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Increased fire severity alters initial vegetation regeneration across *Calluna*-dominated ecosystems

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Abstract

Calluna vulgaris-dominated habitats are valued for ecosystem services such as carbon storage and for their conservation importance. Climate and environmental change are altering their fire regimes. In particular, more frequent summer droughts will result in higher severity wildfires. This could alter the plant community composition of *Calluna* habitats and thereby influence ecosystem function. To study the effect of fire severity on community composition we used rain-out shelters to simulate drought prior to experimental burns at two *Calluna*-dominated sites, a raised bog and a heathland. We analysed species abundance in plots surveyed ca. 16 months after fire in relation to burn severity (indicated by fire-induced soil heating). We found that fire severity was an important control on community composition at both sites. Higher fire severity increased the abundance of ericoids, graminoids and acrocarpous mosses, and decreased the abundance of pleurocarpous mosses compared to lower severity fires. At the raised bog, the keystone species *Sphagnum capillifolium* and *Eriophorum vaginatum* showed no difference in regeneration with fire severity. Species and plant functional type beta-diversity increased following fire, and was similar in higher compared to lower severity burns. Our results further our understanding of the response of *Calluna*-dominated habitats to projected changes in fire

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regimes, and can assist land managers using prescribed fires in selecting burning conditions to achieve management objectives.

1. Introduction

European habitats dominated by the ericaceous shrub *Calluna vulgaris* L. Hull (hereafter *Calluna*), including heathlands and peat bogs, are of conservation and cultural value (European Commission, 1992; Thompson et al., 1995; Fagúndez, 2013). These globally-rare habitats are abundant in the British Isles, where anthropogenic influences, from pre-history to present (forest clearance, managed burning, livestock grazing) have played a significant role in their development, ecological structure and function (Dodgshon and Olsson, 2006). In young *Calluna* stands vigorous resprouting and germination can occur after low to moderately severe fires (Davies et al., 2010; Vandvik et al., 2014). Managed burning has traditionally been used in many regions to promote this new growth to support sheep grazing and high densities of game (mainly red grouse, *Lagopus lagopus scoticus* Latham, but also red deer, *Cervus elaphus* L.; Måren et al., 2010; Allen et al., 2016). More recently, there has been interest in prescribed burning as a land management tool for habitat conservation (Vandvik et al., 2005; Harris et al., 2011) and fire risk reduction (Fernandes et al., 2013).

Wildfires also occur in *Calluna*-dominated habitats (McMorrow, 2011; Davies and Legg, 2016). Whilst managed fires typically cover small areas (ca. 0.1–0.2 ha; Allen et al., 2016), have low fire severity and often leave ground fuels (the moss and litter layer) undisturbed (Grau-Andrés et al., 2017a), wildfires burn larger areas (e.g. 19–4,144 ha; Davies et al., 2016a) often at higher severities that result in greater ground fuel consumption and below-ground heating (Davies et al., 2013, 2016a). Regeneration of ericoids is hindered when fire-induced ground heating is above a critical threshold for survival of plant tissues and

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seeds (Whittaker and Gimingham, 1962; Granström and Schimmel, 1993). High severity wildfires can have a significant impact on the community composition of *Calluna* heathlands and sites can show delayed regeneration over extended periods. For instance, high severity wildfires after drought has been shown to impede *Calluna* regeneration and facilitate dominance of pioneer bryophytes in British blanket bogs (Maltby et al., 1990; Legg et al., 1992). Altered fire regimes associated with climatic and environmental change (Kasischke and Turetsky, 2006; Albertson et al., 2010; Bowman et al., 2011; Moritz et al., 2012; Pausas and Keeley, 2014; Ruffault et al., 2018), including higher severity wildfires because of projected drier summers (Dai, 2013; Cook et al., 2014), may therefore impact on post-fire trajectories and rates of plant community change (Wang and Kemball, 2005; Kettridge et al., 2015). In the UK, extreme wildfire activity and severity following the prolonged summer drought of 2018 has brought the need to better understand the effects of high severity fires on *Calluna*-dominated habitats into sharp focus (Anon, 2018).

Calluna-dominated habitats are widespread in the UK and plant community composition underpins their ecosystem function (Ward et al., 2009) and the provision of important ecosystem services such as cultural value, biodiversity (Thompson et al., 1995), carbon storage (Ostle et al., 2009) and water regulation (Xu et al., 2018). Consequently, there has been increasing interest in understanding peatlands' and heathlands' response to fire (Fagúndez, 2013; Harper et al., 2018). However, no studies to date have focused on the effect of fire severity on peatland and heathland community composition. Increased fire severity has the potential to alter ecosystem function through changes in dominant plant functional types (de Bello et al., 2010; Gray et al., 2013). Further, homogenisation of vegetation communities in *Calluna*-dominated habitats due to environmental and management changes, including alteration to their fire regime, can negatively impact their high conservation value (Ross et al., 2012; Velle et al., 2014) and possibly their resilience (Oliver et al., 2015).

In this study we aimed to investigate how variation in fire severity shapes differences in post-fire vegetation community composition in two distinct *Calluna*-

dominated habitats: a raised bog with deep, saturated peat and a dry heath with thin, organic soils. We achieved a range of fire severities by using rain-out shelters to create experimental drought and lower fuel moisture contents (Grau-Andrés et al., 2018a). We hypothesised that (i) relative to unburnt locations, higher severity fires further alter community composition compared to lower severity fires (Legg et al., 1992; Kettridge et al., 2015); (ii) fire effects on community composition are stronger at the heathland compared to the raised bog due to greater fire severity at the heathland (Grau-Andrés et al., 2018a); and (iii) higher fire severity has a homogenising effect on vegetation community composition, reducing species and functional type diversity (Burkle et al., 2015; Heydari et al., 2017).

2. Material and methods

2.1. Experimental design and measurements

The experiment was completed at two sites in Scotland (UK): Braehead Moss (elevation 270 m, latitude 55.740°N, longitude 3.658°W), a raised bog, and Glen Tanar (elevation 460 m, latitude 57.016°N, longitude 2.974°W), a dry heath. At both sites, mature *Calluna* (*sensu* Gimingham, 1989) formed a dense, continuous stand (mean height = 0.48 m, range = 0.40–0.59 m) above a bryophyte layer dominated by pleurocarpous mosses, predominantly *Hypnum jutlandicum* Holmen & Warncke and *Pleurozium schreberi* (Brid.) Mitt. *Sphagnum capillifolium* (Ehrh.) Hedw. hummocks were frequent at the raised bog, where mean thickness of the moss layer was 10.9 cm (range = 2.6–20.5 cm), compared to 3.5 cm (range = 2.0–5.5 cm) at the heathland. The moss layer covered saturated, deep (up to > 9 m) peat at the raised bog and well-drained peaty podzols with a comparatively thin (ca. 9 cm) organic layer at the heathland.

The experimental design, including the construction and deployment of the rain-out shelters and the completion of the experimental burns, is described in full in Grau-Andrés et al. (2018a). Briefly, nine fires, each covering ca. 30 × 25 m and burnt as head fires, were carried out at the raised bog and ten at the

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heathland between October 2013 and November 2014. In each fire we induced higher fire severity in two 2×2 m plots by lowering pre-fire fuel moisture content using rain-out shelters (Yahdjian and Sala, 2002) relative to two plots burnt under ambient conditions. These plots are referred to as high fire severity and low fire severity plots respectively. Consumption of ground fuels and soil surface heating are indicators of fire severity (see Keeley, 2009) but due to the strong correlation between both measures, we selected the more sensitive fire severity indicator total heat at the soil surface (below the moss layer). Total heat is a measure that integrates both the magnitude and the duration of the heating, and was calculated as the area under the temperature-time curve in each plot from the start of the fire to 50 min after. Soil temperatures were recorded using a single K-type thermocouple per plot, placed centrally. Pre-fire *Calluna* canopy height, a proxy for stand age (Kayll and Gimingham, 1965), was measured five times per plot within the fire area.

Results of the effect of the drought treatment on pre-fire moisture content of different fuel layers and subsequent increase in combustion of ground fuels and fire-induced soil heating are provided in full in Grau-Andrés et al. (2018a). In brief, the drought treatment significantly lowered the mean pre-fire moisture content of the moss and litter layer from 365 to 112 % (dry base) at the raised bog and from 271 to 117 % at the heathland. This led to a significant increase in mean consumption depth of the moss and litter layer in drought-treated plots compared to plots burnt under ambient conditions, both at the raised bog (1.4 vs 0.1 cm) and heathland (2.3 vs 0.7 cm). Fire-induced surface soil heating measured as total heat was significantly greater at drought-treated compared to untreated plots, both at the raised bog (mean 146 vs 40 °C-min) and heathland (mean 1702 vs 307 °C-min). Fore reference, these correspond to mean maximum surface soil temperatures of 15 vs 10 °C at the raised bog and 189 vs 31 °C at the heathland, respectively.

We surveyed regenerating vegetation in October 2015 at the raised bog, when time since burning across the different fires ranged from 307 to 698 days (mean = 509 days), and in April 2015 at the heathland (233–590 days post-burn,
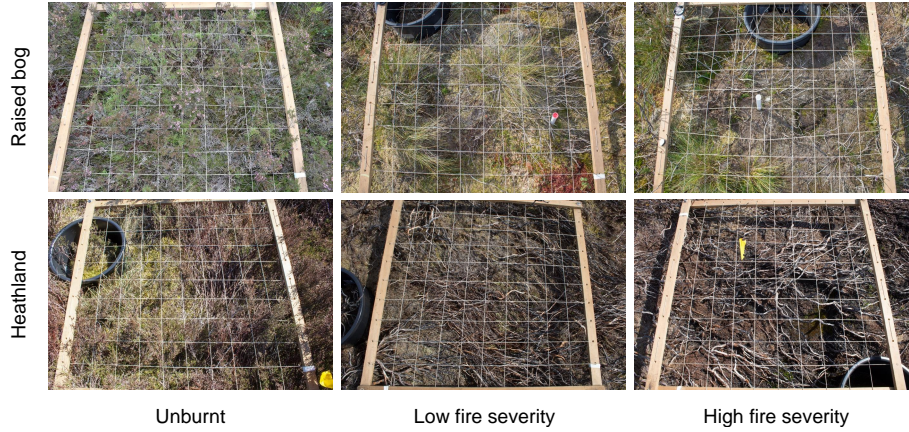
Figure 1: Examples of surveyed plots in each site: unburnt (left), burnt under ambient moisture conditions (centre) and burnt after simulated drought (right).

mean = 453 days). At the same time we also surveyed two adjacent unburnt plots per fire. Surveying was completed using a 1×1 m quadrat with 10×10 cm cells placed centrally in each plot (Figure 1). Presence/absence of species was recorded in each cell, and their cover estimated for the whole quadrat. For ericoids, we recorded the mechanisms of regeneration (seedling or resprout). We also recorded substrate cover information: litter, including dead bryophytes after burning, and duff / bare ground.

