RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

No need to seed: restoring species-rich grassland on former arable fields by natural regeneration

Carl D. Sayer[1,2], Peter Robinson[1], Derek C. G. Sayer[1], Jan C. Axmacher[1]

Abstract

Introduction: Over the last century, agricultural intensification has caused substantial losses of semi-natural species-rich grasslands. One means of restoring grassland habitat is to abandon farmed land, followed by mowing and/or grazing of the established vegetation to facilitate meadow diversification.

Objectives: This study investigated post-abandonment vegetation change for an ex-arable field in eastern England following cessation of crop cultivation in 2005 and commencement of an annual hay meadow mowing regime over 2011–2022.

Methods: Vegetation surveys were undertaken every 2–3 years following 2011, with plants recorded along permanent transects using 1 × 1 m quadrats. In parallel, all plants present in the meadow were recorded via an exhaustive walk-over survey.

Results: After 3–4 years of mowing, weedy annual plants were largely replaced by perennials, with an increase in legumes and a major spread of two orchid species: *Dactylorhiza fuchsii* and *D. praetermissa*. After 11 years of mowing the field had become a species-rich meadow supporting locally scarce species. Communities shifted from a ruderal open vegetation to one encompassing a variety of high conservation value mesotrophic and "unimproved" grassland vegetation types, with British National Vegetation Classification units MG8 (*Cynosurus cristatus–Caltha palustris* grassland), MG5 (*C. cristatus–Centaurea nigra* grassland) and MG4 (*Alopecurus pratensis–Sanguisorba officinalis* grassland) emerging as potential restoration endpoints.

Conclusions: Despite its isolation in an arable agricultural landscape, a rapid decadal-scale post-arable diversification of the meadow's vegetation is evident. The mechanisms facilitating this remain obscure, but it is suspected that deer-mediated seed dispersal may have been important to species arrival.

Implications for Practice: Seeding of grasslands on ex-arable land may not always be required to achieve restoration targets, especially where soils are free-draining and agrochemical applications were not too intensive prior to agricultural management. Natural regeneration combined with hay meadow management may be a cheaper and easier means of restoring high conservation value grasslands compared to the use of commercially derived seed and could be key to recovering this habitat in large landscape-scale projects. More long-term studies of spontaneous hay meadow development following arable farming are urgently needed in the United Kingdom and more generally across Northern and Western Europe.

Key words: ex-arable, hay meadow, natural regeneration, plant conservation, seeding, spontaneous succession

Introduction

Semi-natural grasslands are of key importance to European biodiversity conservation (Dengler et al. 2014; Bardgett et al. 2021) but have experienced major declines in terms of extent and quality over the last century due to agricultural intensification and expansion, combined with extensive associated land drainage schemes (van Dijk 1991; Veen et al. 2009; Wesche et al. 2012). Given this decline and associated negative knock-on effects for other biota (Habel et al. 2019), there is an urgent need and much enthusiasm for grassland restoration. This can involve the improvement of existing sites, as well as the establishment of species-rich grassland on former cropped land (Baasch et al. 2016).

Due to the slow and often limited dispersal abilities of many target plant species, the fragmented nature of remaining high-quality grassland patches, as well as the absence of many desired species in remnant seedbanks at proposed restoration sites (Pywell et al. 2002; Walker et al. 2014), grassland restoration has often seen a strong emphasis on active intervention as opposed to more passive approaches. In this respect, many projects and associated studies have focused on the introduction of regional or commercial seed mixes (Conrad & Tischew 2011; Prach et al. 2014), on introductions of harvested seed and/or of green hay collected from local high conservation value "target" grasslands (Donath et al. 2007; Albert et al. 2019; Wagner et al. 2021), and sometimes the introduction of plug plants

Author contributions: DCGS, CDS conceived the project; CDS, PR undertook the vegetation surveys; CDS wrote the manuscript, with edits provided by JCA, PR; PR undertook the data entry; JCA led on the data analysis.

