may also be important in post-fire recovery. 488 489 Germinable seed-banks and vegetation in steep areas were marginally less similar in burnt areas. This may be due to a loss of germinable seed and/or seedlings on steep slopes after 490 wildfires due to altered abiotic conditions, such as increased erosion and extreme weather 491 conditions (Maltby et al. 1990). 492

All seed-bank studies are dependent on the sampling and germination methods employed. Here, mean seed abundances per m<sup>2</sup> 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 (Lee et al. 2013b; Bossuyt and Honnay 2008). 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 overrepresentation of *Juncus* species in the germinable seed-bank relative to the vegetation 500 (Miller & Cummins 2003; Bossuyt & Honnay 2008; Måren & Vandvik 2009). Species which were not detected in germinable seed-banks here include those with transient seed-banks 501 which would not be expected due to the timing of the sampling, and species which have 502 503 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 504 this study are comparable with those of other studies in similar habitats and are, therefore, 505 considered by the authors to be suitable for comparing the relative frequencies of major 506 species in germinable seed-banks between burnt and unburnt areas. However, inevitably 507 508 some species with low germinable seed abundances and/or clumped distributions may have been overlooked by the sampling regime employed. 509

Here, we focused on differences between sites over a short timeframe (14-18 months postfire) 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 reestablishment of some key species post-wildfire.

The impact of fire on key peatland species may have been overlooked in previous studies 517 due to the overwhelming dominance of C. vulgaris in the seed bank, because of a focus on 518 519 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 520 species such as N. ossifragum and D. rotundifolia which are characteristic of wetter sites, and 521 which, to our knowledge, were not present in previous studies of moorland burning in the 522 UK. The absence of a focus on these species in previous studies may relate to shifting 523 baselines, where species composition post-disturbance is being compared to an already 524

525 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. 526 nigrum), which have been found to be positively associated with prescribed burning in 527 previous UK studies. This may relate to the variable influence of burning at different sites, 528 differences between wildfires and prescribed burning and/or differences in timescales 529 between studies. In conclusion, this study provides evidence of the potential negative impacts 530 of wildfires on key indicator taxa and highlights the need for further studies on a more 531 diverse range of sites in order to quantify potential impacts on key species. 532

## 533 Acknowledgements

This project was commissioned and funded by the Natural Heritage Research Partnership 534 (NHRP) between the Northern Ireland Environment Agency (NIEA) and Quercus, Queen's 535 536 University Belfast (QUB). The NIEA Client Officer was Martin Bradley and input was gratefully received from Richard Wyle. Thanks to land-owners including Forest Service, 537 Northern Ireland Water and the Beltrim Charitable Trust for facilitating site access. Thanks to 538 John Brazil, Lauren Daly, Emma Murphy and Ledicia Santos for assistance with germination 539 trials. Thanks also to Prof. Jim McAdam and Dr. Mel Flexen Agri-Food and Biosciences 540 541 Institute (AFBI), Northern Ireland for assistance with seedling identification and greenhouse logistics. Thanks also to Tancredi Caruso for his advice on statistical analyses and to our 542 anonymous reviewers for their helpful comments. 543

544

## 545 Author contributions:

Research was designed by RK, WIM & NR. Data collection, greenhouse experiments and
data analyses were conducted by RK. Manuscript was written by RK and edited by EB, WIM
and NR.

#### 549 **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.
- 552 Alcamo, J., Moreno, J.M., Nováky, B., Bindi, M., Corobov, R., Devoy, R.J.N., Giannakopoulos, C.,
- 553 Martin, E., Olesen, J.E. & Shvidenko A. 2007. Europe.In: Parry, M.L., Canziani, J.P. Palutikof,
- 554 O.F., van der Linden P.J. & Hanson, C.E. (eds.) Climate Change 2007: Impacts, Adaptation and
- 555 *Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the*
- 556 *Intergovernmental Panel on Climate Change*, pp. 541-580. Cambridge University Press,
- 557 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.
- 560 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.
- 567 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, Finland.
- 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.
- Borcard, D., Gillet, F., & Legendre, P. 2011 *Numerical ecology with R*. Springer Science & Business
  Media, New York, US.