We identified most plants to species level following Stace (2010) for vascular plants and Atherton et al. (2010) and Smith (2004) for bryophytes. Exceptions were lichens (*Cladonia* spp.), which were treated as a single group, an unidentified vascular plant seedling, and three indeterminate species in the genera *Agrostis*, *Luzula* and *Brachythecium*. A full list of species is provided in Appendix A in the Supplementary Material. Similar patterns in species composition emerged from analysing the frequency and cover datasets. We focus here on the frequency data as it better reflects the relative balance between species irrespective of burn status (burnt vs unburnt) where there are large differences in absolute cover. Our data is available online (Grau-Andrés et al., 2018b).

All analyses and plotting were performed in R 3.3.3 (R Core Team, 2017).
Functions in the package *vegan* (Oksanen et al., 2017) were used for multivariate
analyses unless otherwise stated. We calculated species frequency at the plot
level by summing occurrence of each plant species in the 10×10 cm cells of the
quadrat, as % occupancy of grid cells. For examining plant functional types,
we grouped species into broad functional groups (ericaceous shrubs, graminoids,
forbs, pleurocarpous, acrocarpous and *Sphagnum* mosses, *Cladonia* spp., litter
and duff) before calculating abundance in each plot. We used non-metrical multi-
dimensional scaling (NMDS; Kruskal, 1964) on the raw species abundance data to
visualise changes in community composition. We considered rare species, defined
as those present in < 3 plots (5 %) at each site, to be unable to provide meaningful
information about their ecological preferences and they were therefore excluded
from the analysis (McCune et al., 2002). Scree plots of stress against number of
dimensions indicated 3-D NMDS solutions were the best compromise between
ordination accuracy and ease of interpretation. Permutational Multivariate
Analysis of Variance (PERMANOVA; function "adonis") was used to test differ-
ences in community composition between severity treatments and sites. Species
and functional type beta-diversity were estimated by calculating multivariate
homogeneity of group dispersions (a measure of beta-diversity; Anderson et al.,
2006) using the function "betadisper" (Velle et al., 2014). PERMANOVA and
beta-diversity analyses were performed on a distance matrix (function "vegdist")
computed using the Bray-Curtis dissimilarity index (Bray and Curtis, 1957),
commonly used for species abundance data (Anderson et al., 2011). For multiple
comparisons among treatments we used function "pairwise.perm.manova" in
package *RVAideMemoire* (Herv, 2018) for PERMANOVA and "TukeyHSD" for
beta-diversity.

To examine differences in community composition in burnt plots relative to
unburnt, the multivariate analyses included all treatments (unburnt as well as
low and high fire severity plots). To test the effect of environmental covariates
total heat, time since fire and pre-fire *Calluna* height (proxy for stand age,

important control on vegetative regeneration capacity; Kayll and Gimingham, 1965), we also analysed differences in community composition using abundance data that included only burnt plots. In both sets of analyses, we tested whether the effect of fire severity on community composition depended on site by fitting a PERMANOVA with a site $\times$ treatment interaction. We then tested differences in composition and beta-diversity between treatments within each site using separate analyses for each site. In the analyses including only burnt plots we fitted the environmental covariates onto the unconstrained ordination and tested their significance (function "envfit"). To account for the spatial structure of the data (multiple observations in a single fire), significance tests, both for "envfit" and PERMANOVA, were performed using restricted permutations (n = 999) within the grouping variable "fire" (Lepš and Šmilauer, 2003).

3. Results

The NMDS showed a gradient of composition associated with disturbance severity, with unburnt plots at one end of the gradient, high fire severity plots at the other, and low fire severity plots at an intermediate position (Figure 2). PERMANOVA indicated that differences in community composition between treatments within each site were all statistically significant, both for frequency of species (pseudo-$F_{2,51} = 20.7$, $R^2 = 0.45$, $p < 0.001$ at the bog; pseudo-$F_{2,57} = 26.9$, $R^2 = 0.49$, $p < 0.001$ at the heathland) and plant functional type (pseudo-$F_{2,51} = 28.5$, $R^2 = 0.53$, $p < 0.001$ at the bog; pseudo-$F_{2,57} = 36.2$, $R^2 = 0.56$, $p < 0.001$ at the heathland; see full PERMANOVA results in Appendix B.1). Higher abundance of mature ericoids, pleurocarps and liverworts was associated with unburnt plots; *Sphagnum*, graminoids and acrocarps were located at an intermediate position along the severity gradient (sequentially associated with higher fire severity). Forbs were most abundant at the highest severities.

Calluna was the dominant species prior to burning: mean cover in unburnt plots was 63.5±11.9 % at the raised bog and 77.3±17.6 % at the heathland (species frequency and cover in each treatment are provided in Appendix A).
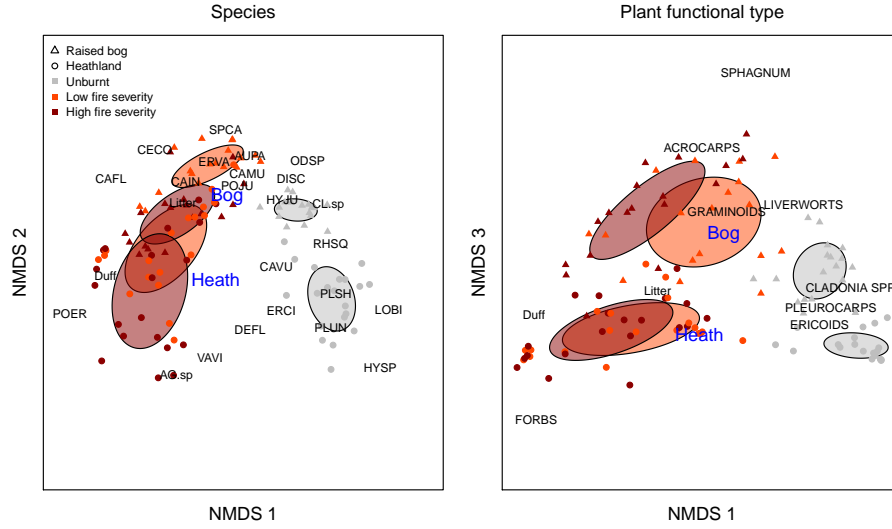
Figure 2: NMDS of frequency of plots (coloured points) and most abundant species (stress = 0.08, left) and all plant functional types (stress = 0.06, right) showing variation related to disturbance severity (horizontal axes) and site (vertical axes). Ellipses indicate group dispersion as standard deviations of treatment centroids in each site. "Bog" and "Heath" are site centroids. Additional NMDS ordinations including third axes and all species are provided in Appendix C. Codes: AG.sp = *Agrostis* spp., AUPA = *Aulacomnium palustre*, CAFL = *Campylopus flexuosus*, CAIN = *Campylopus introflexus*, CAMU = *Calypogeia muelleriana*, CAVU = *Calluna vulgaris*, CECO = *Cephalozia connivens*, CL.sp = *Cladonia* spp., DEFL = *Deschampsia flexuosa*, DISC = *Dicranum scoparium*, Duff = Duff, ERCI = *Erica cinerea*, ERVA = *Eriophorum vaginatum*, HYJU = *Hypnum jutlandicum*, HYSP = *Hylocomium splendens*, Litter = Litter, LOBI = *Lophocolea bidentata*, ODSP = *Odontoschisma sphagni*, PLSH = *Pleurozium schreberi*, PLUN = *Plagiothecium undulatum*, POER = *Potentilla erecta*, POJU = *Polytrichum juniperinum*, RHSQ = *Rhytidiadelphus squarrosus*, SPCA = *Sphagnum capillifolium*, VAVI = *Vaccinium vitis-idaea*.

There was evidence of abundant regeneration following fire with the frequency of seedlings and resprouts ranging 18.7–34.9 %. Regeneration of the dominant ericoids *Calluna* and *Erica cinerea* L. was predominantly from resprouts at the raised bog (61 % of regenerating *Calluna* and all *E. cinerea*), and from seed at the heathland (ca. 100 % for both species) (Appendix D). Graminoids appeared to be more abundant in burnt plots, especially at the heathland where abundance of *Agrostis* spp. was 5.4±10.3 % in unburnt and 11.8±21.1 % in burnt plots. Burning decreased the abundance of pleurocarpous mosses, e.g. frequency of *H. jutlandicum* in unburnt compared to burnt plots was 90.5±10.0 % vs 43.3±28.2 % at the raised bog and 41.0±26.3 % vs 15.7±22.6 % at the heathland. Conversely, frequency of acrocarpous mosses tended to increase with fire, e.g. at the heathland *Polytrichum juniperinum* Hewd. was 1.1±4.9 % in unburnt plots and 4.2±8.7 % in burnt plots.