[1]Department of Geography, University College London, Gower Street, London, U.K.
[2]Address correspondence to C. D. Sayer, email c.sayer@ucl.ac.uk

© *2026 The Author(s).* Restoration Ecology *published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.*
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
doi: 10.1111/rec.70487
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.70487/suppinfo

(Hedberg & Kotowski 2010). Additionally, topsoil removal or deep plowing has been used to reduce soil nutrient availability and accelerate grassland recovery (Pywell et al. 2002; Klimbowska et al. 2007; Resch et al. 2019). The success of these active restoration approaches, either alone or in combination, is variable and dependent on several factors: land use history and local soil conditions (especially soil nutrient status), vegetation communities present prior to restoration (plowed land, commercial grassland, and abandoned farmland), subsequent management activities (e.g. hay cutting and grazing) and climate (Török et al. 2021).

Active approaches to grassland restoration, as mostly promoted in agri-environment schemes, are labor-intensive and often expensive (Török et al. 2011), which limits the spatial extent of restoration efforts. An alternative method of restoring grassland is via natural, spontaneous vegetation regeneration, often combined with limited management interventions like mowing. There may be substantive barriers to achieving a successful outcome with such an approach, however. As many grassland species are dispersal-limited, close proximity of high-quality grasslands is often argued as being essential (Knappová et al. 2012), but this is often not the case, especially in highly fragmented agricultural landscapes. Further, soil seedbanks associated with ex-arable land are generally thought to be of poor quality (Wagner et al. 2017), hence limiting the ease via which target vegetation communities might be re-assembled. For example, for a French river floodplain, Vécrin et al. (2002) showed the seedbank of abandoned arable fields to be highly impoverished, with an absence of seeds from desired species. Equally, for arable land in eastern England that was formerly wet fen grassland, Stroh et al. (2012) showed species associated with an adjacent species-rich target site to be largely absent from the seedbank, with evidence for a major degradation of the seedbank after a relatively short period (circa 6 years) of agricultural conversion. Poor seed longevity of many grassland species in arable fields may be due to physical damage to seeds during cultivation (plowing and harrowing) and/or the negative impacts of agrochemicals (Bekker et al. 1997; Stroh et al. 2012). Indeed, a number of studies have shown the seeds of many characteristic specialist grassland species to be highly short-lived (Kiss et al. 2016; Török et al. 2018).

While there are obstacles to the successful spontaneous restoration of species-rich grassland on abandoned agricultural fields, a number of chrono-sequence and long-term monitoring studies (decadal scales) have nevertheless shown promising results, especially for dry grasslands in Eastern and Central Europe spanning Romania (Ruprecht 2005, 2006), Czech Republic (Lencová & Prach 2011; Prach et al. 2014; Sojneková & Chytrý 2015) and Hungary (Csecserits & Rédei 2001; Albert et al. 2014; Valkó et al. 2016). In a highly replicated study of dry grasslands in the Carpathian Mountains (eastern Czech Republic), Prach et al. (2014) compared restoration outcomes from spontaneous vegetation succession and annual hay cutting with the sowing of regional and commercial seed mixes. While regional seed mixes were advocated to practitioners as producing a more characteristic, less mesic dryland grassland community, spontaneous succession led to the return of a similar number of target grassland species, albeit a little more slowly. Further, for old abandoned arable fields in Transylvania, Kuhn et al. (2025) showed higher restoration potential from seed banks than previously thought for abandoned agricultural fields when viewed at the landscape scale, giving rise to increased optimism on natural regeneration potential.

