Restoration of upland hay meadows over an 11-year chronosequence: an evaluation of the success of green hay transfer

Elizabeth Sullivan (corresponding author) Edge Hill University, St Helens Road, Ormskirk L40 4QP
sullivae@edgehill.ac.uk

Noah Hall, 7 Innisbrook Gardens, Bangor, Co Down, N. Ireland, BT19 1DU noahjoe@live.co.uk

Paul Ashton, Edge Hill University, St Helens Road, Ormskirk L40 4QP ashtonp@edgehill.ac.uk

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Abstract

Grassland restoration has become a key tool in addressing the drastic losses of semi-natural grassland since the mid-twentieth century. This study examined the restoration by green hay transfer of upland hay meadows, a particularly scarce and vulnerable habitat, over an 11-year chronosequence. The community composition of 18 restoration meadows was compared with that of donor reference sites in two study areas in the Pennine region of Northern England. The study investigated: differences in community composition between donor and restoration meadows; transfer of upland hay meadow target species; and the effect of time and isolation from neighbouring meadows on the community composition of the restoration meadows. Results showed that restoration meadows differed from donor meadows in that some target species were easily transferred whilst others were not found in the restoration meadows, or were at low levels of cover. Time had a significant effect on the community composition of the restoration meadows, but the similarity between restoration sites and donor sites did not increase with time; and the effect of isolation was not significant. The study showed that the green hay transfer method increases botanical diversity and is an important first step in meadow restoration. However, further restoration activity, such as seed addition, is likely to be required if restoration sites are to resemble closely the reference donor sites.

Key words: community composition; target species; time; restoration sites; donor sites; similarity

Implications for practice

- Green hay transfer is a valuable technique for the first phase of the restoration of upland hay meadows where site conditions and management regimes are favourable.
- A limited suite of target species can be successfully transferred using this method but, over time, the meadow community should be monitored to assess fluctuations in key species, and decisions should be taken on how and when to introduce missing target species, e.g. by further seed addition.
- The isolation of the restoration site from other similar plant communities does not appear to be a barrier to initial establishment of target species following green hay transfer, though it should be considered in initial decision-making if long-term restoration is to rely on subsequent colonisation from existing populations.

Introduction

Agricultural intensification and abandonment have resulted in a significant reduction in semi-natural habitats, including grasslands (Reidsma et al. 2006; Stoate et al. 2009). During the second half of the twentieth century extensively managed, species-rich grasslands were largely replaced by arable crops, or leys, sown with a few highly productive grass species and enriched with artificial fertilisers (Eriksson et al. 2002; Strijker 2005). Other ecologically important grasslands, formerly managed as low intensity hay meadows, were lost due to early mowing for silage instead of mid-summer cutting for hay. Over time this practice significantly reduces floral diversity as few plants can set seed (Smith et al. 2008). The outcome of these changes has been that there are very few extant areas of species-rich grassland, and that the ones that do remain are often small and fragmented in their distribution (Fuller 1987; Cousins et al. 2007; Krauss et al. 2010). Species-rich grasslands support an extremely diverse flora and fauna (Wilson et al. 2012; Habel et al. 2013) and provide a range of important ecosystem services, such as the provision of nectar sources and habitats for pollinators (Byrne & delBarco-Trillo 2019) and nutrient cycling (Peciña et al. 2019).

The conservation response to the drastic loss of semi-natural habitats has included legislation to protect sites from development or agricultural conversion, and agri-environment schemes which encourage farmers to enter a management agreement in return for payments (Ridding et al. 2015; Fry et al. 2017; Hermoso et al. 2018). This has been a worldwide approach which has involved considerable expenditure, but there are concerns about the effectiveness of such schemes in ensuring the long-term persistence of some habitats and species (Batáry et al. 2015; Ansell et al. 2016; Ó hUallacháin et al. 2016). Where species-rich grasslands are small, or the surrounding farmland is intensively managed, it has been shown to be difficult to maintain the target habitat or species even when a low input management regime is in place on the site itself. (Batáry et al. 2015; Mathar et al. 2016). Increasing the numbers of species-rich sites, and the connectivity between them, has been highlighted as key to ensuring that grassland habitats, and species that are grassland specialists, can be retained in the longer term (Cousins et al. 2007; Arponen et al. 2013; Deák et al. 2018). The importance of increasing the species-rich grassland resource has been recognised through the inclusion of grassland restoration options in agri-environment schemes, so incentives are available for farmers and landowners to participate in enhancing diversity on their farm holding (Török et al. 2011).

Previous studies of grassland restoration have often focused on the re-creation of grassland habitats on former arable fields (Conrad & Tischew 2011; Lencová & Prach 2011; Prach et al. 2014; Boecker et al. 2015) or grasslands which have been abandoned and left unmanaged (Buisson et al. 2015; Galvánek & Lepš 2008; Ruprecht 2006). The current study addresses restoration of agriculturally improved upland hay meadows which, to date, have been less well studied. Upland hay meadows are a particularly vulnerable grassland type in Europe; they are listed under Annexe I of the Habitats Directive, with only circa 2000 km² remaining (Rodwell et al. 2013). Targets have been set for the restoration of this habitat by the UK Government because there are now very few sites in the UK (Smith et al. 2017). These remaining sites have a very fragmented distribution, so it would be expected that dispersal of key species is limited. Upland hay meadows are usually characterised by relatively low productivity, though they are botanically diverse with a high proportion of forbs (Critchley et al. 2007; Reiné et al. 2014). Traditionally, upland meadows were cut annually for field-dried hay, and grazed in the late summer and autumn, and in some cases in the spring, before being 'shut up' to allow the grass crop to grow (Smith et al. 2000; Mauchamp et al. 2014).