Excluding unburnt plots from analysis allowed us to test the effect of the environmental covariates fire-induced soil heating (as total heat), time since fire and pre-fire *Calluna* height (proxy for stand age) on the community composition of burnt plots. Only total heat was significantly correlated with the NMDS ($R^2 = 0.32$, $p < 0.01$ at the raised bog; $R^2 = 0.37$, $p < 0.001$ at the heathland) (Figure 3). Increased fire severity was generally associated with higher abundance of ericoids, graminoids and acrocarpous mosses, while pleurocarpous mosses were more abundant at low fire severities. However, there were some differences in species response between the sites. For example, higher abundance of *E. cinerea* was associated with lower fire severity plots at the raised bog and with high severity plots at the heathland. At the raised bog, the dominant graminoid *E. vaginatum* occupied an intermediate position along the fire severity gradient, indicating low sensitivity to fire severity; at the heathland, in contrast, *Agrostis* spp. and *D. flexuosa* were more frequent in higher fire severity plots. At both sites, high frequency of pleurocarps such as *H. jutlandicum* and *P. schreberi* was associated with low fire severity, while acrocarps such as *Campylopus introflexus* (Hedw.) Brid. tended to show a strong positive response to higher fire severity. *S. capillifolium* at the raised bog seemed insensitive to fire severity as indicated by
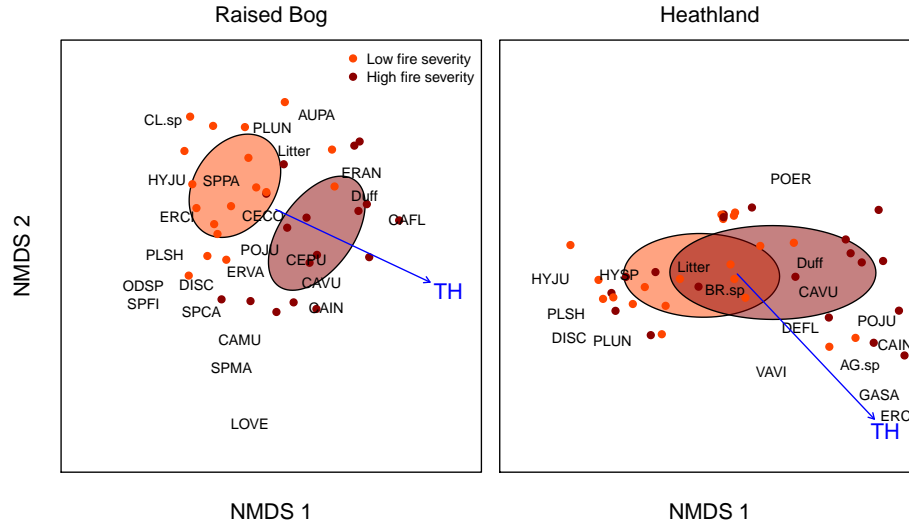
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Figure 3: NMDS of burnt plots at the raised bog (stress = 0.09) and the heahtland (stress = 0.05), showing most abundant species. Coloured dots are low and high fire severity plots; ellipses indicate standard deviation. Arrow point to most rapid change in the covariate total heat ("TH"). Species codes: BR.sp = *Brachythecium* spp., GASA = *Galium saxatile*, CEPU = *Ceratodon purpureus*, SPFI = *Sphagnum fimbriatum*, SPMA = *Sphagnum magellanicum*, SPPA = *Sphagnum papillosum*, ERAN = *Eriophorum angustifolium*, LOVE = *Lophozia ventricosa*; rest as in Figure 2. See Appendix C for supplementary NMDS including axes 3 and all species.

its intermediate location along the fire severity gradient. PERMANOVA showed that species community composition was significantly different in low compared to high severity plots, both at the raised bog (pseudo-$F_{1,34}$ = 8.8, R^2 = 0.21, p < 0.001) and the heathland (pseudo-$F_{1,38}$ = 4.3, R^2 = 0.10, p < 0.001; see details in Appendix B.2). When analysing the data grouped by plant functional type, community composition was also significantly different between fire severity treatments at both sites (pseudo-$F_{1,34}$ = 11.1, R^2 = 0.25, p < 0.001 at the raised bog; pseudo-$F_{1,38}$ = 5.2, R^2 = 0.12, p < 0.001 at the heathland).

We found some evidence that the effect of burning on community composition was stronger at the heathland than at the raised bog, as indicated by the significant interaction between site and treatment in the PERMANOVA of

species data including both unburnt and burnt plots (pseudo-$F_{2,113}$ = 1.4, p = 0.03). This is illustrated by the larger distance between unburnt and burnt plots at the heathland compared to the raised bog in the NMDS (Figure 2). Conversely, PERMANOVA of data including only burnt plots showed non-significant interactions between site and treatment, both for species (pseudo-$F_{1,72}$ = 0.9, p = 0.16) and plant functional type (pseudo-$F_{1,72}$ = 0.2, p = 0.61; see full model details in Appendix B; NMDS including both sites is provided in Appendix C).

Burning increased species beta-diversity at both sites, shown by the greater heterogeneity in community composition in burnt compared to unburnt plots (Table 1). At the raised bog, beta-diversity was significantly higher in both low and high fire severity plots compared to unburnt plots, while at the heathland only high fire severity plots had significantly higher beta-diversity than unburnt. Analysis of beta-diversity in burnt plots only revealed that higher severity burning increased heterogeneity of community composition at the heathland but not at the raised bog compared to lower severity fire. We found similar patterns when analysing the community data grouped by plant functional type, except for significantly greater beta-diversity in low fire severity vs unburnt plots at the heathland.

4. Discussion

Our results support the hypothesis that in *Calluna*-dominated habitats, relative to unburnt locations, higher severity fires have a greater effect on community composition than lower severity fires (Figure 2). Increased fire severity was generally associated with higher abundance of ericoids, graminoids and acrocarpous mosses. While burning altered species community composition more at the heathland than at the raised bog, presumably because of the higher fire severity recorded at the heathland (Grau-Andrés et al., 2018a), variation in fire severity had a similar effect size on altering community composition at both sites. Nevertheless, within-site variation in fire severity had a greater

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Table 1: Beta-diversity (as multivariate group dispersion) for the different treatments and sites. Within each combination of dataset (species or plant functional type; unburnt and burnt plots or burnt plots only) and site, different letters indicate statistical differences between treatments ($\alpha = 0.05$). Model and multiple comparison results are reported in full in Appendix E.

	Unburnt	Low fire severity	High fire severity
Species - Unburnt and burnt plots			
Raised Bog	0.16 a	0.24 b	0.24 b
Heathland	0.25 a	0.27 ab	0.34 b
Plant functional type - Unburnt and burnt plots			
Raised Bog	0.11 a	0.19 b	0.18 b
Heathland	0.09 a	0.24 b	0.31 b
Species - Burnt plots only			
Raised Bog		0.24 a	0.24 a
Heathland		0.27 a	0.34 b
Plant functional type - Burnt plots only			
Raised Bog		0.19 a	0.18 a
Heathland		0.24 a	0.31 b

effect on community composition at the raised bog, where the severity treatment explained 21 % of the variation in community composition compared to 10 % at the heathland (Figure 3). It is possible that increased removal of the deeper, more continuous pleurocarpous moss layer with higher severity burning at the raised bog resulted in a greater competitive advantage for vascular and acrocarpous moss species than at the heathland, where there may have been more opportunities to establish pre-burning in a drier and likely more disturbed habitat (fire, grazing). Previous studies have shown that pre-fire *Calluna* stand age determines regeneration capacity (Davies et al., 2010; Harris et al., 2011). However, stand age did not significantly affect community composition here, likely because our experiment considered a very limited range of stand age.

Calluna was most abundant at moderate to high fire severities as illustrated by its position along the total heat gradient in the NMDS (Figure 3). *Calluna* regeneration in mature plants is predominantly through resprouting from stem bases but this ability declines as plants age (Kayll and Gimingham, 1965) or when stem bases are damaged by prolonged heating during severe burns (Granström and Schimmel, 1993; Schimmel and Granström, 1996). In such situations regeneration from seed becomes dominant (Legg et al., 1992). More severe burns may actually promote *Calluna* seedling germination via cues including temperature pulses (Whittaker and Gimingham, 1962), chemicals present in smoke and ash (Måren et al., 2010), and through improved substrate conditions (Mallik et al., 1984; Davies et al., 2010). *Calluna* regenerated predominantly through resprouts at the raised bog but from seeds at the heathland. Higher fire severity at the latter site is a possible explanation for this trend. Maximum temperatures at the soil surface in high fire severity plots averaged 189 °C at the heathland (compared to only 15 °C at the raised bog; Grau-Andrés et al., 2018a) suggesting the potential for damage to plant tissues during the heathland burns and consequent impacts on regeneration (Schimmel and Granström, 1996).

Other ericoids had contrasting responses to fire severity at the raised bog compared to the heathland, suggesting ecological differences between species within this group were important in explaining post-fire response. For example, *E. cinerea* was associated with moderate-low fire severity at the raised bog but with high fire severity at the heathland. Given the much higher maximum temperatures in high fire severity plots at the heathland and that both *E. cinerea* and *Calluna* regenerated predominantly from seeds at this site, this suggests that *E. cinerea* seeds tolerate higher fire severity than *Calluna* seeds (e.g. due to the larger size of *E. cinerea* seeds; Tavşanoğlu and Pausas, 2018), and/or that they benefit further from germination cues from stronger fire effects (e.g. temperature pulses that break dormancy; Whittaker and Gimingham, 1962). Further research will need to investigate the relative contribution of the different response mechanisms of ericoids to variation in fire severity (thermal and chemical germination cues, seed mortality, resprouting capacity).

Higher fire severity increased the abundance of graminoids at the heathland but had a negligible effect on graminoids at the raised bog. *Agrostis* spp. and *D. flexuosa* are early colonists and their positive response to increased fire severity at the heathland was likely due to decreased competition from *Calluna*, as this responded negatively to high fire severity at the site. Coherent with this interpretation, Hobbs and Gimingham (1984), working on a similar habitat, reported high post-fire abundance of *D. flexuosa* when regeneration of *Calluna* was slow. However, the dominant graminoid at the raised bog, *E. vaginatum*, was equally abundant across the severity gradient. *E. vaginatum* protects its basal meristems within dense tussocks and can thus regenerate after moderately-severe fires (Innes, 2014).

Bryophytes showed a general tendency of higher abundance of acrocarps at increased fire severity and higher abundance of pleurocarps at low fire severity. Fire favours short-term acrocarp establishment, while pleurocarps tend to more slowly recover their pre-fire dominance (Hobbs and Gimingham, 1984; Vandvik et al., 2005; Harris et al., 2011). These contrasts are explained by the different life strategies of bryophytes: acrocarps are often fast-developing "colonists" with high spore production and dispersal while pleurocarps tend to invest on vegetative persistence and regeneration (During, 1979). High severity fires that damage vegetative structures and spores stored on the ground select for species with wide spore dispersal (Clement and Touffet, 1990; Esposito et al., 1999) therefore controlling community composition. *S. capillifolium*, the dominant *Sphagnum* at the raised bog, was weakly associated with the fire severity gradient at the raised bog, suggesting that the species has a degree of resilience to fire (Lee et al., 2013; Grau-Andrés et al., 2017b) likely due to its high water retention traits (Shetler et al., 2008) and its capacity to regenerate from deep below the moss surface (Taylor et al., 2017). Moreover, our findings add to the current knowledge base on the effects of burning on peat-forming species such as *Eriophorum* spp. and *Sphagnum* spp. (Lee et al., 2013; Davies et al., 2016b; Milligan et al., 2018).