Studies of grassland development on ex-arable land are less common for Northern and Western European grasslands, although promising results have come from Germany (Conrad & Tischew 2011) and Sweden (Öster et al. 2009). In the United Kingdom, such studies appear restricted to a short-term (4 years), multi-site field experiment undertaken by Pywell et al. (2002) in southern England. This compared natural plant regeneration with seeding and concluded, at least over the short timescale of the study, that seeding preceded by deep cultivation was most successful. Nonetheless, the study also recognized that continued monitoring was required to be sure that the conclusions of the study were upheld in the longer term. A pioneer of English hay meadow restoration, Miriam Rothschild, emphasized the key importance of a good seedbank and poor soils not subjected to fertilizer input for formerly cropped fields, noting that, in some restorations, a "*delightful*" aspect was the appearance of rare plants which were not present in added seed mixtures, but which apparently "*came in from the cold*" (Feltwell 1992). Inspired by Rothschild's comments and responding to a need for more studies of natural regeneration potential for Northern and Western European grasslands, we document the spontaneous response of vegetation to mowing and time for a small former arable field in eastern England, United Kingdom, and evaluate success against likely British mesotrophic grassland conservation targets. The implications of our study for species-rich hay meadow restoration on ex-arable land are considered.

Methods

Study Site

Sayer's Old Meadow (hereafter Old Meadow) is located in the village of Bodham in North Norfolk, eastern England, and covers an area of 1.7 ha (Fig. 1). It is situated in a predominantly arable agricultural landscape interspersed by small patches of deciduous woodland and improved grassland, with most farmed fields enclosed by hedgerows. The meadow slopes downward from both its north (high of 66 m asl) and south sides (high of 67 m asl) to a low point of 64 m asl in the center. Maximum average daily temperature ranges from 7.4°C in January to 21°C in August, and mean annual precipitation is approximately 636 mm, with highest rainfall typically occurring during autumn and winter (date range for Weybourne 1991–2020—MetOffice 2024). Geological parent material consists of Upper Cretaceous Chalk bedrock, overlain by chalk-rich boulder clay, with the soil being free-draining, sandy, and slightly acidic (LandIS® 2024).

Old Meadow was used as permanent pasture for milking cows until the 1950s. From around 1950 to the early 1970s it was plowed up and used, on rotation, for arable crops (including

