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Effects of Long-Term Removal of Sheep Grazing on the Seedbanks of High-Level Grasslands and Blanket Bogs

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ABSTRACT

Many areas of vegetation in the British uplands have reduced species diversity as a result of sheep overgrazing. It has been suggested that abandonment or re-wilding strategies might be used to reverse this. A likely first step would be the removal or reduction of grazing livestock from upland areas, with a presumption that this would lead to a recovery in species richness. However, we do not know if this would work, or the timescales involved. One of the important areas where more knowledge is needed is information on the size and composition of soil seedbanks as regeneration from zseed is a likely pathway of recovery. Here, we compared seedbanks in both grazed and ungrazed plots in five experiments at Moor House NNR in the northern Pennines; these sheep grazing exclusion experiments were started 52 and 63/64 years ago. Soil samples (n=10) were collected from both grazed and ungrazed plots in each experiment, and seed emergence counted in glasshouse trials. We detected only seeds of common species and very few dicotyledonous species. This suggests that the soil seedbank is unlikely to be a reliable source of the less common species for ecological restoration in these upland communities, suggesting an extinction debt. Therefore, seed addition and the creation of suitable safe-sites for germination may be needed in conjunction with grazing controls to allow the establishment of plants that will increase the species richness of the vegetation. However, this interventionist restoration approach remains to be tested.

Keywords: Blanket bog, Grassland, Restoration, Seedbank, Sheep grazing, Species diversity

Introduction

The rationale for this work is based on the "wet desert" hypothesis put forward by Frank Fraser Darling back in the 1950s, which basically stated that high sheep grazing had reduced species diversity in upland plant communities (Darling, 1955). This has been highlighted recently by George Monbiot, who has described upland vegetation as "sheep-wrecked" (Monbiot, 2013). If the wet desert hy-

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pothesis is correct, we would expect that if sheep grazing is reduced then species diversity should increase again. This expectation is at the basis of recent suggestions that the agricultural use of the uplands should be reduced or re-wilded. The simplest approach to start this process would be the reduction or cessation of livestock grazing (Crumley, 2000; Marrs *et al*., 2018; 2020; Sandom *et al*., 2013; Stewart *et al*., 2005).

However, recent analysis of vegetation in long-term exclosure experiments at Moor House NNR in the northern Pennines has provided conflicting support for this hypothesis. On the one hand, a review of the properties of species that thrive once grazing is removed are the most nutritious, but they take a relatively long time to re-establish themselves, especially in grasslands (Marrs *et al*., 2020). Moreover, a recent analysis of the vegetation change in the continuously-grazed plots showed a general decline in many species groups over the timescale of the experiments (started between 1954 and 1972), but where sheep were removed there were both increases in some species (herbs, mosses, sedges) but faster reductions in grasses and liverworts (Milligan *et al*., 2016). These authors suggested that restoration to pre-treatment levels would probably require some form of intervention to create safe-sites (sensu Harper, 1977) for seed/spore germination (Milligan *et al*., 2016). However, a fundamental question before such work is undertaken is a requirement to know if there are either enough, or indeed any, seed/spores of the target species in the soil seed/diaspore bank.

Here, we revisit five of the high-level experiments at Moor House, three grassland and two blanket bog sites. Detailed descriptions of vegetation change within these experiments have been published elsewhere (Marrs *et al*., 1988; Milligan *et al*., 2016; Rawes, 1981; 1983). Each site has a grazed plot and an ungrazed comparator (see Marrs *et al*., 1986 for detailed experimental methods). However, due to policy changes and grazing rights ownership over the long time-course of these experiments the sheep grazing intensity has been reduced. In the 1960s the overall grazing pressure was ca. 4.4 sheep ha^{-1} across all vegetation types, but in 1972, grazing density was more than halved to ca. 2.0 sheep ha^{-1}, and it was halved again to ca. 1.0 sheep ha^{-1} in the early 2000s (Marrs *et al*., 2018; 2020; Milligan *et al*., 2016; 2018). In addition, the sheep distribution within the sites varies across the different plant communities with 11.6-23.2% greater densities on the most-grazed grassland communities compared to the least grazed blanket bog ones (Rawes & Welch, 1969). Thus, here our comparison is an ungrazed treatment *versus* a grazed treatment as the control, which was subject to the "business-as-usual" grazing pressure for that area.