Grassland restoration aims to reduce competitive agricultural grasses and re-introduce specialist species that are representative of the target grassland type (Conrad & Tischew 2011; Waldén et al. 2017). Methods of restoration for degraded grasslands vary but the use of green hay transfer has been successful in the establishment of some specialist meadow species (Kirkham et al. 2013; Bischoff et al. 2018). However, there have been few evaluations of the success of green hay transfer in upland hay meadows, and the effects of change in the community composition of restored upland hay meadow vegetation over time are largely unknown. Analyses of change over time are important because some plants can establish more quickly than others, and there can be increases in the number of species establishing over time (von Gillhaussen et al. 2014; Engst et al. 2017). This study seeks to address gaps in the knowledge through the analysis of the community composition of 18 upland hay meadows restored by green hay transfer, over an 11-year chronosequence, as part of a regional restoration programme (Gamble et al. 2012; Robinson & Gamble 2014). Data from multiple sites, which were restored at different times, are of particular value because this enables analysis of both spatial and temporal patterns, and the consideration of variables such as the extent of isolation of meadows, community composition at different stages since restoration and similarity to the donor site.

Measurements of the success of grassland restoration can be based on comparisons with a reference site or plot, the numbers of target species transferred through the restoration process, or the extent to which the restored sites match a particular vegetation classification, e.g the British National Vegetation Classification (NVC) (Rodwell 1992; Walker et al. 2004; Conrad & Tischew 2011; Kirkham et al. 2013). This study used the donor sites as reference sites, and an analysis of the target species was also undertaken. Target species are those found in long-established meadows which have had low fertiliser input, and which are representative of the region in which the restoration is taking place (Baasch et al. 2016). Less attention was given to comparisons with vegetation classification types because the study was carried out over two geographical regions, with variations in soil types and climate. These variations were expected to affect the community composition of the donor sites, with few sites conforming to the 'typical' vegetation classification. Instead the focus was on the resemblance between donors and restoration sites and change over time in the meadow vegetation.

Meadow restoration has become an important conservation activity led by government-funded schemes and Non-Governmental Organisation projects (Walker et al. 2004; Gamble et al. 2012; Rothero et al. 2016; Hosie et al. 2019). Donor and restoration sites have a fragmented distribution and are often isolated from similar habitats, thus restricting potential seed sources following the initial restoration (Pacha & Petit 2007). Previous studies of grassland restoration have shown that the presence of semi-natural grassland communities in the surrounding landscape are critical to the success of restoration (Jongepierová et al. 2007; Řehounková & Prach 2008). However, where there is a limited availability of potential restoration sites with suitable soil conditions, management regimes and landowner permissions, site isolation may not be a primary consideration in restoration practice. At the same time the importance of spatial population structures of grassland species has been largely overlooked (Harzé et al. 2018). The present study addresses this gap in the knowledge by investigating whether isolation of restoration sites has an impact on community composition.

Our study evaluated the green hay restoration method by testing the following hypotheses: (1) Green hay spreading results in a community composition in the restoration meadows which is similar to that of the donor meadows, (2) Target species are transferred from donor site to restoration site during green hay transfer, (3) Time since restoration increases the similarity of the community composition of restoration sites to that of donor sites, (4) Isolation decreases the similarity of the community composition of restoration sites to that of donor sites.

Methods

Study regions and sites

The study was carried out in two regions of Northern England: the Forest of Bowland (53°58'N, 2°26'W) and the Yorkshire Dales (54°23'N, 2°16'W) (Fig 1). The Forest of Bowland has a mean annual precipitation of 1294 mm and a mean annual temperature of 12.7°C (Met Office 2018a). In the Yorkshire Dales the mean annual precipitation is 898 mm and the annual mean temperature is 11.7°C (Met Office 2018b). The Forest of Bowland has a varied bedrock known as the 'Bowland Series' which consists largely of millstone grits, limestone, sandstone and shale. In the Yorkshire Dales carboniferous limestone is the dominant bedrock, interspersed in places with shale and sandstone (Brenchley & Rawson 2006).

The study included 11 donor meadows and 18 restoration sites across the two regions. The study sites varied in size from 0.4-6.93 hectares (Tables 1 and 2). Some of the donor sites (Table 1) are protected under UK legislation as Sites of Special Scientific Interest (SSSIs) or form part of a Special Area of Conservation (SAC) under EU legislation (Table 1). The sites were notified for their upland hay meadow/mountain hay meadow habitat and belong to the Triseto-Polygonion alliance (Rodwell et al. 2007). Within the UK National Vegetation Classification, they are classified as MG3 *Anthoxanthum odoratum-Geranium sylvaticum* communities (Rodwell 1992) although there is some variation within the two regions. The restoration meadows (Table 2) had all been restored since 2007 using green hay transferred from a local donor site.

Restoration methods

The soil type, aspect and altitude of candidate restoration sites were matched as far as possible to those of the donor sites. Soil potassium (K) and phosphorus (P) were required to be below the UK Soil Index 2 (DEFRA 2018). Management of the candidate restoration meadows was expected to be a low input regime with no artificial fertiliser addition, low livestock densities and an annual late summer cut for hay.