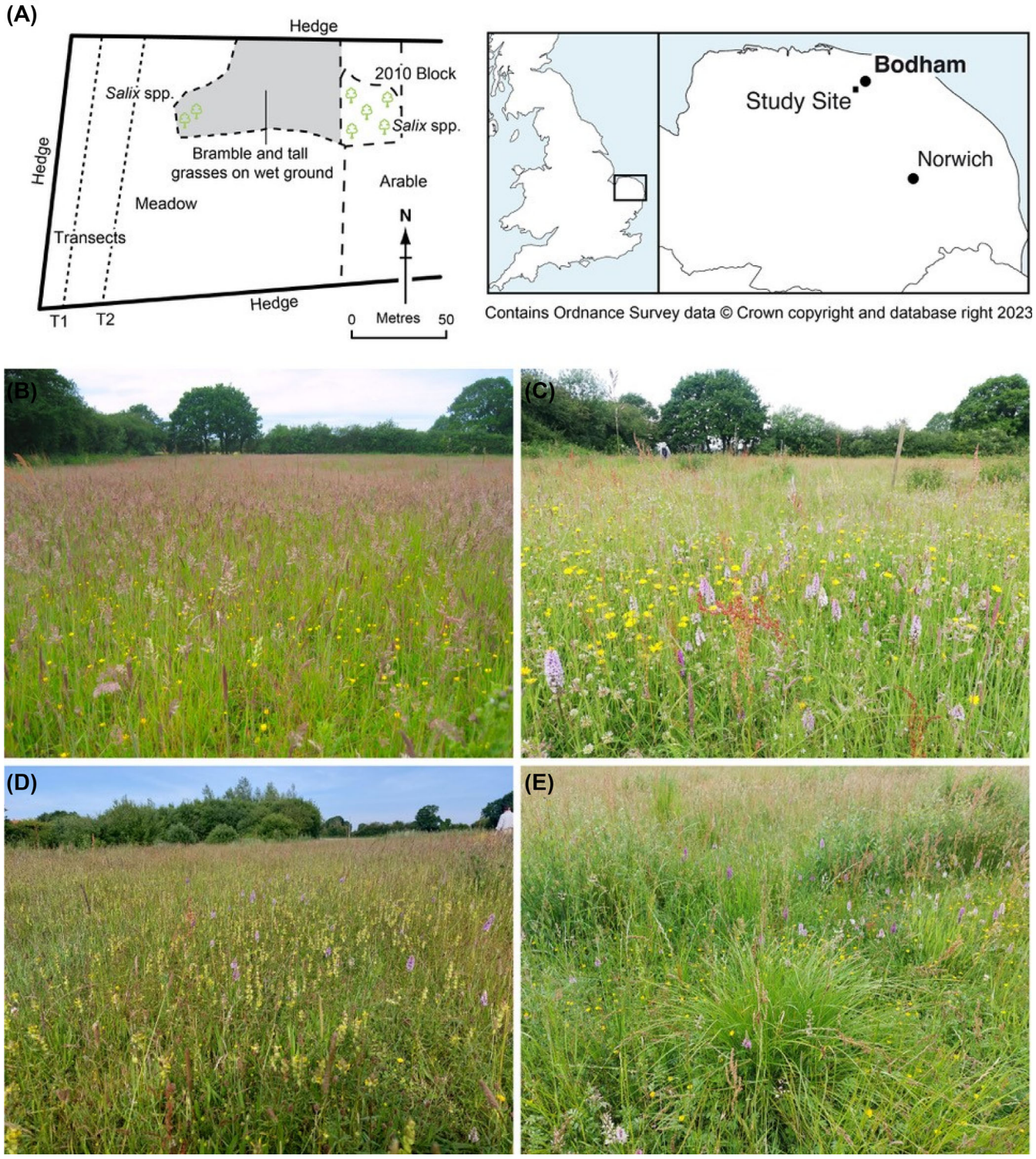


Figure 1. Location of Sayer's Old Meadow (A). Looking west in 2014 (B) and the same view in 2019 (C). Photos from 2022 showing a dense patch of *Rhinanthus minor* (D) and a tussock of the locally scarce *Carex paniculata* (E).

wheat, barley, mangles, and suedes) followed by sowing with Perennial ryegrass (*Lolium perenne*) and grazing by a small bovine herd. During this time, artificial fertilizers were also occasionally applied to the field. After the early 1970s, Old Meadow became a permanent arable field used for growing wheat, barley, oats, sugar beet (on rotation), and on one occasion

potatoes. Oil seed rape (*Brassica napus* subsp. *oleifera*) was added to the aforementioned crops after the late 1990s. During this phase of arable, the field was subject to regular annual use of fertilizers and other agrochemicals. Following the harvest of a final rape crop in 2005, the field was left fallow for 6 years. Due to waterlogging, a small northern section of the field (Fig. 1A) was only plowed over and cropped on one occasion between the 1950s and 1995. This area has long been dominated by tall grasses, Bramble (*Rubus fruiticosus* agg.) and Grey willow (*Salix cinerea*), with frequent standing water present in winter–spring.

Conservation-focused management of the meadow commenced in 2011 after the 6-year fallow period with the majority of the field subject to annual cutting and removal of material (as hay bales) in August–September. Only the small wet area in the north of the field and an adjacent north-eastern block of former arable land (left to woodland development—largely *Salix* spp.) were exempt from this management (Fig. 1A). Between 2011 and 2022, Common Ragwort (*Jacobaea vulgaris*) was hand-picked and removed annually from the meadow prior to mowing due to its toxicity to cattle when included in hay.