Our aims were to test whether (a) the seedbank in these long-term experiments could assist restoration efforts to improve plant species diversity, and (b) assuming so, did sheep removal affect seedbank quality. Hence, this study compared the plant species composition of the vegetation and seedbanks in the five high-altitude, sheep-grazing experiments on the Moor House National Nature Reserve (Table 1, Fig. 1). Each experiment had two plots, an ungrazed plot where sheep were fenced out and a plot subject to "business-as-usual" sheep grazing pressures (Milligan *et al*., 2016). The experiments can be viewed in two groups, grassland and high-level bog. The grassland group contained three experiments set up on Hard Hill, Little Dun Fell and Knock Fell, and the high-level bog group contained two experiments at Silverband and Troutbeck Head (Marrs *et al*., 1986; Milligan *et al*., 2016). The three grassland experiments were set up between

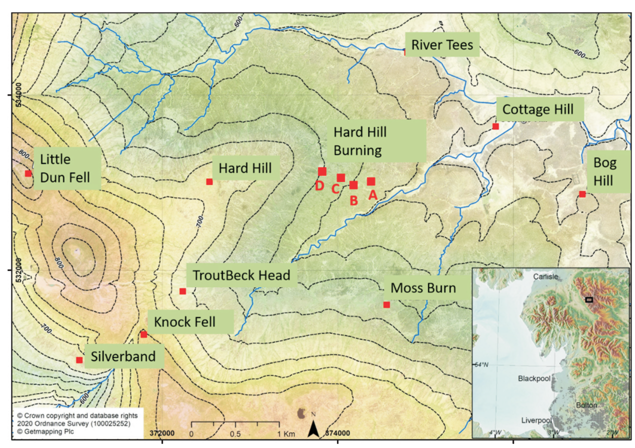

Fig. 1. Locations of all long-term vegetation experiments on Moor House NNR in northern England.

Table 1. Locations and summary of experimental history of the five sites at Moor House NNR

Group	Site name (Code)	British National Grid reference	Elevation (m)	Year fence erected	Year of vegetation recording (no. of years ungrazed)
High-level grassland	Hard Hill (HH)	NY 72576 33034	690	1954	2015 (61)
	Little Dun Fell (LDF)	NY 70475 33104	830	1954	2016 (62)
	Knock Fell (KF)	NY 71794 31267	750	1955	2014 (59)
High-level bog	Silverband (SB)	NY 71059 30975	690	1966	2015 (49)
	Troutbeck Head (TB)	NY 72236 31760	690	1966	2014 (48)

1954 and 1955 and the high-level bogs in 1966 (Marrs *et al*., 1986), thus there is consistency between experiments within each group.

In the 1960s Eddy *et al*. (1968) classified the communities on both Hard Hill and Little Dun Fell as a *Festucetum*, an *Agrosto-Festucetum* on Knock Fell, and an *Eriophoretum* on both Silverband and Troutbeck Head. Milligan *et al*. (2016) reclassified the *Festucetum* as H19a (*Vaccinium myrtillus-Cladonia arbuscula* heath: *Festuca ovina-Galium saxatile* sub-community, Rodwell, 1991), the *Agrosto-Festucetum* as CG10 (*Festuca ovina-Agrostis capillaris-Thymus praecox* grassland community, Rodwell, 1992) and the Eriophoretum as M20b (*Eriophorum vaginatum* blanket and raised mire: *Calluna vulgaris-Cladonia* spp. sub-community, Rodwell, 1991) under the UK National Vegetation Classification. Soil types also differed ranging from acidic deep peats on the high-level bog to brown-earth soils at Knock Fell (Eddy *et al*., 1968; Heal & Smith, 1978; Rawes & Welch, 1969).