Sites were prepared before restoration by mowing and removal of the grass cuttings, followed by harrowing (Robinson & Gamble 2014). The donor sites (used as the reference sites in this study) were then mown in dry weather conditions, and a maximum of one third of the green hay crop (by area) was transferred and spread on the recipient site (the restoration sites in this study) as quickly as possible after mowing to prevent seed loss and wilting (Robinson and Gamble 2014). The timings of green hay spreading varied according to weather conditions and contractor availability (Table 2). Donor and restoration sites were considered suitable if they were within an hour’s travel time and had similar site conditions. Travel time, rather than distance between donor and restoration site, was of particular importance to ensure the green hay was in the best condition. It was sometimes possible to spread green hay from one donor site onto two adjacent recipient sites. Examples are: hay from BDM2 was spread onto BRM2 and BRM3; and hay from YDM5 onto YRM6 and YRM7.

Site survey

Vegetation surveys were carried out in donor and restoration sites in June 2018. In each site twelve 1 m x 1 m quadrats were placed randomly (using a randomised function in Excel) for independent data collection with sufficient statistical power in subsequent analyses. Edge effects were minimised by excluding a 5 m wide border within field boundaries. Sampling points were located using a GPS, accurate to +/- 3 m. Vascular plants were identified to species level using the nomenclature of Stace (2010) and the percentage cover of each plant species was recorded.

Data analysis

Community composition and transfer of target species

All data analysis was carried out in R version 3.5.1 (R Development Core Team 2018). To investigate differences in community composition between the donor meadows and the restoration sites Non-Metric Multi-Dimensional Scaling (NMDS) was carried out using the vegan package (Oksanen et al. 2016) on the Hellinger transformed mean site percentage cover values for all 29 sites (i.e. 11 donor and 18 restoration sites). Following this initial exploration Indicator Species Analysis (ISA) was undertaken using the labdsv package (Roberts 2016) to identify whether any target species (Supplement S1) were influential in differences between the composition of donor and restoration meadows in each region. The ISA was undertaken separately for each region because field observations, along with differences in climate and soil types, indicated that there were regional variations in meadow community composition. A permutational significance test using 499 permutations was used to determine which indicator species were significant.

Comparisons were made of mean percentage cover by site of meadow target species in donor and restoration meadows. These were taken from the UK Joint Nature Conservation Committee’s guidance for the monitoring of upland hay meadows (JNCC 2004) (Supplement S1). The frequency of site records for each species was compared, along with records of target species at the restoration sites prior to restoration. The pre-restoration survey information was incomplete in the Yorkshire Dales as three site records were unavailable.

Effect of time and isolation on community composition

A Pearson's product-moment correlation test was carried out, following tests for normality, to investigate the relationship between time since restoration and Bray Curtis similarity between pairs of donor and restoration sites. Bray Curtis was used because it takes into account abundances as well as species presence. The effects of time since restoration and isolation on the community composition of the restoration sites were investigated using Redundancy Analysis (RDA) in the vegan package (Oksanen et al. 2016). Time since restoration was included in the model as the number of years since green hay transfer took place. Isolation was calculated using Hanski's Connectivity Index (Hanski 1994) for each restoration meadow. Euclidean distances between each restoration meadow and all species-rich meadows in Natural England's Priority Habitat Inventory Layer (https://data.gov.uk/dataset/4b6ddab7-6c0f-4407-946e-d6499f19fcde/priority-habitat-inventory-england) within a 2 km radius of the restoration meadow were measured in QGIS (QGIS Development Team 2019). The Priority Habitat Layer (PHL) includes all grassland types of conservation interest but has been developed from a wide range of surveys and datasets, some of which were collected over 20 years ago, so there may have been changes in the agricultural management of the qualifying meadows in the PHL. A 2 km radius was chosen because this covers maximum dispersal distances for grassland plants (Sullivan et al. 2018) but also accounts for the fact that some grassland seeds may be dispersed by animal or vehicle movements. Hanski's Index was calculated using the following equation:

$$CI_i = \Sigma_{i \neq j} \exp(-\alpha d_{ij}) \times A_j^{a}$$

where d is the distance between each restoration site and neighbouring meadows; A is the area of neighbouring meadow sites; α is a constant relating to dispersal ability (1/ migration distance); and a

is a scaling parameter which defines the density area relationship. In this case α was 0.5 because 2 km was taken as the migration distance and the scaling parameter (*a*) was also 0.5 because the increase in population will be less than proportional with the increase in site area if all meadow plant species are considered. Location (Bowland or Yorkshire Dales) was also included as constraining variable in the RDA. Permutational significance testing of the whole model (999 permutations) and of the individual constraining variables was undertaken (each 999 permutations).

Results

Community composition and transfer of target species

A total of 98 plant species were recorded in 312 quadrats. Species recorded in each region are listed in Supplements S2 and S3. The NMDS analysis of community composition in all 29 donor and restoration meadows (Fig 2) revealed differences in the composition of the two regions, Bowland and Yorkshire Dales. There was a clear separation between donor and restoration meadows in Bowland but there was some overlap between the Yorkshire Dales donor and restoration meadows. The ISA results (Table S1) revealed that five of the significant indicator species for the Bowland donor meadows: *Sanguisorba officinalis* (great burnet), *Alchemilla xanthochlora* (pale lady's mantle), *Lathyrus pratensis* (meadow vetchling), *Filipendula ulmaria* (meadowsweet) and *Scorzoneroides autumnalis* (autumn hawkbit) were target species for upland hay meadows, whilst one target species, *Rhinanthus minor* (yellow rattle), was found to be a significant indicator for the Bowland restoration sites. In the Yorkshire Dales two target species, *S. officinalis* and *Geranium sylvaticum* (wood cranesbill), were significant indicators for the donor meadows but the significant indicator species identified for the restoration meadows were not target species. These results indicate that some target species, with the exception of *R. minor*, do not appear to have been successfully transferred. The Bray Curtis similarity index analysis showed that the five meadows with the greatest degree of similarity to their donor meadows were in the Yorkshire Dales (Table S2) and all of these were a minimum of six years since restoration.