Our results agree with previous studies in heathlands that have shown that species diversity declines with time since fire because of increased competitive

dominance of *Calluna* and pleurocarpous mosses (Vandvik et al., 2005; Harris et al., 2011; Welch, 2016), although empirical data on peatlands is limited. Disturbance by fire can reduce competition from *Calluna* and pleurocarpous mosses and thus promote establishment and growth of other species (Mallik and Gimingham, 1983; Hobbs and Gimingham, 1984; Davies et al., 2010; Harris et al., 2011; Velle et al., 2014). Burning increased short-term heterogeneity of community composition (beta-diversity) at both sites (Table 1). However, the effect of fire severity on beta-diversity do not support the hypothesis that higher severity fires homogenise community composition, e.g. through domination of fast-colonising species (Burkle et al., 2015; Kelly et al., 2016), although the fire severity we achieved in our experimental fires was much lower than that possible during wildfires (Maltby et al., 1990; Davies et al., 2013). Notably, species and plant functional type beta-diversity was actually greater in high compared to low severity plots at the heathland, while there was no difference between treatments at the raised bog. The increased severity range in high fire severity plots (e.g. total heat ranged 0–489 °C-min at the raised bog and 69–9968 °C-min at the heathland; Grau-Andrés et al., 2018a) compared to low fire severity plots (0–204 °C-min at the raised bog and 41–780 °C-min at the heathland) may have increased microhabitat heterogeneity and therefore species beta-diversity (Burkle et al., 2015).

Management implications

The empirical evidence we provide linking fire severity with community composition suggests that managers could manipulate fire severity by paying close attention to burning conditions, especially moisture and wind speed, to achieve different management objectives. At the raised bog, higher severity fires were associated with greater abundance of *Calluna* and acrocarpous mosses, including invasive *C. introflexus*, while low fire severity plots had greater abundance of pleurocarpous mosses. The keystone peatland species *Sphagnum* and *E. vaginatum* were unaffected by the range of fire severity achieved. Our results suggest that, if the objective of prescribed burning in bogs is to decrease cover of

competitive *Calluna* to facilitate expansion of peat-forming species, lower severity fires are preferable since they are conducive to slower *Calluna* regeneration and adequate recovery of *Sphagnum* and *E. vaginatum*. Further, considering that a higher abundance of vascular plants can promote carbon loss from peatlands (Walker et al., 2016; Dieleman et al., 2017), lower severity burning leading to slower recovery of *Calluna* may help preserve below-ground carbon stores.

At the heathland, higher fire severity was associated with increased abundance of ericoids *Calluna*, *E. cinerea* and *V. vitis-idaea* and graminoids *Agrostis* spp. and *D. flexuosa*, likely a consequence of improved substrate (higher bare ground cover due to greater consumption of pleurocarpous mosses and litter). Managers seeking fast *Calluna* recovery may therefore achieve better results when burning under drier conditions leading to greater consumption of ground fuels. However, soils should remain above a critical moisture threshold to prevent ignition of organic soil layers that greatly hamper heathland vegetation recovery, increase carbon loss and pose a substantial fire control risk (Maltby et al., 1990; Davies et al., 2013). At both sites, community composition was substantially different in low compared to high severity burning. This, together with the greater species beta-diversity after burning, suggests that managers seeking to increase habitat diversity at the landscape level should consider burning under different conditions to achieve a range of fire severities.

5. Conclusions

Higher severity fires further differentiated post-fire vegetation community composition from unburnt, compared to lower severity fires, in a *Calluna*-dominated raised bog and a heathland. Within-site variation in fire severity had a greater effect at the raised bog, but general trends in species response were similar at both sites. Within the fire severity range considered, higher severity fires did not homogenise community composition. Our results can inform management strategies in peatlands and heathlands dominated by dwarf shrubs. In the context of greater wildfire severity associated with projected changes in

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climate, our findings suggest an increase in the cover of vascular plants, which may have important implications for ecosystem functioning and services such as conservation and carbon storage. However, longer-term data on rates and extents of recovery to pre-fire conditions are required to confirm this. Taken together, our results suggest that greater fire severity than that achieved with our treatments, i.e. wildfires after extensive drought that ignite the organic soil, may be required to induce substantial shifts in vegetation community composition and decrease diversity (Maltby et al., 1990; Kettridge et al., 2015).

Acknowledgements

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Supplementary Material for "Increased fire severity alters initial vegetation regeneration across **Calluna**-*dominated ecosystems"*.

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Appendix A. Species frequency and cover per treatment

Table A.1: Species frequency and cover (standard deviation in parenthesis) per treatment in Braehead Moss.

Group	Species	Code	Unburnt % F	Unburnt % C	No-drought % F	No-drought % C	Drought % F	Drought % C
Ericoids	*Calluna vulgaris* (L.) Hull	CAVU	100.0 (0.0)	63.8 (11.9)	18.7 (13.0)	1.2 (0.9)	34.9 (16.2)	2.0 (1.5)
	Erica cinerea L.	ERCI	4.6 (5.8)	1.1 (1.1)	2.7 (4.6)	0.4 (0.6)	0.8 (1.8)	0.2 (0.4)
	Vaccinium oxycoccos L.	VAOX	1.0 (3.1)	0.2 (0.4)	0.7 (2.1)	0.1 (0.3)	0.5 (1.5)	0.1 (0.2)
Graminoids	*Eriophorum angustifolium* Honck.	ERAN	0.6 (1.2)	0.2 (0.4)	0.3 (1.2)	0.1 (0.3)	0.7 (1.5)	0.2 (0.4)
	Eriophorum vaginatum L.	ERVA	27.1 (12.4)	9.0 (5.8)	30.7 (19.6)	10.1 (8.1)	32.8 (18.3)	10.1 (8.4)
Pleurocarps	*Hypnum jutlandicum* Holmen & E. Warncke	HYJU	90.5 (10.0)	60.3 (20.7)	60.8 (27.0)	18.9 (16.9)	25.8 (16.2)	3.9 (4.1)
	Pleurozium schreberi (Brid.) Mitt.	PLSH	14.6 (19.2)	2.4 (3.9)	3.9 (8.0)	0.8 (1.7)	3.2 (6.0)	0.4 (0.8)
	Plagiothecium undulatum (Hedw.) Schimp.	PLUN	2.3 (3.3)	0.7 (0.7)	0.2 (0.4)	0.2 (0.4)	0.3 (0.7)	0.2 (0.4)
	Rhytidiadelphus squarrosus (Hedw.) Warnst.	RHSQ	0.1 (0.2)	0.1 (0.2)	0.6 (1.2)	0.2 (0.4)	0	0
Sphagnum	*Sphagnum capillifolium* (Ehrh.) Hedw.	SPCA	11.4 (12.9)	3.8 (5.1)	16.1 (19.5)	6.8 (10.0)	14.1 (16.9)	4.9 (8.2)
	Sphagnum fallax (H. Klinggr.) H. Klinggr.	SPFA	0	0	0.1 (0.2)	0.1 (0.2)	0.6 (1.8)	0.1 (0.3)
	Sphagnum fimbriatum Wilson	SPFI	0.9 (3.1)	0.3 (0.6)	1.9 (3.7)	0.3 (0.5)	0.5 (0.8)	0.3 (0.5)
	Sphagnum magellanicum Brid.	SPMA	1.3 (3.2)	0.3 (0.6)	1.7 (3.5)	0.4 (0.6)	2.1 (7.6)	0.9 (3.5)
	Sphagnum papillosum Lindb.	SPPA	0	0	1.7 (5.6)	0.5 (1.2)	1.4 (4.6)	0.2 (0.4)
Acrocarps	*Aulacomnium palustre* (Hedw.) Schwägr.	AUPA	6.2 (9.1)	0.7 (0.7)	5.4 (9.1)	0.5 (0.7)	2.4 (3.4)	0.6 (0.5)
	Campylopus flexuosus (Hedw.) Brid.	CAFL	0.4 (1.2)	0.2 (0.4)	4.5 (5.7)	0.8 (0.7)	11.2 (17.5)	1.2 (0.9)
	Campylopus introflexus (Hedw.) Brid.	CAIN	10.2 (9.4)	1.1 (0.9)	13.1 (11.1)	2.4 (2.6)	33.2 (24.0)	7.2 (8.1)
	Ceratodon purpureus (Hedw.) Brid.	CEPU	0	0	0.2 (0.5)	0.1 (0.2)	1.3 (1.4)	0.5 (0.5)
	Dicranum scoparium Hedw.	DISC	1.8 (2.4)	0.6 (0.5)	2.0 (4.9)	0.3 (0.5)	1.3 (2.1)	0.3 (0.5)
	Leucobryum glaucum (Hedw.) Ångstr.	LEGL	0.1 (0.3)	0.1 (0.3)	0	0	0.4 (1.2)	0.1 (0.3)
	Polytrichum juniperinum Hedw.	POJU	27.6 (23.4)	1.6 (1.1)	26.7 (22.0)	2.0 (2.0)	36.6 (24.0)	3.2 (3.0)
Liverworts	*Calypogeia muelleriana* (Schiffn.) Müll. Frib.	CAMU	0.8 (2.2)	0.3 (0.6)	0.5 (0.7)	0.4 (0.5)	0.8 (1.5)	0.3 (0.5)
	Cephalozia connivens (Dicks.) Lindb.	CECO	0.4 (1.2)	0.2 (0.4)	1.8 (1.8)	0.6 (0.5)	1.8 (2.6)	0.5 (0.5)
	Lophozia ventricosa (C.E.O. Jensen) H. Buch	LOVE	0.7 (1.8)	0.2 (0.4)	0.2 (0.7)	0.1 (0.2)	0.8 (1.8)	0.3 (0.5)
	Odontoschisma sphagni (Dicks.) Dumort.	ODSP	5.2 (7.4)	1.0 (1.1)	0.5 (1.5)	0.2 (0.4)	0.3 (0.8)	0.1 (0.3)
Other	*Cladonia* spp.	CL.sp	6.8 (9.6)	1.2 (1.1)	0.5 (1.0)	0.2 (0.4)	0.3 (1.0)	0.1 (0.2)
	Duff	Duff	7.6 (11.0)	3.0 (4.0)	20.4 (17.8)	10.9 (12.0)	59.3 (26.6)	36.8 (24.9)
	Litter	Litter	53.1 (18.4)	22.4 (15.7)	85.0 (13.3)	47.3 (20.1)	69.1 (18.1)	34.9 (19.6)
	Vascular seedling	Seedl.v	0.4 (0.9)	0.2 (0.4)	0.8 (1.5)	0.4 (0.5)	1.1 (1.4)	0.5 (0.5)

Table A.2: Species frequency and cover (standard deviation in parenthesis) per treatment in Glen Tanar.