Vegetation Surveys

Vegetation surveys of the meadow were undertaken every 2 years in 2011–2019. Covid-19 prevented the planned survey for 2021 and hence 2022 was used as the next feasible survey year. In all surveys, plants were recorded along two permanent south–north transects (Fig. 1A), located on the eastern side of the field (around 10 and 30 m from the field edge hedgerow, respectively), covering the main (north to south) moisture gradient at the site, using 1 × 1 m quadrats spaced at 10 m intervals. Both transects had 12 quadrats giving 24 permanent plots in total. In parallel, all plants on the meadow were recorded via an exhaustive walk-over survey, which was terminated when no further plants could be found in at least 10–15 minutes of searching. This took around 2–3 hours for two people in each year. Efforts were made to cover all areas of the meadow by walking along parallel lanes of approximately 5 m width. Finally, to track the first occurrence and early spread of Common spotted orchid (*Dactylorhiza fuchsii*) (2013–2016), Southern marsh orchid (*D. praetermissa*) (2013–2016), and Yellow rattle (*Rhinanthus minor*) (2016–2021), individual plant occurrences were recorded (to an accuracy of 3–5 m) using a hand-held Garmin Etrex Global Positioning System (GPS). These species were targeted for a detailed study of distribution change as the earliest locally scarce species (orchids, especially *D. praetermissa*), and for being a key hemiparasitic species (*R. minor*). Surveys continued until 2015 for *D. fuchsii* and *D. praetermissa*, and until 2021 for *R. minor*, after which occurrences of these species were too frequent for the task to be practical. All plant identifications followed Stace (2024). Over the period of this study, the 1 km^2 area (monad) within which Old Meadow resides was subjected to extensive plant surveys spanning all habitats (primarily hedges, field margins, and arable fields). These data afforded the opportunity to assess each Old Meadow species in terms of local occurrence and rarity.

Data Analysis

Alpha-diversity of all plots along the two transects was calculated using a number of diversity measures: Observed species richness per quadrat (hereafter species density), Shannon diversity in its exponential form (Jost 2006), Simpsons diversity, and the dominance-based Berger-Parker Index. As all diversity indices were highly correlated (Pearson correlation, $p < 0.001$ in all cases), we only consider patterns for observed species density and Shannon diversity in this manuscript. Temporal diversity changes were analyzed using an ANOVA with a Scheffé post hoc test, calculated using the IBM SPSS Statistics for Windows (Version 29) software package. We also assessed changes in γ-diversity, as the entire meadow plant species pool, by combining walkover survey and quadrat data. We furthermore determined the degree of local species rarity by identifying species appearing in the meadow which were not present in the extensive survey data available for Old Meadow's 1 km^2 monad. To characterize vegetation heterogeneity within surveys and temporal changes in species composition, we used a correspondence analysis (CA), performed using the CANOCO 5 software package (ter Braak & Šmilauer 2010). In a second step, we split each of the two transects into two sections (0–60 and 70–120 m). For each section, we then recorded the frequency (number of "present" records for each plant species across all quadrats in each transect section), leading to four data points of frequency data for each census year. This data was then analyzed by the MAVIS 1.03 software package (CEH 2016). MAVIS provides weightings for plant communities, as defined by the British National Vegetation Classification (NVC) system (Rodwell 1992), that each of the data points is most closely associated with. The NVC system was used as it forms the basis for many vegetation-based conservation targets and decisions. We were particularly interested to establish the degree to which the meadow flora was changing toward NVC mesotrophic meadow communities with high conservation significance, namely MG4 *Alopecurus pratensis–Sanguisorba officinalis*, MG5 *Cynosurus cristatus–Centaurea nigra*, and MG8 *C. cristatus–Caltha palustris* grassland (Rodwell 1992). To obtain this information, the transect section × plant community matrix based on the MAVIS output formed the foundation of a second CA.