Comparisons of the percent cover and frequency of target upland hay meadow species (Table 3; Fig 3) showed that *R. minor*, *Euphrasia spp.* (eyebright species) and *Leonotodon hispidus* (rough hawkbit) were recorded most frequently and at the highest levels of percent cover in the restoration sites. *R. minor* was recorded at all donor and restoration meadows (Fig 3). The annual species, *R. minor* and *Euphrasia* spp, showed increases in mean percent cover when compared with donor sites. Some target species, including *A. xanthochlora* and *G. sylvaticum*, were not recorded at all in the restoration sites and some, e.g. *F. ulmaria* and *S. officinalis*, were only recorded at low levels of percentage cover in the restoration sites. These analyses support the findings from the ISA that some target species were transferred successfully whilst others were not.

When comparisons were made between the restoration sites pre- and post-restoration (Table 3) some species, e.g. *A. xanthochlora* and *G. sylvaticum*, were present before restoration but were lost after restoration though this was only at one site. Other species, e.g. *Centaurea nigra* (common knapweed) and *Lotus corniculatus* (bird's-foot trefoil), were present at low frequencies pre-restoration and saw moderate increases after restoration; and some species, e.g. *Euphrasia* spp and *L. hispidus*, were not present pre-restoration but were recorded at high frequencies post-restoration.

Effect of time and isolation on community composition

The relationship between time since restoration and Bray Curtis similarity was not significant (r = 0.328, P = 0.185) indicating that similarity to the reference site (i.e. donor site) does not increase with time since restoration (Fig 4). The redundancy analysis (RDA) model was significant following a permutation test (P = 0.007) whilst testing of constraining variables found that time since restoration was significant ($P = 0.009$) as was location ($P = 0.017$) but isolation (Hanski Connectivity Index) was not significant ($P = 0.515$). The RDA plot (Fig 5) indicates that sites are clustered together by location but are less clustered by time since restoration, particularly the sites restored six years ago and those restored three years ago. Axis 1 (RDA1 in Fig 5) was significant ($P = 0.004$) with sites clearly distributed along this axis by location, and to a lesser extent, by time since restoration. Examination of the variance inflation factors for the constraining variables did not indicate strong collinearity so the interpretation of the significance of the model was considered to be reliable.

Discussion

This study set out to evaluate the green hay method of meadow restoration by investigating its effect on the community composition of restored sites over time. The analysis has shown that, whilst some target species have been successfully established in the restoration meadows, others have not, and the composition of the restoration and donor meadows was different. Time was shown to have a significant effect on community composition but, overall, restoration meadows had not become more similar to their donors over the study period. Isolation from neighbouring hay meadows had not had a significant effect on the community composition of the restoration sites.

Community composition of donor and restoration meadows

The restoration meadow sites had a different community composition to the donors, so the first hypothesis of the study was not supported. Target species for upland hay meadows such as *A. xanthochlora*, *G. sylvaticum* and *S. officinalis* were identified as significant indicators for the donor sites but were not recorded or were recorded at low levels of cover with a patchy distribution in the restoration meadows. Analysis of the target species did show that most species had seen an increase in records when compared with presence on the sites pre-restoration, although this was often at a low level of cover. Some target species had established successfully, including *R. minor*, which was a significant indicator species in the Bowland restoration sites. *Euphrasia* spp, *L. hispidus* and *S.*

autumnalis were also recorded at high frequencies in the restoration sites, despite a lack of records of *Euphrasia* spp. and *L. hispidus* in the sites prior to restoration. Thus, the second hypothesis is only partially supported. Previous studies of grassland restoration involving some of these species were variable. For example, a study by Pywell et al. (2003) which included results from 25 studies of grassland restoration on former arable and species poor grasslands found that *S. officinalis* was a poor coloniser but also recorded that *R. minor* and *L. hispidus* were consistently poor colonisers. Kirkham et al. (2013) recorded an increase in *L. hispidus* but also saw increases in *R. minor* and *S. officinalis* albeit at low levels of cover.

Explanations for the variation in success of transfer of key species could include differences in phenology. Bischoff et al. (2018) reported that target species in Cnidion floodplain meadows were typically late flowering and were transferred more effectively with an October hay cut. However, early cutting was also associated with the transfer of additional species to the target ones for this habitat. In the two study regions agri-environment scheme prescriptions state an earliest cutting date of 15 July. *S. officinalis* is a relatively late flowering species with seeds expected to ripen from mid-August onwards, so a mid-July hay cut would be too early to capture seeds from this species. However, the timing of the hay transfer varied from mid-July to late August so should have included seed from later-flowering seeds on at least some of the sites. *G. sylvaticum*, a key target species for the Yorkshire Dales meadows, would be expected to have set seed by mid-July (Kirkham et al. 2013; Fitter and Peat 1994). Based on this information, the timing of the hay cut should not have prevented seed transfer, but further research on timings of hay cut and transfer, which consider locally important species' traits, would be valuable.