Group	Species	Code	Unburnt		No-drought		Drought	
			% F	% C	% F	% C	% F	% C
Ericoids	*Calluna vulgaris* (L.) Hull	CAVU	100.0 (0.0)	77.3 (17.6)	19.9 (17.9)	0.8 (0.4)	22.4 (20.0)	0.8 (0.5)
	Erica cinerea L.	ERCI	16.3 (22.4)	1.3 (2.3)	6.9 (16.2)	0.4 (0.5)	8.0 (16.7)	0.4 (0.6)
	Erica tetralix L.	ERTE	1.3 (4.4)	0.2 (0.4)	0	0	0	0
	Vaccinium myrtillus W.D.J. Koch	VAMY	2.6 (5.6)	0.2 (0.4)	0.9 (4.2)	0.0 (0.2)	0.2 (0.7)	0.1 (0.4)
	Vaccinium vitis-idaea W.D.J. Koch	VAVI	3.2 (6.2)	0.3 (0.5)	1.4 (3.0)	0.2 (0.4)	6.0 (13.0)	0.6 (0.6)
Graminoids	*Agrostis* spp.	AG.sp	5.4 (10.3)	0.7 (1.1)	9.6 (19.8)	1.0 (1.4)	13.9 (22.7)	1.0 (1.3)
	Agrostis capillaris L.	AGCA	0.3 (1.2)	0.1 (0.3)	0	0	0.1 (0.7)	0.0 (0.2)
	Deschampsia flexuosa (L.) Trin.	DEFL	8.5 (12.8)	1.6 (2.5)	3.0 (5.3)	0.4 (0.7)	3.6 (6.4)	0.5 (1.0)
	Luzula spp.	LU.sp	0	0	0.1 (0.5)	0.1 (0.3)	0.1 (0.5)	0.1 (0.3)
Forbs	*Galium saxatile* L.	GASA	0	0	0.6 (2.3)	0.1 (0.3)	0.4 (1.0)	0.1 (0.3)
	Potentilla erecta(L.) Raeusch.	POER	0.3 (1.1)	0.1 (0.3)	2.8 (6.1)	0.2 (0.4)	2.1 (5.1)	0.2 (0.4)
Pleurocarps	*Brachythecium* spp.	BR.sp	0	0	0.6 (1.3)	0.1 (0.4)	0.5 (1.5)	0.1 (0.4)
	Hypnum jutlandicum Holmen & E. Warncke	HYJU	41.0 (26.3)	10.6 (15.3)	22.2 (26.1)	2.4 (6.1)	9.2 (16.7)	1.3 (2.5)
	Hylocomium splendens (Hedw.) Schimp.	HYSP	33.0 (33.5)	14.8 (22.9)	1.0 (1.3)	0.5 (0.5)	1.4 (3.6)	0.2 (0.4)
	Kindbergia praelonga (Hedw.) Ochyra	KIPR	12.4 (21.3)	9.6 (19.5)	0	0	0	0
	Pleurozium schreberi (Brid.) Mitt.	PLSH	57.8 (30.0)	33.2 (28.7)	12.3 (12.9)	1.2 (1.2)	10.6 (17.4)	0.8 (1.0)
	Plagiothecium undulatum (Hedw.) Schimp.	PLUN	17.0 (23.3)	2.0 (3.5)	7.2 (14.8)	0.7 (1.4)	0.7 (1.8)	0.2 (0.4)
	Rhytidiadelphus squarrosus (Hedw.) Warnst.	RHSQ	2.0 (3.2)	0.4 (0.5)	1.1 (3.9)	0.1 (0.3)	0.3 (1.3)	0.1 (0.3)
Acrocarps	*Campylopus introflexus* (Hedw.) Brid.	CAIN	0	0	1.5 (4.9)	0.1 (0.4)	2.0 (4.0)	0.4 (0.5)
	Dicranum scoparium Hedw.	DISC	1.2 (1.9)	0.5 (0.5)	0.3 (0.6)	0.2 (0.4)	0.2 (0.7)	0.1 (0.3)
	Polytrichum juniperinum Hedw.	POJU	1.1 (4.9)	0.0 (0.2)	2.2 (6.2)	0.2 (0.4)	6.2 (10.4)	0.6 (0.7)
Liverworts	*Lophocolea bidentata* (L.) Dumort.	LOBI	1.5 (2.2)	0.4 (0.5)	0.2 (0.5)	0.1 (0.4)	0.0 (0.2)	0.0 (0.2)
Other	*Cladonia* spp.	CL.sp	0.3 (0.9)	0.1 (0.4)	0	0	0	0
	Duff	Duff	0.6 (1.7)	0.1 (0.3)	49.6 (27.9)	32.0 (29.6)	71.0 (31.9)	59.8 (39.4)
	Litter	Litter	32.2 (25.6)	21.1 (27.5)	84.2 (14.5)	55.4 (26.1)	55.1 (36.4)	33.5 (32.2)
	Vascular seedling	Seedl.v	0	0	0.2 (0.8)	0.1 (0.3)	0.3 (0.8)	0.2 (0.4)

Appendix B. PERMANOVA of community composition based on frequency data

Appendix B.1. Burnt and unburnt plots

Appendix B.1.1. Species data

Table B.1: PERMANOVA testing the effect of the interaction between site (Breahead Moss and Glen Tanar) and treatment (unburnt, low fire severity and high fire severity plots) on species community composition.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
site	1	3.38	3.38	44.24	0.18	0.001
treatment	2	7.08	3.54	46.36	0.37	0.001
site:treatment	2	0.33	0.17	2.19	0.02	0.029
Residuals	108	8.25	0.08		0.43	
Total	113	19.04			1.00	

Table B.2: Results of the PERMANOVA testing the effect of treatment (unburnt, low fire severity and high fire severity plots) on species community composition at the raised bog site.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
treatment	2	2.24	1.12	20.74	0.45	0.001
Residuals	51	2.76	0.05		0.55	
Total	53	5.00			1.00	

Table B.3: Pairwise comparisons for PERMANOVA at the raised bog site (see Table B.2) to determine differences in species community composition between treatments.

	drought	nodrought
nodrought	0.001	
unburnt	0.001	0.001

Table B.4: PERMANOVA testing the effect of treatment (unburnt, low fire severity and high fire severity plots) on species community composition at the heathland site.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
treatment	2	5.17	2.59	26.85	0.49	0.001
Residuals	57	5.49	0.10		0.51	
Total	59	10.66			1.00	

Table B.5: Pairwise comparisons for PERMANOVA at the heathland site (see Table B.4) to determine differences in species community composition between treatments.

	drought	nodrought
nodrought	0.022	
unburnt	0.002	0.002

Appendix B.1.2. Plant functional type data

Table B.6: PERMANOVA testing the effect of the interaction between site (Breahead Moss and Glen Tanar) and treatment (unburnt, low fire severity and high fire severity plots) on community composition of plant functional types.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
site	1	1.75	1.75	35.38	0.13	0.001
treatment	2	6.44	3.22	65.33	0.47	0.001
site:treatment	2	0.06	0.03	0.59	0.00	0.590
Residuals	108	5.33	0.05		0.39	
Total	113	13.58			1.00	

Table B.7: PERMANOVA testing the effect of treatment (unburnt, low fire severity and high fire severity plots) on plant functional type community composition at the raised bog site.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
treatment	2	1.89	0.94	28.48	0.53	0.001
Residuals	51	1.69	0.03		0.47	
Total	53	3.57			1.00	

Table B.8: Pairwise comparisons for PERMANOVA at the heathland site (see Table B.7) to determine differences in plant functional type community composition between treatments.

	drought	nodrought
nodrought	0.001	
unburnt	0.001	0.001

Table B.9: PERMANOVA testing the effect of treatment (unburnt, low fire severity and high fire severity plots) on plant functional type community composition at the heathland site.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
treatment	2	4.62	2.31	36.17	0.56	0.001
Residuals	57	3.64	0.06		0.44	
Total	59	8.26			1.00	

Table B.10: Pairwise comparisons for PERMANOVA at the heathland site (see Table B.9) to determine differences in plant functional type community composition between treatments.

	drought	nodrought
nodrought	0.018	
unburnt	0.002	0.002

Table B.11: PERMANOVA testing the effect of the interaction between site (Breahead Moss and Glen Tanar) and treatment (low fire severity and high fire severity) on species community composition.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
site	1	2.29	2.29	25.83	0.24	0.001
treatment	1	0.97	0.97	10.95	0.10	0.001
site:treatment	1	0.08	0.08	0.87	0.01	0.156
Residuals	72	6.38	0.09		0.66	
Total	75	9.72			1.00	

Table B.12: PERMANOVA testing the effect of treatment (low vs high fire severity) on species community composition at the raised bog site.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
treatment	1	0.58	0.58	8.85	0.21	0.001
Residuals	34	2.24	0.07		0.79	
Total	35	2.83			1.00	

Table B.13: PERMANOVA testing the effect of treatment (low vs high fire severity) on species community composition at the heathland site.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
treatment	1	0.46	0.46	4.26	0.10	0.001
Residuals	38	4.14	0.11		0.90	
Total	39	4.60			1.00	

Appendix B.2.2. Plant functional type data

Table B.14: PERMANOVA testing the effect of the interaction between site (Breahead Moss and Glen Tanar) and treatment (low fire severity and high fire severity) on community composition of plant functional types.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
site	1	1.50	1.50	22.33	0.21	0.001
treatment	1	0.92	0.92	13.77	0.13	0.001
site:treatment	1	0.02	0.02	0.24	0.00	0.609
Residuals	72	4.83	0.07		0.66	
Total	75	7.26			1.00	

Table B.15: PERMANOVA testing the effect of treatment (low vs high fire severity) on plant functional type community composition at the raised bog site.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
treatment	1	0.47	0.47	11.21	0.25	0.001
Residuals	34	1.44	0.04		0.75	
Total	35	1.91			1.00	

Table B.16: PERMANOVA testing the effect of treatment (low vs high fire severity) on plant functional type community composition at the heathland site.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
treatment	1	0.46	0.46	5.21	0.12	0.001
Residuals	38	3.39	0.09		0.88	
Total	39	3.85			1.00	