Materials and Methods

Seedbank assessment

In April 2018, ten random positions were located in both the grazed and ungrazed plots at each of the five experiments. Sampling was done after a severe winter and hence it would be expected that any seeds in the seedbank would have experience substantive natural chilling. At each position, the surface vegetation was removed, and three soil cores sampled using an auger (5 cm diameter, 7 cm depth) and pooled. At the time of the sampling the intervention had been in place for 63/64 years for the grasslands and 52 years for the high-level bogs.

We used the general seedling emergence method described by Ghorbani *et al*. (2006) and Lee *et al*. (2013). The individual soil samples (n=100) were spread individually over a 1 cm deep layer of horticultural sand in a seed tray (21.5×16 cm); these trays were positioned randomly on benches fitted with permanently-saturated capillary matting in an unheated glasshouse (Ghorbani *et al*., 2006; Lee *et al*., 2013). Emerging seedlings were identified, counted and removed over four months. Where identification was uncertain at the time of counting, the seedling was transplanted into a separate pot and grown on for twelve months so that an accurate identification could be made. Seedling densities per quadrat were corrected to numbers m^{-2}. Control trays containing horticultural sand were included to identify seed contamination in the substrate and species which may have gained access to the glasshouse. No other pre-treatment (gibberellin or smoke treatment) was given, following (Thompson & Grime, 1997). The few individuals that were detected in these control trays were non-moorland species and were discounted in subsequent analyses. Nomenclature follows Stace (2019).

Vegetation assessment

At each site the abundance of plant species has been monitored at approximately 10-year intervals using point quadrats (Marrs *et al*., 1986) and all data are available in Rose *et al*. (2020). The vegetation data for both the grazed and ungrazed plot from the five experiments were extracted from this database for the latest sampling date to be as comparable as possible with the seedbank sampling. At the time of vegetation sampling the intervention had been in place for between for between 59 and 61 years (grasslands) and 48/49 years (high-level bog).

Statistical assessment

Seedbanks are very difficult to assess in these upland habitats because often very few seeds germinate in tests (Lee *et al*., 2013) as a result of a combination of poor seed production because of low temperatures and wet conditions coupled with poor incorporation into the surface soils as a result of litter accumulation (Ghorbani *et al*., 2006). Accordingly, here we only analyse the total number of germinable seed detected in each sample. To do this we used a generalised linear model (function 'glm, R Core Team, 2019) with a poisson error distribution (Crawley, 2013). Model reduction was tested but the full interaction model was selected as the Minimum Adequate Model (MAM). Thereafter, data on seed densities were viewed in two ways. Where species were present in the seedbank of both grazed and ungrazed treatments we compared the densities in each treatment using the non-parametric Wilcoxon rank-sum test ('wilcox.test' function, Crawley, 2013; R Core Team, 2019). Otherwise, we present qualitative information on the presence/absence of species in both vegetation and seedbanks in the two grazing treatments at each site.

Results

The total number of seeds detected was low (Fig. 2) but were in the same order of magnitude as those detected in similar studies from slightly lower elevations at Moor House, but an order of magnitude lower than those in blanket bogs at the southern end of the Pennines (Lee *et al*., 2013). For the analysis of the total number of germinable seeds the additive model was selected as the MAM for the grassland sites, and the interaction model for the high-level bogs (Table 2). For grasslands, the greatest seed densities were at Hard Hill and Knock Fell (no significant difference between them) and Little Dun Fell had the least (Fig. 2C); there was a marginally greater seed density ($P<0.06$) in the ungrazed treatment (Fig. 2F). In the high-level bogs, there was no significant site differences between the grazed treatment at the two sites, but com-