- 574 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.
- 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.
- 579 Bradshaw, S.D., Dixon, K.W., Hopper, S.D., Lambers H. & Turner, S.R. 2011. Little evidence for
- 580 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 (2<sup>nd</sup> ed)*, pp. 151-153. Springer, New York, US.
- Burnham, K.P. & Anderson, D.R. 2004. Multimodel Inference Understanding AIC and BIC in
  Model Selection. *Sociological Methods and Research* 33: 261-304.
- 585 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.
- 588 Crawley, M.J. 2013. *The R book (2<sup>nd</sup> ed)*. John Wiley & Sons, Chichester, UK.
- 589 Csontos, P. 2007. Seed-banks: ecological definitions and sampling considerations. *Community* 590 *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.
- 597 Freckleton, R. 2011. Dealing with collinearity in behavioural and ecological data: model averaging
  598 and the problems of measurement error. *Behavioural Ecology and Sociobiology* 65: 91-101.
- 599 Graae, B.J., Alsos, I.G. & Ejrnaes, R. 2008. The impact of temperature regimes on development,
- 600 dormancy breaking and germination of dwarf shrub seeds from arctic, alpine and boreal sites.
- 601 *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 (3<sup>rd</sup> ed)*. Botanical Society of the British Isles, London, UK.
- Johnson, J.B. & Omland, K.S. 2004. Model selection in ecology and evolution. *Trends in Ecology & Evolution* 19: 101-108.
- J.N.C.C. 2006. *Common standards monitoring guidance for upland habitats*. Joint Nature
  Conservation Committee, London, UK
- 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.
- 624 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.

- 630 Legendre, P. & Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of
  631 species data. *Oecologia* 129: 271-280.
- Legendre, P., Oksanen, J. &. ter Braak, C.F.J. 2011. Testing the significance of canonical axes in
  redundancy analysis. *Methods in Ecology and Evolution* 2: 269–27.
- Littlewood, N., Anderson P., Artz, R., Bragg, O., Lunt, P. & Marrs, R. 2010. *Peatland biodiversity*.
   *Scientific Review*. IUCN UK Peatland Programme, UK.
- 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.
- 640 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.
- Maltby, E., Legg C.J. & Proctor M.C.F. 1990. The ecology of severe moorland fire on the North York
- 647 Moors: effects of the 1976 fires, and subsequent surface and vegetation development. *Journal of*648 *Ecology* 78: 490-518.
- Møller, A. and 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:
- **657 351-362**.

- 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
- 662 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.
- 669 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.
- 680 Summerfield, R.J. 1974. *Narthecium Ossifragum* (L.) Huds. *Journal of Ecology* 62: 325-339.
- Tsaliki, M. & Diekmann, M. 2009. Fitness and survival in fragmented populations of *Narthecium ossifragum* at the species' range margin. *Acta Oecologica* 35: 415-421.
- 683 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-
- 685 151.

- 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.
- 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.
- 691 Vandvik, V., Heegaard, E., Måren, I.E. & Aarestad, P.A. 2005 Managing heterogeneity: the
- 692 importance of grazing and environmental variation on post-fire succession in heathlands. *Journal*693 *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.

Supplementary material

Appendix 1. Table S1. Details of study site locations, characteristics and management (pdf format). Appendix 2. Table S1. Details of study site locations, characteristics and management (csv format). Appendix 3. Table S2. Relative frequency of species in vegetation and germinable seed-bank (pdf format).

Appendix 4. Table S2. Relative frequency of species in vegetation and germinable seed-bank (csv format).

Appendix 5. Germinable seed-bank dataset summarised at quadrat level (csv format).