Appendix C. Supplementary NMDS ordination based on frequency data

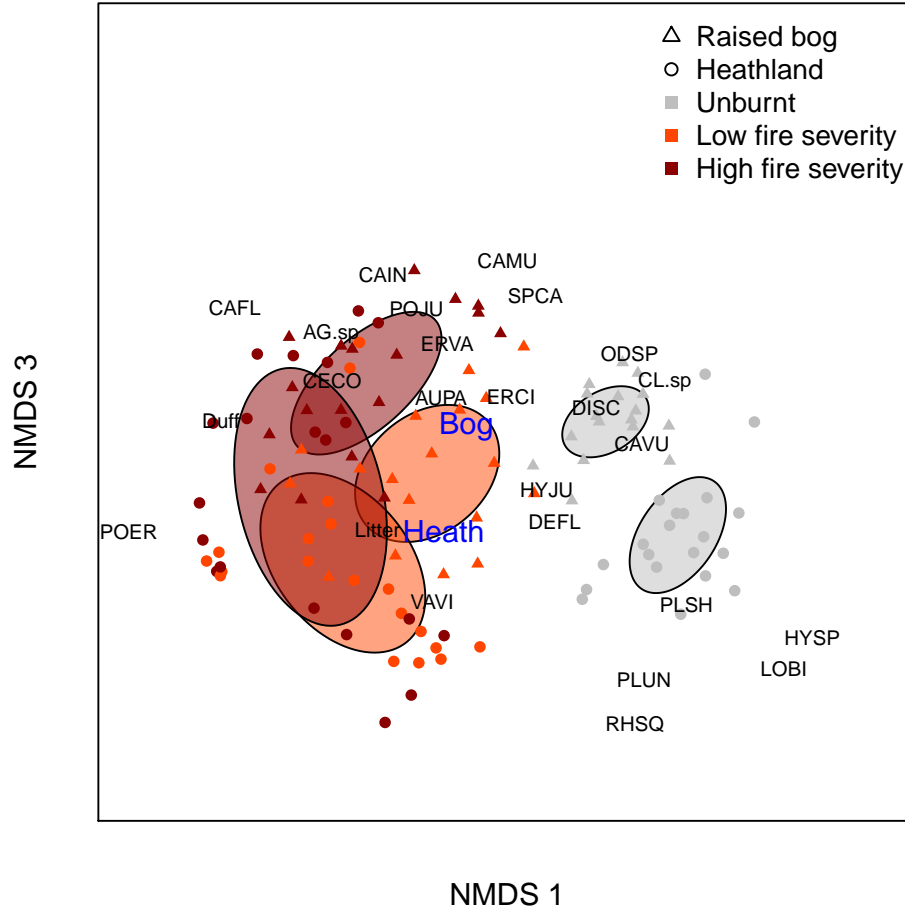*Appendix C.1. Burnt and unburnt plots*

Figure C.1: NMDS for species data complementing Figure 2 with axis 3. For an approximation of how much variation each axis explains, variance of plots along axes 1, 2 and 3 was 0.27, 0.16 and 0.11, respectively.
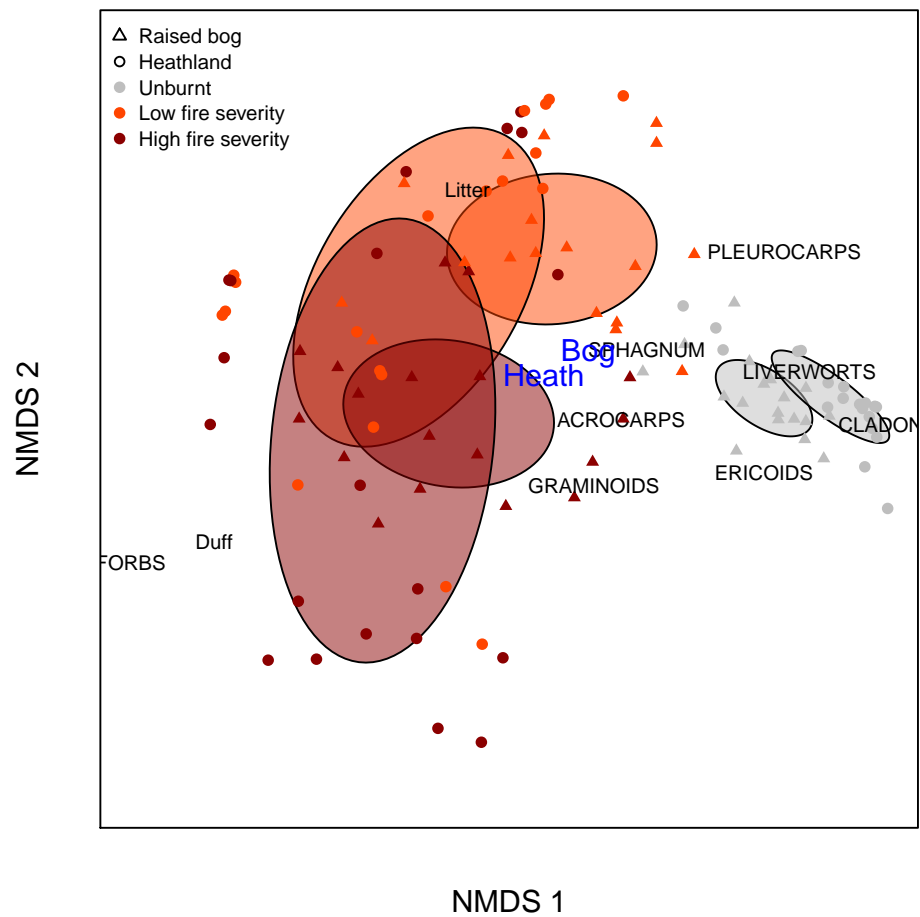
Figure C.2: NMDS for plant functional type data complementing Figure 2, showing axis 2. Variance of plots along axes 1, 2 and 3 was 0.25, 0.12 and 0.08 respectively.
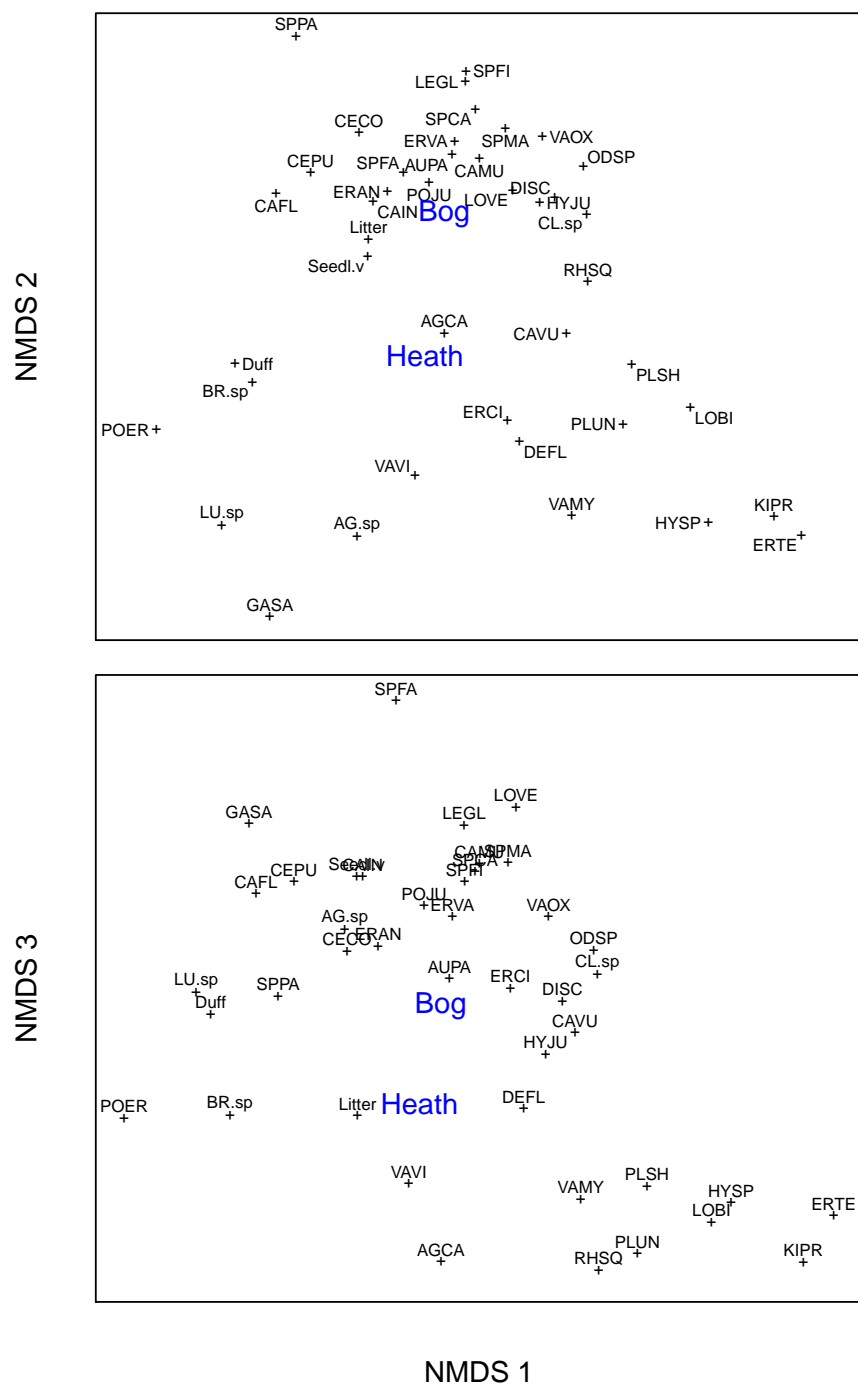
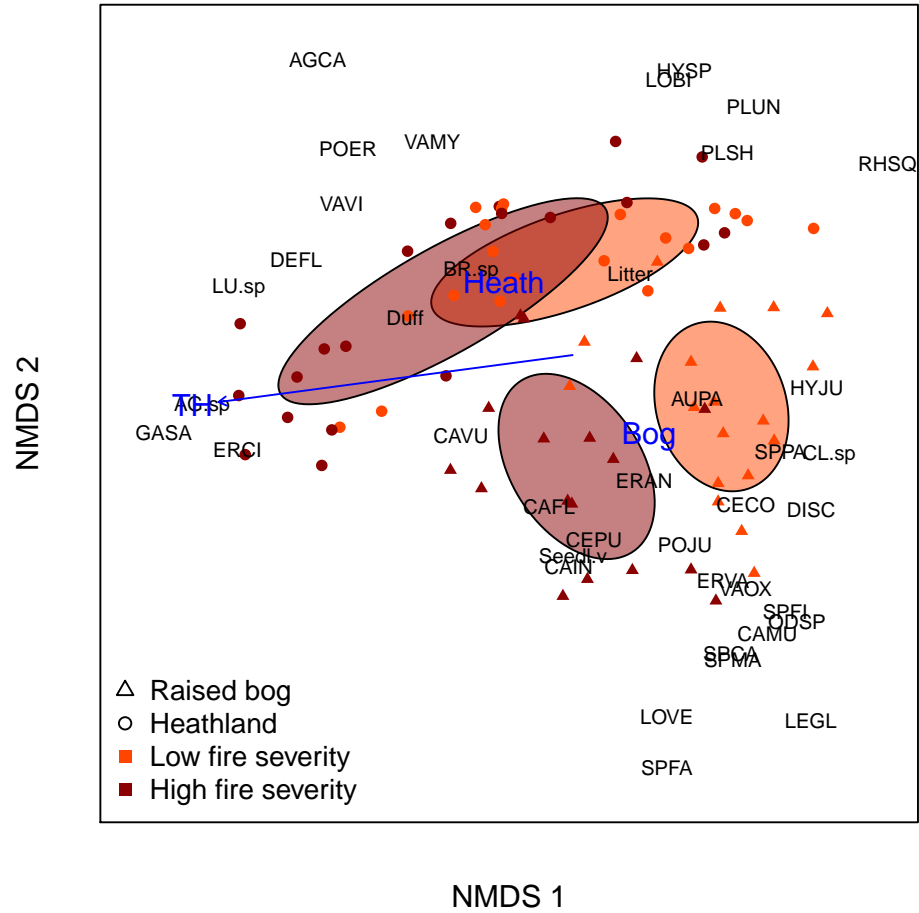Figure C.3: NMDS complementing Figure 2 with all species and the three axes.