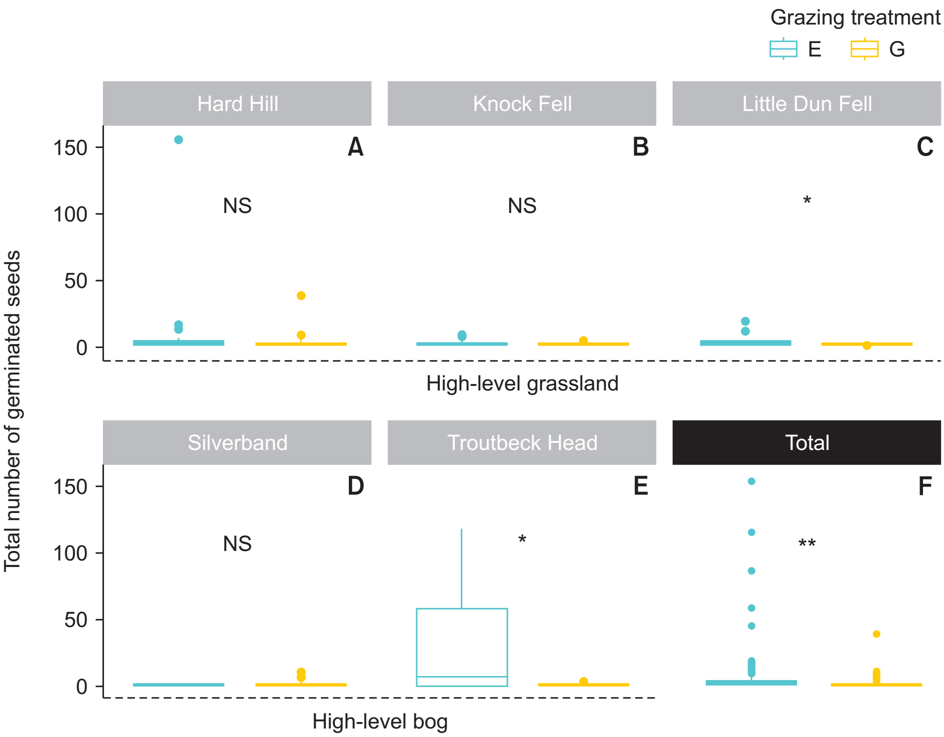

Fig. 2. Total number of seeds of all species in both grazed and ungrazed plots in long-term experiments in three grasslands and two bogs at Moor House NNR. E, enclosure; G, grazed; NS, not significant. Significance: *P<0.05; **P<0.01.

Table 2. Results for the minimum adequate model derived from mixed-effects modelling of total seed density in grazed and ungrazed plots

Group	Variable	Estimate±SE	Z-value	*P*-value
	Hard Hill (Int)	2.140±0.109	19.73	<0.001***
ΔDev=1.2%	Knock Fell	−0.511±0.177	2.88	0.004**
ΔAIC=5.6	Little Dun Fell	−1.735±0.280	−6.19	<0.001***
	Silverband	−0.365±0.170	2.16	0.031*
	Troutbeck Head	−2.140±0.334	−6.40	<0.001***
	Ungrazed	1.095±0.125	8.74	<0.001***
	Knock Fell×Ungrazed	−0.822±0.224	3.67	<0.001***
	Little Dun Fell×Ungrazed	0.356±0.313	1.14	NS
	Silverband×Ungrazed	−3.786±0.532	−7.12	<0.001***
	Troutbeck Head×Ungrazed	2.374±0.345	6.89	0.205

SE, standard error; Dev, deviance; AIC, akaike information criterion; NS, not significant.
The change in deviance (%) and AIC relative to the null model are presented and significance denoted as: *P<0.10; **P<0.01; ***P<0.001.
The intercept is denoted as (Int).

pletely opposing responses in the ungrazed treatment, Silverband having a much lower seed density and Troutbeck Head a much greater one than their grazed counterparts (Fig. 2E).