Habitat	Species	richness	% of vegetation	Most common species (% of quadrats in which species is detected)		
	Vegetation	Vegetation Seed-bank		Vegetation	Seed-bank	
Blanket bog	33	21	58%	Calluna vulgaris (99%) Eriophorum vaginatum (82%) Erica tetralix (62%)	Calluna vulgaris (99%) Erica tetralix (68%) Juncus effusus (21%)	
Dry heath	35	19	40%	Calluna vulgaris (95%) Erica cinerea (81%) Potentilla erecta (77%)	Calluna vulgaris (100%) Erica cinerea (86%) Carex binervis (55%)	
Wet heath	25	17	44%	Molinia caerulea (92%) Erica tetralix (84%) Trichophorum germanicum (80%) Calluna vulgaris (80%)	Calluna vulgaris (92%) Erica tetralix (68%) Erica cinerea (68%)	

**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.

**Table 2.** Model averaged results of Generalised Linear Mixed Models (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 were given as "Habitat1/Habitat2" where the habitat after the "/" was the reference condition.

Model (response distribution)	$\sum \omega_i$	$\beta \pm \text{s.e.}$	Z value	p
Explanatory variables		•		
a) Total germinable seed abundan	ice (negative b	pinomial)	0.500	0.010
Slope	1.00	$-0.253 \pm 0.100$	2.522	0.012
Altitude	0.94	$-0.200 \pm 0.109$	1.838	0.066
Burning	0.49	$-0.099 \pm 0.145$	0.685	0.493
Julian Date	0.37	$-0.052 \pm 0.091$	0.564	0.573
Heat load	0.27	$-0.020 \pm 0.053$	0.371	0.711
Grazing	0.11	$-0.015 \pm 0.069$	0.219	0.827
Soil Nitrogen	0.06	$-0.003 \pm 0.023$	0.125	0.901
Burning*Grazing	0.06	$0.015 \pm 0.074$	0.201	0.841
b) Non- <i>Calluna vulgaris</i> germinah	le seed abund	lance (negative binor	nial)	
Altitude	1.00	$-0.547 \pm 0.131$	4.158	< 0.001
Burning	1.00	$-0.523 \pm 0.196$	2.653	0.008
nH	0.94	$0.323 \pm 0.123$ $0.217 \pm 0.123$	1 767	0.077
Slope	0.77	0.217 = 0.123 $0.250 \pm 0.223$	1 1 1 8	0.264
Heat load	0.76	$-0.142 \pm 0.1223$	1 166	0.243
Julian date	0.70	$0.112 \pm 0.122$ $0.070 \pm 0.123$	0.571	0.568
Burning*Slope	0.29	$-0.081 \pm 0.125$	0.166	0.500
Soil phosphorus	0.18	$0.001 \pm 0.100$ $0.017 \pm 0.061$	0.100	0.022
Soil pitrogen	0.10	$0.017 \pm 0.001$	0.274	0.818
Grazing	0.12	$-0.002 \pm 0.0017$	0.230	0.815
Orazing	0.12	$-0.009 \pm 0.047$	0.190	0.045
c) Germinable seed-bank species 1	richness (nega	tive binomial)		
Burning	1.00	$-0.163 \pm 0.080$	2.036	0.042
Slope	1.00	$0.199 \pm 0.078$	2.535	0.011
Burning*Slope	0.91	$-0.127 \pm 0.081$	1.568	0.117
Heat load	0.86	$-0.060 \pm 0.042$	1.406	0.159
Habitat – Bog/Dry Heath	0.71	$-0.196 \pm 0.161$	1.217	0.224
Habitat – Bog/Wet Heath	0.71	$-0.186 \pm 0.152$	1.219	0.223
Habitat – Dry Heath/Wet Heath	0.71	$0.011 \pm 0.104$	0.104	0.917
Altitude	0.65	$-0.066 \pm 0.067$	0.988	0.323
Julian Date	0.39	$0.028 \pm 0.045$	0.616	0.538
Soil nitrogen	0.29	$-0.016 \pm 0.035$	0.457	0.648
Soil phosphorus	0.29	$0.019 \pm 0.039$	0.481	0.631
Soil pH	0.11	0.019 = 0.029 0.004 + 0.019	0 234	0.815
Grazing	0.06	$-0.001 \pm 0.011$	0.112	0.911
d) Jaccard Similarity of germinab	le seed-banks	s and vegetation (Ga	ussian)	
Habitat – Bog/Dry Heath	1.00	$-0.003 \pm 0.038$	0.077	0.938
Habitat – Bog/Wet Heath	1.00	$0.114 \pm 0.037$	3.035	0.002
Habitat – Dry Heath/Wet Heath	1.00	$0.117 \pm 0.038$	3.097	0.002
Julian Date	0.91	$-0.025 \pm 0.014$	1.699	0.089
Burning	0.90	$0.002 \pm 0.021$	0.100	0.921
Slope	0.90	$0.054 \pm 0.027$	1.987	0.047
Burning*Slope	0.90	$-0.059 \pm 0.029$	2.014	0.044
Soil pH	0.89	$-0.023 \pm 0.015$	0.015	0.113
Altitude	0.44	$-0.010 \pm 0.015$	0.692	0.489
Soil Phosphorus	0.27	$-0.004 \pm 0.009$	0.448	0.654