Another reason for the lack of establishment of target species could be the extent of soil disturbance at the restoration site. Seeds or green hay spread on bare soil with tilling/ploughing have been shown to be effective, particularly when nutrient levels were relatively high (Kiehl et al. 2010; Bischoff et al.

2018). The Bowland and Yorkshire Dales restoration sites were not subjected to this degree of disturbance, although they were prepared by mowing, or a period of intensive grazing, followed by chain harrowing, so newly added species would have to compete with existing common grassland species to some extent. The effect of competitive species has been explored by Fry et al. (2017) who found that a number of early colonising species were the primary constraint in the establishment of target species. These species, which included *Trifolium pratense* (red clover) and *Ranunculus acris* (meadow buttercup), were seen to be more influential in limiting the growth of target species than soil chemistry or the microbial community, and could affect success for several years after seed had been transferred. These species were common in both Bowland and the Yorkshire Dales in donor and restoration meadows (including being present on many restoration meadows prior to restoration) so may have influenced some of the target species at the restoration sites.

Effect of time since restoration on community composition

Time since restoration was found to have had a significant effect on the community composition in the restoration meadows which supports the third hypothesis of the study. The RDA showed that most of the meadows which had been restored in the same year had a similar community composition. This could be explained by the fact that some species were transferred easily but failed to establish over the longer term, whilst others only became established later. For example, *L. corniculatus* was recorded in sites restored two, three, five and six years ago but not in sites restored earlier than this, whereas *Conopodium majus* (pignut) was only recorded in sites restored six years ago or earlier. It has been suggested that *C. majus* does not flower until the tuber has reached a critical size which could take several flowering seasons (Thompson and Baster 1992). Species-specific characteristics such as this could influence the composition of the restoration meadow communities over time and more research on the population dynamics of key species could help to inform restoration success.

The effect of time on the community composition of restored meadows is complex. Although meadows restored in the same year had a similar community composition, the restoration meadows did not become more similar to the donor meadows over the study period. For species that were not easily transferred through green hay, the transient nature of grassland species seedbanks (Bekker et al. 2000; Wallin et al. 2009) and the fact that some perennial species produce relatively small quantities of seed, may explain why the missing species do not become established. For example, seedbank analyses of *R. minor* and *G. sylvaticum* revealed that both species had a transient seedbank but there was a mean seedbank density of 309 seeds per m^2 for *R. minor* compared with 6 seeds per m^2 for *G. sylvaticum.* (Fitter and Peat 1994). It would be expected, therefore, that species with a limited and transient seedbank would be unlikely to become established over time following green hay restoration, and that further restoration activity or dispersal from local populations may also be required. Pywell et al. (2007) suggested a phased approach to grassland restoration which included initially sowing *R. minor* to reduce the effect of competitive species, followed by seeding with specialist plants. The hemi-parasitic species *R. minor* and *Euphrasia* spp. were both present at high levels of cover across the restoration sites so seeding would not be necessary where they are easily transferred from donor sites. However, further seeding with selected target species may now be required. This has been recognised by the conservation organisations involved in the restoration of the study sites, and other meadows in the study area. These organisations set out to use several restoration methods, including initial green hay transfer, and anticipated that further seeding or plug planting of particular species may be required later in the process (Gamble et al. 2012).

Effect of isolation on community composition

Isolation from neighbouring hay meadows did not have a significant effect on the community composition of the restoration sites so the fourth hypothesis of the study cannot be accepted. It is possible that isolation may be a more significant influence in the future and may prevent colonisation by particular meadow species. The distribution of the restoration meadows in relation to other species-rich meadows in the study area is variable, so it may also affect some sites more than others. The role of dispersal in achieving restoration success was emphasised by Helsen et al. (2013) who found that spatial isolation slows down restoration and that sites need to be physically interconnected. Waldén et al. (2017) recorded an increase in grassland specialists over time in sites which had been restored 6-23 years before their study but, importantly, they also noted that the presence of a local species pool in other semi-natural grassland fragments was significant. Burmeier et al. (2011) found that target meadow species did colonise new areas successfully after several years following green hay transfer to strips of a restoration site, but this was recorded at a small scale within a meadow. Dispersal of seeds is affected by many factors including dispersal mechanisms, and, although seeds which are dispersed following ingestion or attachment to animals or machinery can travel many kilometres, those which are unassisted or even dispersed by wind may only be dispersed over short distances of several metres or less (Coulson et al. 2001; Thomson et al. 2011). It seems unlikely, therefore, that the missing target species will easily colonise sites which are not immediately adjacent to upland hay meadows in future years.

The analysis also showed that location (study region) had had a significant effect on the community composition of the restoration meadows. The two study regions are close together geographically but there are differences in soil types and climate, particularly in terms of precipitation, with the Bowland region having much higher rainfall (see Methods). This finding illustrates the importance of the choice of donor site, an aspect of grassland restoration which has also been highlighted elsewhere (McDonald 2001; Wallin et al. 2009).

This study set out to investigate whether green hay transfer could be effective in achieving species-rich upland grassland sites which were similar to the donor community. The method was found to be successful in transferring several target species, but it did not enable the establishment of a grassland community which closely resembled that of the donor sites, even after 11 years of low input agricultural management. These findings reflect those of green hay restoration studies in other circumstances, such as on lowland and ex-arable sites (Sengl et al. 2017; Albert et al. 2019), suggesting that green hay transfer can be a valuable first step in grassland restoration, or can be used more generally to increase the diversity of species-poor grassland, providing that management is sympathetic. Assuming that the goal is to develop a species-rich grassland community which is akin to meadows or pastures with little or no agricultural improvement, then it is likely that further interventions will be required to introduce the target species that are not readily transferred by green hay. Grasslands vary widely in their local site conditions and in terms of the influences of the surrounding landscape matrix. A greater understanding of these factors, as well as the ecological requirements and population dynamics of the target species, will help to inform successful restoration in the longer-term.