In the grasslands, 17 species were present in both vegetation and seedbank (Table 3), seven of these were only found at Knock Fell, and of these four were graminoids and three dicotyledons (*Potentilla erecta*, *Rumex acetosa*, and *Sagina procumbens*), note *S. procumbens* was also found in the seedbank at the Hard Hill ungrazed plot. Of this group *Anthoxanthum odoratum*, *Luzula campestris/multiflora*, *Poa humilis* and *S. procumbens* were not detected in the seedbank of the ungrazed plots and *R. acetosa* was only detected in the seedbank of the grazed plot, where it was not found in the vegetation. Ten common species were detected in the vegetation of at least

Table 3. Species that were detected (+) in both the vegetation and the soil seedbank in the three grassland sites

No of sites	TC	Species	Vegetation						Soil seedbank					
			Hard Hill		Little Dun Fell		Knock Fell		Hard Hill		Little Dun Fell		Knock Fell	
			G	UG	G	UG	G	UG	G	UG	G	UG	G	UG
1	Gr	*Anthoxanthum odoratum*					+	+					+	
	Gr	*Deschampsia cespitosa*					+	+					+	+
	Gr	*Luzula campestris/multiflora*					+	+					+	
	Gr	*Poa humilis*					+	+					+	
	D	*Potentilla erecta*					+	+					+	+
	D	*Rumex acetosa*					+	+						+
	D	*Sagina procumbens*						+		+			+	
2	Gr	*Agrostis canina/vinealis*			+		+	+		+		+	+	+
	Gr	*Agrostis capillaris*			+		+	+					+	+
	Gr	*Nardus stricta*	+	+			+		+	+	+			
3	Gr	*Avenella flexuosa*	+	+	+	+	+	+		+	+	+	+	
	Gr	*Carex bigelowii*	+	+	+	+	+	+	+	+	+	+		+
	Gr	*Festuca ovina*	+	+	+	+	+	+	+	+	+		+	
	Gr	*Juncus squarrosus*	+	+	+		+	+	+	+	+	+	+	+
	D	*Cerastium fontanun*		+	+		+						+	
	D	*Galium saxatile*	+	+	+	+	+	+	+	+	+	+		
	D	*Vaccinium myrtillus*	+	+	+	+	+	+				+		

TC, taxonomic class; G, grazed; UG, ungrazed; Gr, graminoid, D, dicotyledon.
The species are ranked by the number of sites in which they were detected in the vegetation. Species are ranked by TC.

two sites and they were all detected in the seedbank of at least one treatment at each site (Table 3); six were graminoids and four dicoytledons. Of particular interest were those species that were present in the vegetation but not in the seedbank; three species at Hard Hill (*Empetrum nigrum*, *Eriophiorum vaginatum*, and *Vaccinium vitis-idaea*), two species at Little Dun Fell (*Chamaenerium angustifolium* and *Festuca vivipara*) but twenty one species at Knock Fell, the site with the greatest species diversity (Milligan *et al*., 2016). Of these species missing from the Knock Fell seedbank eighteen were dicotyledons, two were graminoids and one was a clubmoss (*Seliginella selaginoides* [lesser clubmoss]) (Table 4). Only *Juncus bulbosus* and *J. effusus* were detected in the seedbank of grassland sites but were not present in the vegetation (Table 4).

In the high-level bogs six graminoids plus *Calluna vulgaris* were found in both vegetation and soil seedbank, but *C. vulgaris* was absent from the Silverband seedbank (Table 5). Seven species, one fern, two graminoids and four dicotyledons were detected in the vegetation but not in the soil seedbank and seven species, six graminoids and one dicotyledon (*Galium saxatile*) were detected in the soil seedbank, but not in the vegetation (Table 5).