**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.

<b>Model</b> Explanatory variables	DF	Explained variance (%)	Pseudo-F	Р
<b>a) Germinable seed-bank</b> (Const 12.1%, residual df = 111, pseud	rained varian $o-F = 3.057$ ,	ce = 10.6 %, Conditi p = 0.001)	onal variance (S	Site) =
Soil pH	1	5.1	7.350	0.005
Soil phosphorus	1	1.9	2.723	0.010
Burning	1	1.4	2.004	0.010
Habitat	2	2.1	1.510	0.060
<b>b) Vegetation cover</b> (Constrained residual df = $109$ , pseudo- $F = 3$	variance = 1 .485, $p = 0.0$	6.2 %, Conditional v 05)	ariance (Site) =	11.3%,
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 phosphorus	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. 1 Locations of field sites.



**Fig. 2** Mean seed abundance per m<sup>2</sup> 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.



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.

#### Supporting information for the article

Kelly, R., Boston, E.M., Montgomery, W.I.M. & Reid.N. 2016. The role of the seed-bank in the recovery of temperate heath and blanket bog following wildfires. Applied Vegetation Science.

**Table S1.** Details of study site locations, characteristics and management. Habitats were classified into into classes using the JNCC National Vegetation Classification system for UK habitats. Annex I habitats included were "blanket bog" (*n*=75), "Northern Atlantic wet heaths with *Erica tetralix*" (*n*=25) and "European dry heaths" (*n*=22). Data on area and dates of wildfires were supplied by the European Forest Fire Information System – EFFIS (http://effis.jrc.ec.europa.eu) of the European Commission Joint Research Centre and are derived from MODIS satellite data.

Site/Area of Special	No. of	Latitude	Longitude	Altitude	pН	EU Annex 1	Management	Total area of	Dates of
Interest (ASSI's)	quadrats	(WGS 1984)	(WGS 1984)	range (m)	range	Habitats		wildfire (km <sup>2</sup> )	fires
Cuilcagh	18	54.2354	-7.7498	198 - 396	3.9 - 5.8	Blanket bog, Dry Heath, Wet Heath	Low intensity cattle and sheep grazing	1.4	02/05/2011
Eastern Mournes	34	54.1655	-5.9620	202 - 554	4.0-4.8	Blanket bog, Dry Heath, Wet Heath	Low intensity sheep grazing/ recreational use (hill-walking)	9.9	10/04/2011 01/05/2011
Glennasheevar	11	54.4342	-7.9590	184 - 245	4.1 - 4.3	Blanket bog, Wet Heath	Low intensity sheep grazing	3.7	02/05/2011
Mullaghcarn	20	54.6783	-7.2176	218 - 505	3.9 - 4.2	Blanket bog, Dry Heath	Low intensity sheep grazing at 70% of site	12.0	23/04/2011 02/05/2011
Slieve Beagh	19	54.3411	-7.1926	241 - 352	3.9 - 4.2	Blanket bog	Low intensity sheep grazing at 66% of site	23.7	01/05/2011
Slieveanorra	20	55.1072	-6.2510	232 - 345	3.9 - 4.2	Blanket bog	Low intensity cattle grazing at 33% of site	1.1	22/04/2011