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TABLES

Table 1 Details of donor meadows including area in hectares (ha) and elevation in metres above sea level (m asl); SSSI = site of special scientific interest (UK designation); SAC = special area of conservation (EU designation)

Site code	Site name	Area (ha)	Elevation (m asl)
Forest of Bowland			
BDM1	Black House Farm 1	1.63	177
BDM2	Bell Sykes (SSSI/SAC) 1	2.70	167
BDM3	Bell Sykes (SSSI/SAC) 2	1.48	151
BDM4	Black House Farm 2	2.67	181
BDM5	Bell Sykes (SSSI/SAC) 3	1.43	148
Yorkshire Dales			
YDM1	Fothering Holme (SSSI/SAC)	2.10	335
YDM2	Swaledale	1.84	250
YDM3	Foxhole Rigg (SSSI)	3.80	150
YDM4	Sawyersgarth	2.56	247
YDM5	Myersgarth	3.90	190
YDM6	Hetton	7.80	180

Table 2 Details of restoration sites including area in hectares (ha), elevation in metres above sea level (m asl), year and month of restoration, nearest upland hay meadow in kilometres (km) and the code for donor meadow

Site code	Site name	Area (ha)	Elevation (m asl)	Year restoration	Month restoration	Nearest meadow (km)	Donor

BRM1	Stephen Park	1.76	235	2012	Mid-Aug	0.834	BDM1
BRM2	Bell Sykes 4	4.46	188	2012	Mid-Aug	0.001	BDM2
BRM3	Bell Sykes 5	1.22	190	2012	Mid-Aug	0.001	BDM2
BRM4	New Laithe	5.53	227	2015	Late-July	2.565	BDM3
BRM5	Lower Stony Bank 1	1.00	225	2015	Early-Sep	0.952	BDM4
BRM6	Long Bank	2.30	161	2015	Late July	8.242	BDM4
BRM7	Lower Stony Bank 2	6.93	222	2016	Mid Aug	1.088	BDM1
BRM8	Bambers 1	1.75	203	2016	Early Aug	1.090	BDM5
BRM9	Bambers 2	1.99	206	2016	Early Aug	1.275	BDM5
YRM1	Arkengarthdale	1.40	296	2007	Late July	0.677	YDM1
YRM2	Dagger Stones	2.64	215	2009	Mid July	1.182	YDM2
YRM3	Low Wilkinson 1	0.90	197	2009	Mid Aug	0.197	YDM3
YRM4	Low Wilkinson 2	3.00	140	2009	Mid July	0.002	YDM3
YRM5	Littondale	0.40	253	2010	Late Aug	0.002	YDM4
YRM6	Newbiggin 1	1.20	181	2012	Late Aug	2.595	YDM5
YRM7	Newbiggin 2	1.00	186	2012	Late Aug	2.595	YDM5
YRM8	Hills Lane	2.70	185	2013	Late July	0.846	YDM6
YRM9	Hurst Holme	5.40	147	2013	Late July	1.894	YDM6

Table 3 Mean site percent cover of target species (source: JNCC 2004) in donor and restoration meadows (both regions) and number of restoration sites where target species were recorded [1]pre- and post-restoration

	Mean % cover donor sites	Mean % cover restoration sites	Donor sites present (*N* = 11)	[1]Sites present pre-restoration (*N* = 15)	Sites present post-restoration (*N* = 18)
Alchemilla xanthochlora	0.48	0.00	4	1	0
Centaurea nigra	6.55	0.91	5	2	5
Conopodium majus	1.62	0.63	6	2	6
Euphrasia spp.	8.62	10.43	10	0	17
Filipendula ulmaria	4.98	0.10	5	0	4
Geranium sylvaticum	1.30	0.00	3	1	0
Lathyrus pratensis	5.82	0.46	10	1	9
Leontodon hispidus	4.04	1.32	8	0	18
Lotus corniculatus	0.51	1.30	2	2	5
Persicaria bistorta	0.00	0.30	0	0	2
Rhinanthus minor	14.63	26.53	11	2	18
Sanguisorba officinalis	9.49	0.25	9	1	5
Scorzoneroides autumnalis	3.94	1.29	9	3	11
Succisa pratensis	0.00	0.02	0	0	1

[1]Note that the pre-restoration data is incomplete for the Yorkshire Dales meadows. Data for three sites are missing but two of these sites were known to be very species-poor before restoration.