Figure C.4: NMDS for species including both sites and all species. By analysing both sites together, comparison of the effect of fire severity across sites is possible, but differences in response of species at each site (Figure 3) are masked. Table B.11 complements this figure.
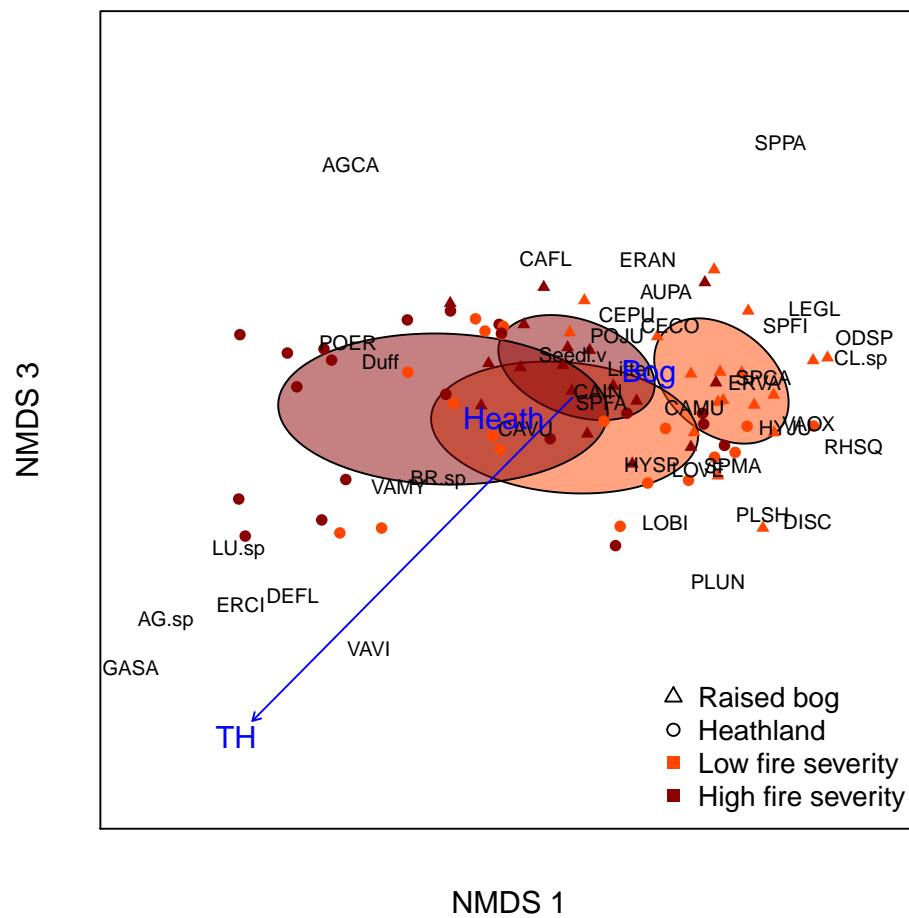
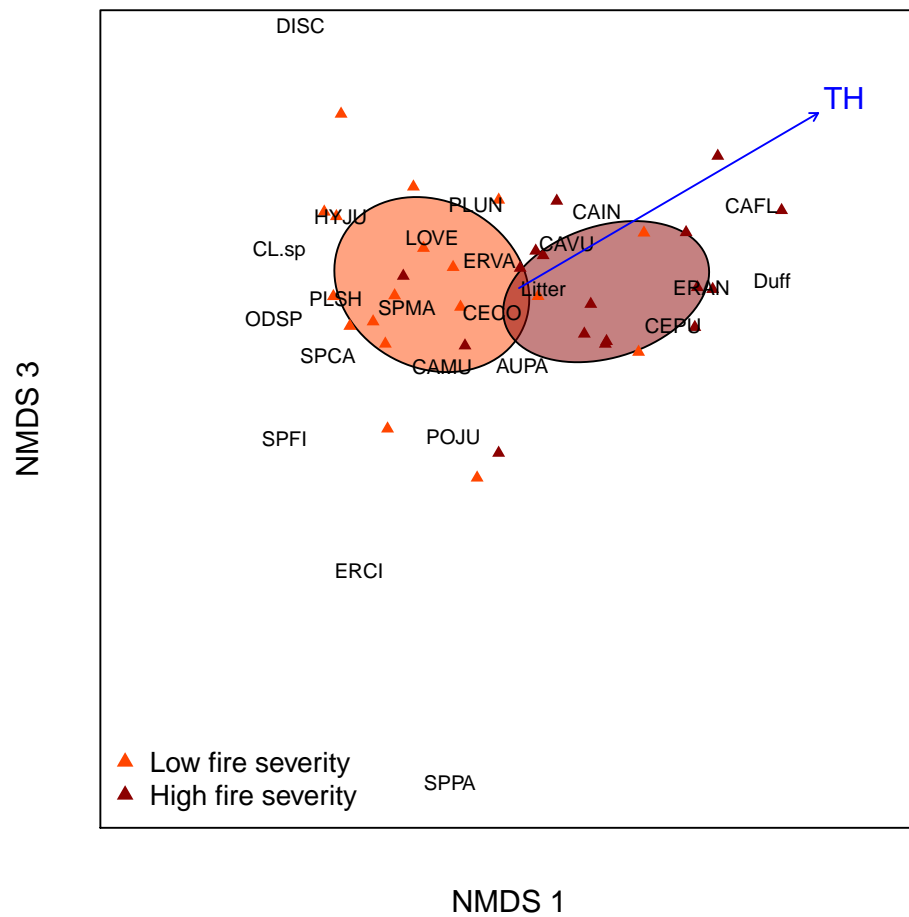Figure C.5: NMDS complementary to Figure C.4, showing axes 1 vs 3.