Discussion

There is no doubt that the plant species diversity has declined over the last century or so as a result of a combination of factors including high levels of sheep-grazing plus the impacts of atmospheric pollution including SO2 and N on the vegetation (Monteith *et al*., 2016; Rose *et al*., 2016), although there is some evidence that pollutant damage is reducing (Mitchell *et al*., 2017). In the experiments reported here, there has been a reduction in many species-groups within the grazed plots over time, but herbs, mosses, and sedges have expanded when sheep-grazing was stopped (Milligan *et al*., 2016). Indeed, Marrs *et al*. (2020) have recently shown that a few species have increased in the ungrazed plots, but it has taken between 10-20 years in blanket bog for this to occur, and up to 60 years in the grasslands. Given, these results, it has been suggested that any rapid increase in biodiversity will come from either exogenous or endogenous processes, or indeed both (White, 1979; Marrs, 1988). Due to the size of the areas of vegetation involved exogenous processes require that the propagules (seeds/spores) can disperse from sites some distance from the study area, and endogenous processes rely on seed production within the existing

Table 4. Species that were detected (+) either (1) in the vegetation, or (2) the soil seedbank in the three grassland sites

Fraction	Site	TC	Treatment	Hard Hill (HH)		Little Dun Fell (LDF)		Knock Fell (KF)	
				G	UG	G	UG	G	UG
Vegetation only	HH	Gr	*Eriophorum vaginatum*		+				
		D	*Empetrum nigrum*	+	+				
		D	*Vaccinium vitis-idaea*	+	+				
	LDF	Gr	*Festuca vivipara*			+			
		D	*Chamaenerion angustifolium*				+		
	KF	LC	*Selaginella selaginoides*					+	
		Gr	*Carex caryophyllea*					+	
		Gr	*Festuca rubra*					+	+
		D	*Achillea millefolium*					+	+
		D	*Alchemilla glabra*						+
		D	*Anemone nemorosa*						+
		D	*Cardamine pratensis*					+	
		D	*Cirsium paulstre*						+
		D	*Crepis capillaris*						+
		D	*Euphrasia* spp.					+	
		D	*Galium sterneri*					+	
		D	*Geum rivale*					+	+
		D	*Minuartia verna*					+	+
		D	*Oxalis acetosella*					+	+
		D	*Saxifraga hypnoides*					+	+
		D	*Scorzoneroides autumnalis*					+	
		D	*Taraxacum officinale* agg.						+
		D	*Thymus druceii*					+	+
		D	*Trifolium repens*					+	
		D	*Viola lutea*					+	
		D	*Viola riviniana*					+	
Seedbank only	All	Gr	*Juncus bulbosus*	+				+	
		Gr	*Juncus effusus*			+		+	+

TC, taxonomic class; G, grazed; UG, ungrazed; Gr, graminoid, D, dicotyledon.
Species are ranked by TC.

vegetation. Irrespective of which of these processes occur, once the seed arrives within the vegetation they have to travel through the existing vegetation and litter to reach the soil surface for immediate germination if safe-sites are available (sensu Harper, 1977) or incorporation into the soil propagule bank for future germination (Ghorbani *et al*., 2006; Thomson *et al*., 1997). The obvious way to assess the regeneration potential of the vegetation is to measure the size and composition of the soil seedbank (González-Alday *et al*., 2009; Putwain & Gillham, 1990, Wagner *et al*., 2018).

Here, we compared the seedbank in both grazed and ungrazed plots in five experiments at Moor House and the results were disappointing in that the seedbanks were relatively small, but in the same order of magnitude as other studies at this site (Lee *et al*., 2013), and for the most part contained common species that were present in the vegetation, or were abundant nearby (e.g. the *Carex* and *Juncus species*). There were very few dicotyledonous species in the seedbank, especially at Knock Fell, the site with the greatest vascular plant diversity. These results show that seedbanks cannot necessarily be relied upon

Table 5. Species that were detected (+) in (1) both vegetation and soil seedbank, (2) only in the vegetation, or (3) only in the soil seedbank in the two high-level bog experiments