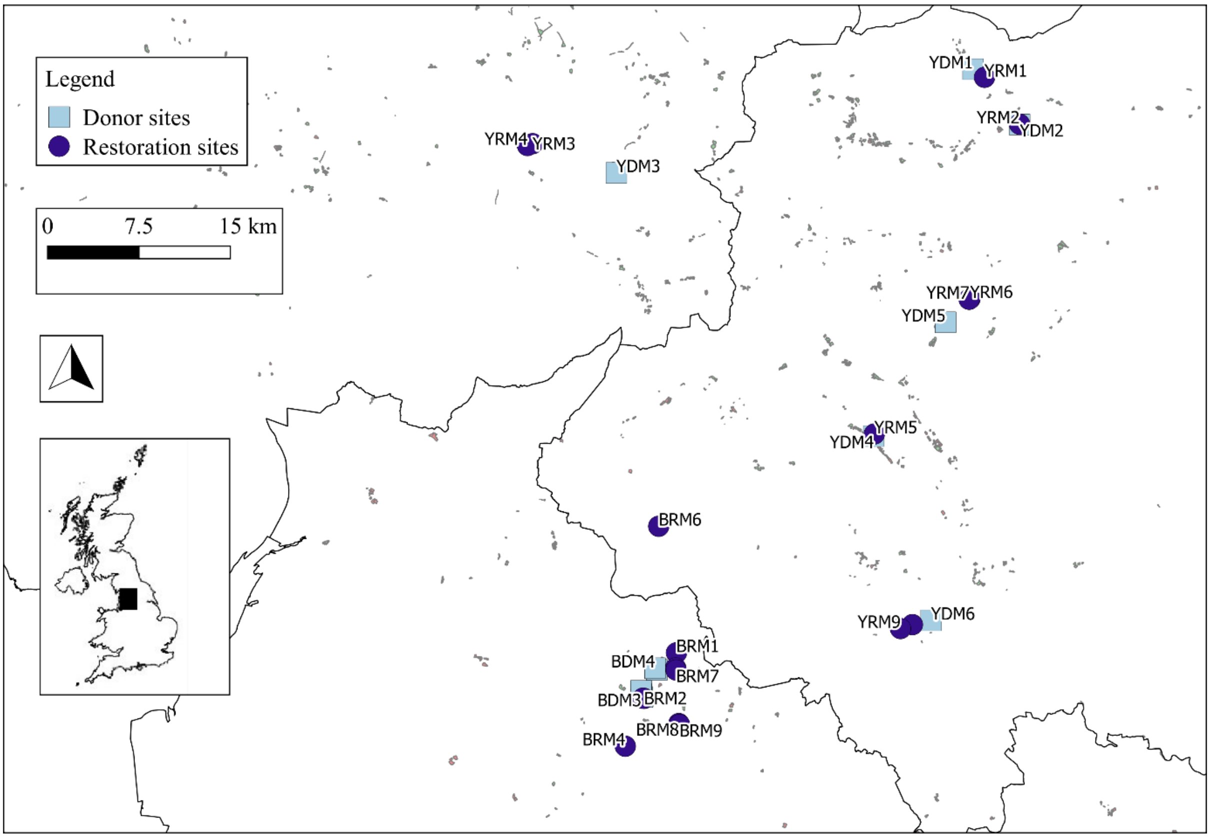

Fig 1 Donor and restoration sites in Bowland and the Yorkshire Dales, northern England, alongside species rich hay meadows from Natural England's Priority Habitat Inventory Layer

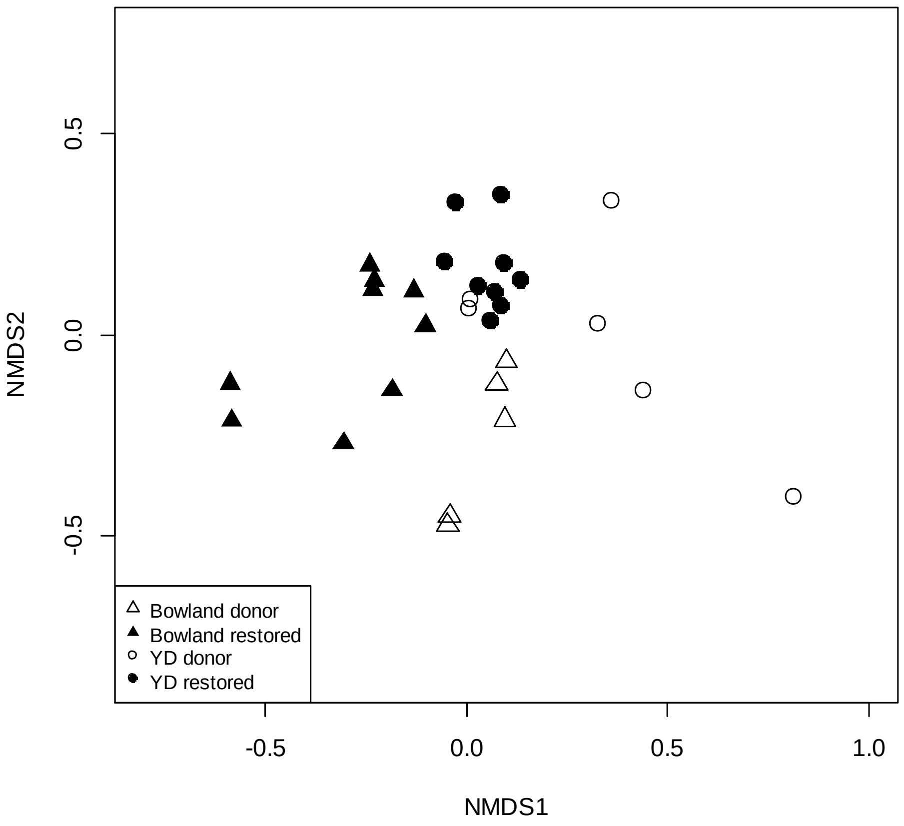

Fig 2 NMDS ordination of the community composition of donor and restoration sites in the Bowland and Yorkshire Dales study areas. Stress = 0.14