Figure C.6: NMDS for species data at the raised bog site complementing Figure 3, showing axes 1 vs 3. Variance of plots along NMDS axes 1, 2 and 3 was 0.10, 0.09 and 0.04 respectively.
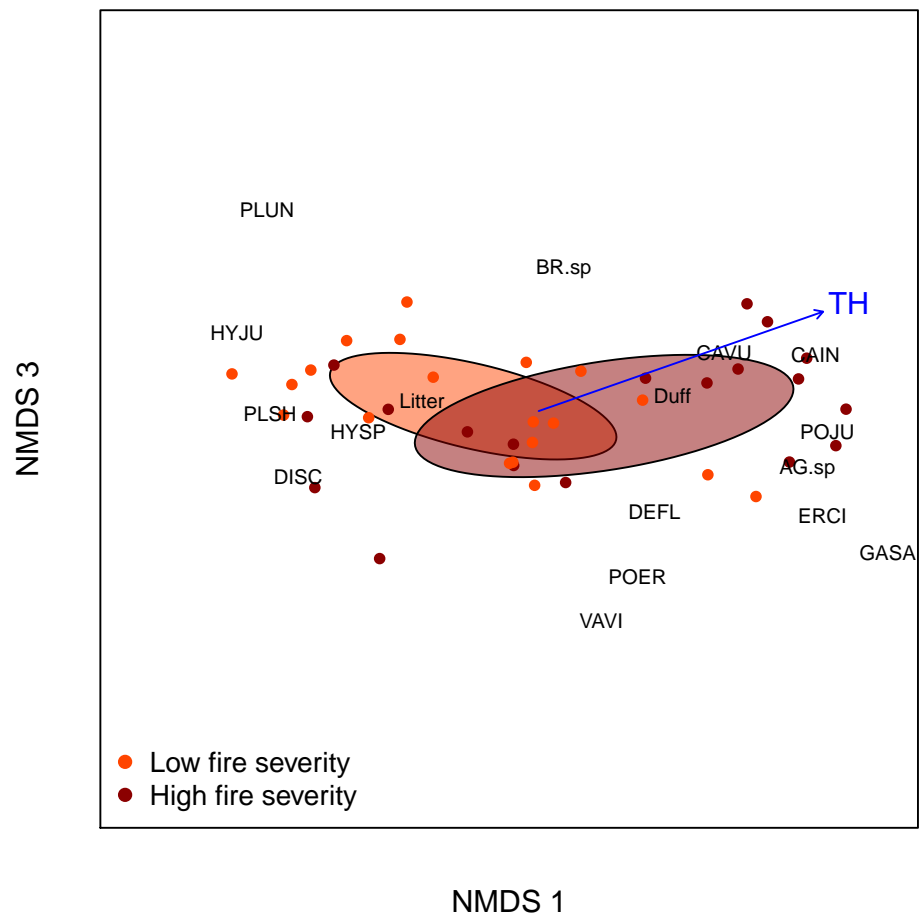
Figure C.7: NMDS for species data at the heathland site complementing Figure 3, showing axes 1 vs 3. Variance of plots along NMDS axes 1, 2 and 3 was 0.31, 0.06 and 0.03 respectively.
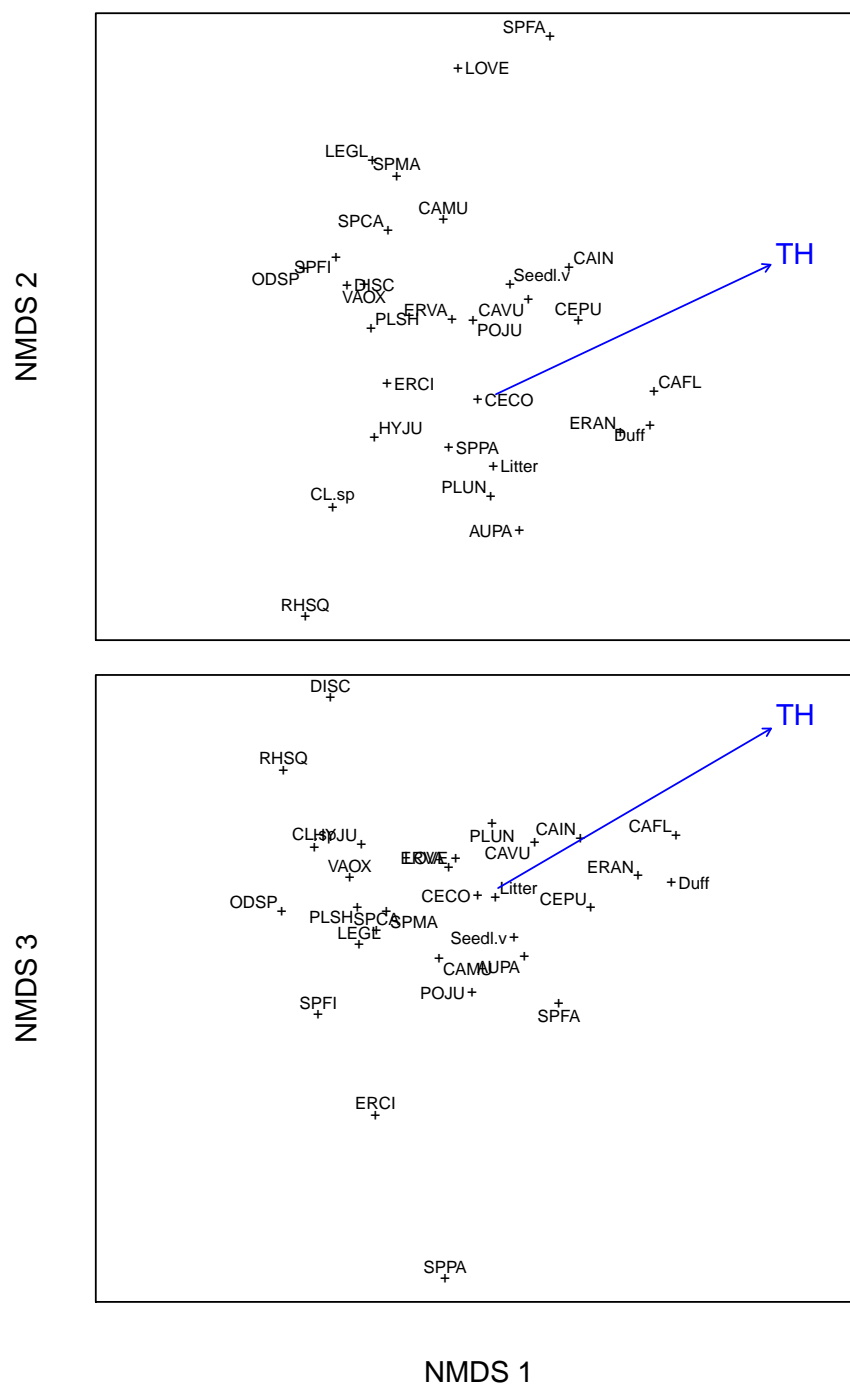
Figure C.8: NMDS for frequency data at the raised bog site complementing Figure 3, showing all species and axes.
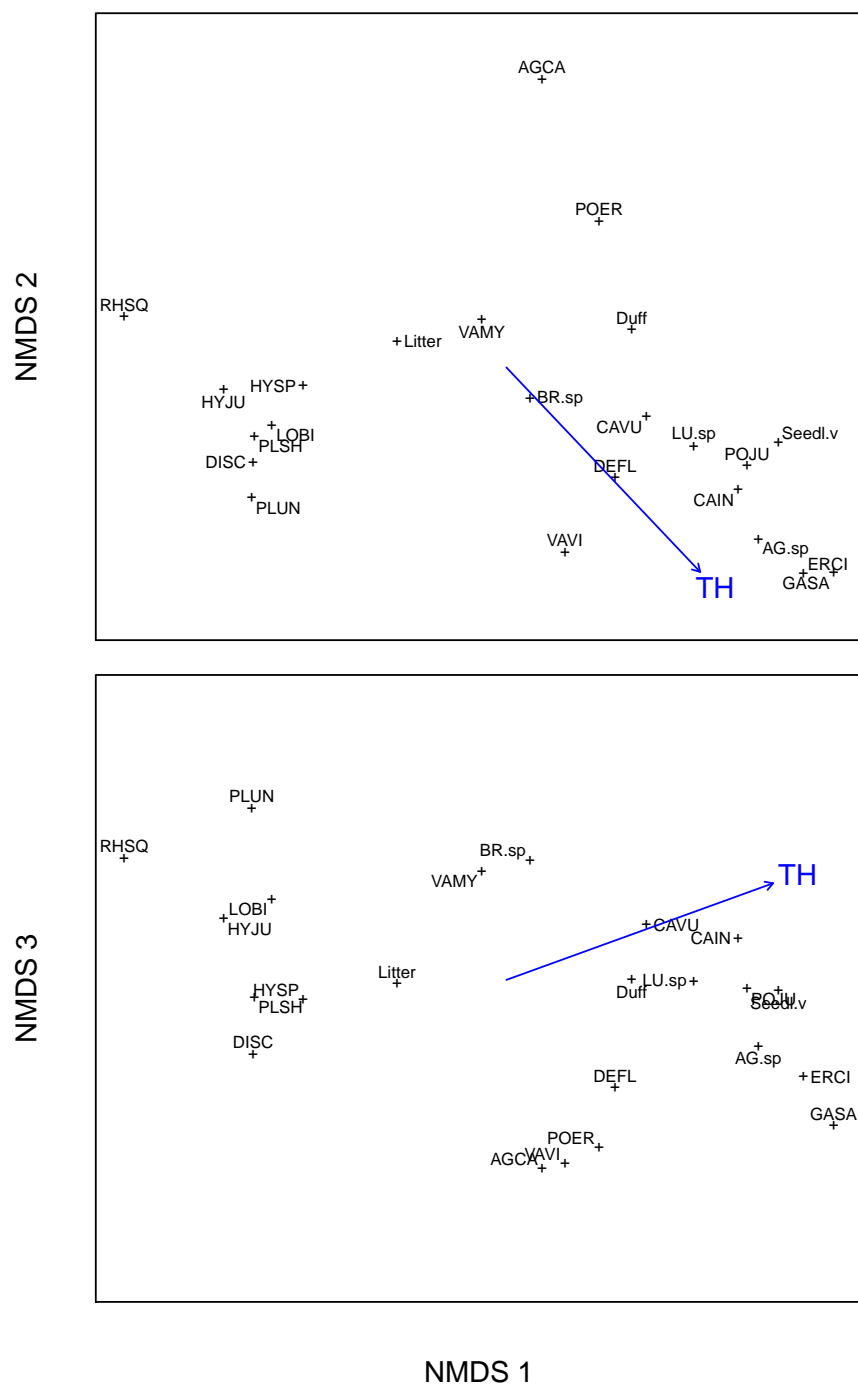
Figure C.9: NMDS for frequency data at the heathland site complementing Figure 3, showing all species and axes.

Appendix D. Proportion of resprouts and seedlings in regenerating *Calluna* and *E. cinerea*

Table D.1: Average frequency of regenerating forms of dominant ericoids per plot (SD in parenthesis).

Regenerating Ericoid	Drought	No-drought
Raised bog		
Calluna resprout	22.3 (21.0)	10.9 (10.2)
Calluna seedling	13.3 (9.5)	8.1 (6.5)
E. cinerea resprout	0.8 (1.8)	2.7 (4.6)
E. cinerea seedling	0	0
Dry heath		
Calluna resprout	0	0.1 (0.3)
Calluna seedling	22.4 (20.0)	19.8 (17.9)
E. cinerea resprout	0	0
E. cinerea seedling	8.0 (16.7)	6.8 (16.2)

Appendix E. Beta-diversity based on frequency data

The following tables provide model details summarised in Table 1.

Appendix E.1. Burnt and unburnt plots

Appendix E.1.1. Species data

Table E.1: Details of the analysis testing overall differences in beta-diversity of species community composition between treatments (unburnt, low fire severity and high fire severity plots) at the raised bog site.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	2	0.07	0.035	9.92	0.000
Residuals	51	0.18	0.004		

Table E.2: Details of the analysis testing overall differences in beta-diversity of species community composition between treatments (unburnt, low fire severity and high fire severity plots) at the heathland site.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	2	0.09	0.045	4.71	0.013
Residuals	57	0.55	0.010		

Table E.3: Details of the analysis testing overall differences in beta-diversity of plant functional type community composition between treatments (unburnt, low fire severity and high fire severity plots) at the raised bog site.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	2	0.07	0.035	8.99	0.000
Residuals	51	0.20	0.004		

Table E.4: Details of the analysis testing overall differences in beta-diversity of plant functional type community composition between treatments (unburnt, low fire severity and high fire severity plots) at the heathland site.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	2	0.49	0.247	28.28	0.000
Residuals	57	0.50	0.009		

Appendix E.2. Burnt plots only

Appendix E.2.1. Species data

Table E.5: Test of differences in beta-diversity of species community composition between low vs high fire severity treatments at the raised bog site.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	1	0.00	0.00	0.01	0.915
Residuals	34	0.15	0.00		

Table E.6: Test of differences in beta-diversity of species community composition between low vs high fire severity treatments at the heathland site.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	1	0.05	0.05	4.44	0.042
Residuals	38	0.42	0.01		

Appendix E.3. Plant functional type data

Table E.7: Test of differences in beta-diversity of community composition of plant functional types between low vs high fire severity treatments at the raised bog site.

	Df	Sum Sq	Mean Sq	F value	Pr($>$F)
Groups	1	0.00	0.00	0.07	0.786
Residuals	34	0.17	0.01		

Table E.8: Test of differences in beta-diversity of community composition of plant functional types between low vs high fire severity treatments at the heathland site.

	Df	Sum Sq	Mean Sq	F value	Pr($>$F)
Groups	1	0.05	0.05	4.45	0.042
Residuals	38	0.39	0.01		