Distribution	TC	Fraction	Vegetation				Soil seedbank			
		Site	Silverband		Troutbeck Head		Silverband		Troutbeck Head	
		Treatment	G	UG	G	UG	G	UG	G	UG
Vegetation & Soil seedbank	Gr	*Avenella flexuosa*	+	+	+	+	+		+	
	Gr	*Eriophorum vaginatum*	+	+	+	+			+	
	Gr	*Festuca ovina*	+	+	+	+	+	+	+	
	Gr	*Juncus squarrosus*			+		+		+	+
	Gr	*Nardus stricta*	+	+	+		+			
	Gr	*Trichophorum cespitosum*	+	+	+	+			+	
	D	*Calluna vulgaris*		+	+	+			+	+
Vegetation only	F	*Dryopteris dilatata*		+						
	Gr	*Carex nigra*	+	+	+					
	Gr	*Eriophorum angustifolium*	+	+	+	+				
	D	*Empetrum nigrum*	+	+	+	+				
	D	*Rubus chamaemorus*		+	+	+				
	D	*Vaccinium myrtillus*	+	+	+	+				
	D	*Vaccinium vitis-idaea*				+				
Soil seedbank only	Gr	*Agrostis vinealis*					+			
	Gr	*Carex bigelowii*					+			
	Gr	*Carex curta*					+			
	Gr	*Carex echinata*					+			
	Gr	*Juncus bulbosus*					+			
	Gr	*Juncus effusus*					+			
	D	*Galium saxatile*						+		
	Gr	*Trichophorum cespitosum*								
	Gr	*Trichophorum germanicum*								

TC, taxonomic class; G, Grazed; UG, Ungrazed; Gr, Graminoid, D, Dicotyledon.
Species are ranked by taxonomic class TC.

to provide the diversity of seed germination to provide new species to increase plant species biodiversity. It also suggests that some plant species within the existing vegetation may not be providing sufficient viable seed on a regular basis for them to be incorporated into the soil seedbank. This is certainly possible in these relatively harsh conditions (Heal, 1978). Pigott (1968), for example, showed that low temperatures prevented viable fruit set in *Cirsium acaule* in upland communities. It is also possible that any seed that is produced is prevented from entering the seedbank by the vegetation/litter depth (Ghorbani *et al*., 2006). These results are in line with previous work on similar habitats in Belgium (Bossuyt & Hermy, 2003) which gives some indication of how different species may perform in grasslands, and Thompson and Grime (1997), Morin and Payette *et al*. (1988) and Vander-Kloet (1988) give information on the longevity of some species in the seedbank. Taken together, it appears these communities suffer may from an extinction debt (Gonzalez, 2013) as the species that persist do not have the means to regenerate without help. Recent research shows that extinction debts may last for centuries (Isbell *et al*., 2019).

Thus, it is unlikely that the diversity of these upland communities will be increased quickly in the future unless there are positive interventions to (a) increase the seed input into the communities and (b) create suitable germinations sites. Such safe-sites can be created through a combination of methods to create bare patches, for example through the use of herbicides, fire or mechanical damage by cutting, rotavating, screefing screefing or introduction of species such as Wild Boar (*Sus scrofa* L.) that forage by creating soil disturbance (Bueno *et al*., 2010, Critchley *et al*., 2013, Humphrey & Coombs, 1997; Lee *et al*., 2013; Miles, 1974; Milligan *et al*., 2004). However, these suggestions need further experimental testing to assess their feasibility.

Author Contributions

HL, KC and RHM designed the seedbank study and sampled the seedbanks, HL, KC and HMcA performed the seedbank assessments, RR and JO'R assessed the vegetation and along with MF and RHM produced the vegetation database, MF provided an applied perspective and all contributed to writing the manuscript.

Conflict of Interest

RHM is President of the Heather Trust, this is an ambassadorial role only.

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