#### Supporting information to the paper

Kelly, R., Boston, E.M., Montgomery, W.I.M. & Reid.N. 2016. The role of the seed-bank in the recovery of temperate heath and blanket bog following wildfires. *Applied Vegetation Science*.

**Table S2.** Relative frequency of species in vegetation and germinable seed-bank, showing percentage of quadrats in which species were detected. Species are ranked in order of frequency in the vegetation. Species recorded in 0% of quadrats are given as "not detected" to indicate that they may be present in low numbers but undetected.

Species	Percentage of quadrats (%)				
	Vegetation	Germinable			
		seed-bank			
Calluna vulgaris	94.3	97.5			
Erica tetralix	61.5	62.3			
Eriophorum vaginatum	57.4	4.9			
Trichophorum germanicum	43.4	Not detected			
Eriophorum angustifolium	41.0	0.8			
Potentilla erecta	40.2	15.6			
Molinia caerulea	39.3	2.5			
Vaccinium myrtillus	39.3	Not detected			
Erica cinerea	28.7	34.4			
Narthecium ossifragum	21.3	Not detected			
Deschampsia flexuosa	18.0	9.8			
Carex pilulifera	16.4	5.7			
Polygala serpyllifolia	13.9	Not detected			
Agrostis canina	13.1	13.1			
Nardus stricta	11.5	9.0			
Empetrum nigrum	10.7	0.8			
Galium saxatile	10.7	3.3			
Agrostis capillaris	8.2	1.6			
Carex panicea	8.2	1.6			
Luzula multiflora	6.6	Not detected			
Carex binervis	5.7	15.6			
Ulex gallii	5.7	Not detected			
Carex echinata	4.9	7.4			
Drosera rotundifolia	4.1	0.8			
Juncus squarrosus	3.3	4.9			
Juncus effusus	3.3	23.0			
Carex viridula	2.5	3.3			
Carex nigra	2.5	Not detected			
Juncus acutiflorus	1.6	1.6			
Danthonia decumbens	1.6	Not detected			
Festuca.vivipara	1.6	Not detected			
Holcus lanatus	1.6	Not detected			
Holcus mollis	1.6	Not detected			
Myrica gale	1.6	Not detected			
Epilobium palustre	0.8	3.3			
Juncus bulbosus	0.8	23.0			
Anthoxanthum odoratum	0.8	Not detected			
Betula pubescens	0.8	Not detected			
Carex rostrata	0.8	Not detected			
Cirsium dissectum	0.8	Not detected			
Drosera intermedia	0.8	Not detected			
Juncus conglomeratus	0.8	Not detected			
Listera cordata	0.8	Not detected			
Oxalis acetosella	0.8	Not detected			
Salix repens	0.8	Not detected			
Schoenus nigricans	0.8	Not detected			
Sorbus aucuparia	0.8	Not detected			
Rumex acetosella	0.8	Not detected			
Trifolium repens	0.8	Not detected			
Vaccinium oxycoccos	0.8	Not detected			
Viola riviana	0.8	Not detected			
Sagina procumbens	Not detected	0.8			
Juncus bufonius	Not detected	1.6			