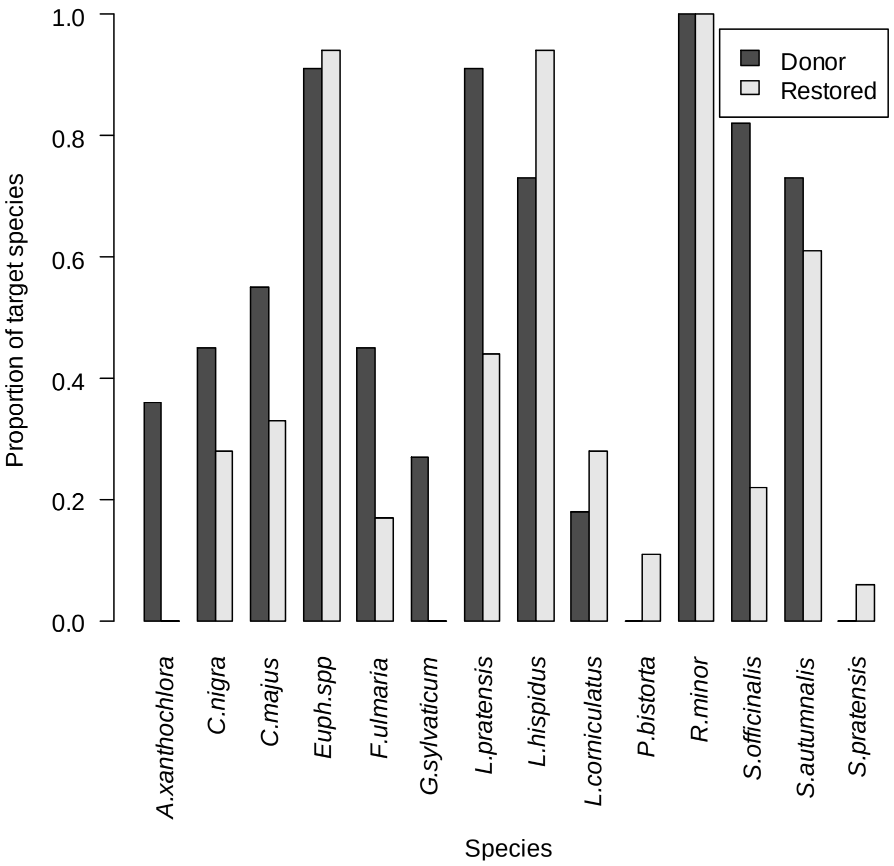

Fig 3 Target species in the donor and restoration meadows in Bowland and the Yorkshire Dales. The chart shows the proportion of donor ($n = 11$) and restoration sites ($n = 18$) in which the target species were found.

658

659 **Fig 4** Change in mean pairwise Bray-Curtis similarity index values for donor and restoration sites

660 over the 11 years of the restoration period

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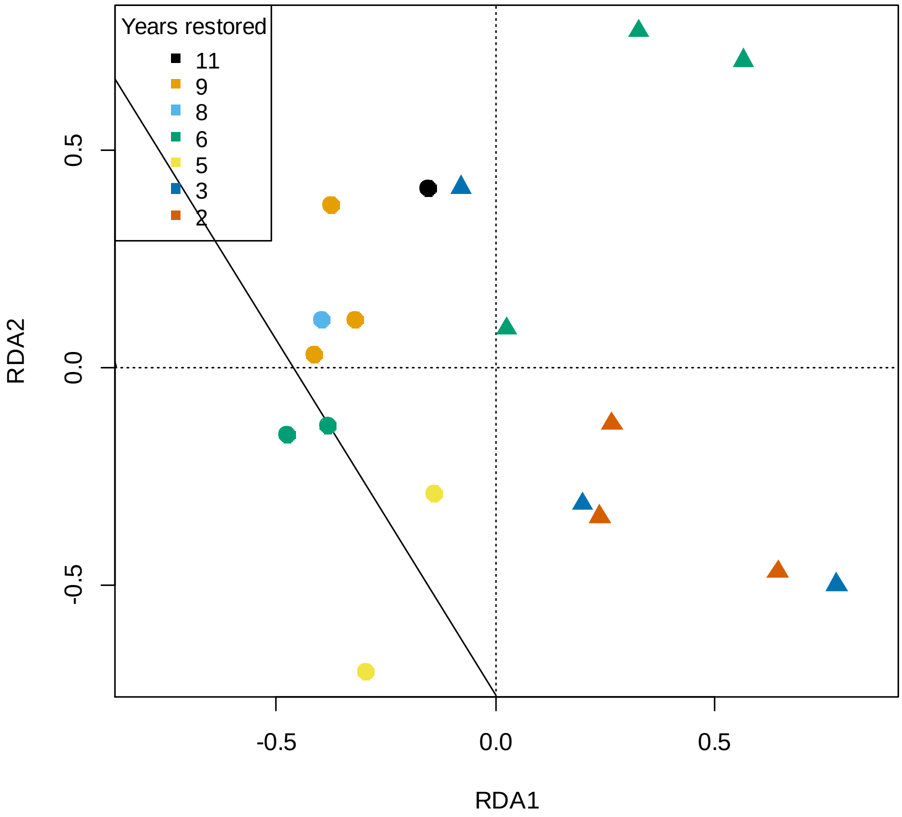

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Fig 5 RDA of community composition of Bowland and Yorkshire Dales restoration meadows constrained by time since restoration and isolation (Hanski Connectivity Index) and location. Circles represent sites in Yorkshire Dales, triangles are Bowland sites. Number of years since restoration are represented by colours shown in figure legend. Adjusted $R^2 = 0.14$.