Results

Species Diversity Change

In total, combining all surveys, 156 plant species, including vascular plants and mosses, were recorded in the meadow between 2011 and 2022. Of these, 86 and 154 were found in the quadrat and walk-over surveys, respectively. Diversity varied greatly between individual quadrats along the transects in each year, with this heterogeneity partly masking between-year diversity variation. Nonetheless, both plant species density (species/m^2) and Shannon diversity were significantly lower over the period

2011–2013 in comparison to the period 2017–2022, with a clear trend of year-on-year diversity increase visible (Fig. 2). The overall species pool (γ-diversity) (Table 1) also showed an increasing trend over the study period. In 2011, a total of 63 species were found in the meadow, which increased gradually to 86 species by 2022. The number of new species recorded for the meadow (Table 1, Table S1) was very high for the 2013, 2015, and 2017 surveys (19, 17, and 18 new species, respectively), but lower for the 2019 and 2022 surveys (six and eight new species, respectively).

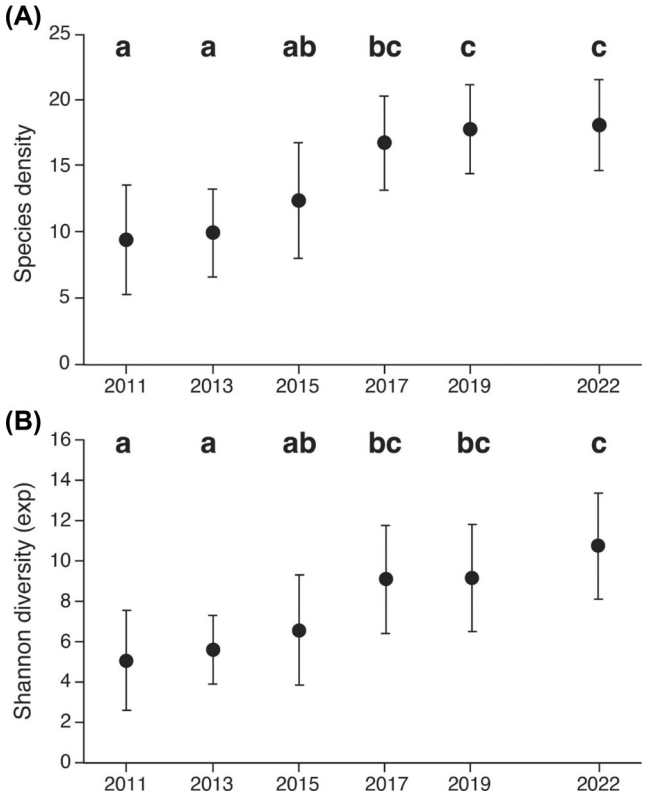


Figure 2. Temporal change in average species density (A) and Shannon diversity (exponential form) (B) for the quadrats in Sayer's Old Meadow over 2011–2022. Error bars show plot-based ± SD and letters above them indicate statistically significant differences between years ($p < 0.05$, based on an ANOVA using the Scheffé post hoc test).

Changing Meadow Composition and Species Rarity

In combination, the quadrat-based CA (Fig. 3) and walk-over survey species lists show clear successive vegetation shifts for the meadow.

In the CA, the plots on the first axis (7.8% explained variance) follow a distinct temporal pattern, with early survey plots and species located at high axis values and later survey plots and species at low axis values. In the early years post-mowing (2011 and 2013), the quadrats were dominated by the grasses *Holcus lanatus*, *Poa trivialis*, and *Agrostis stolonifera*, as well as ruderal species, especially *Equisetum arvense*, *Cirsium arvense*, *Potentilla anserina*, and to a lesser extent *Epilobium hirsutum*. Many typical arable weed species present in the meadow flora in 2011 (walk-over survey data only) were lost by 2013 and not seen subsequently, including *Anagallis arvensis*, *Papaver rhoeas*, *Triplerospermum inodorum*, and *Polygonum aviculare* (Table S1). The year 2013 saw the first arrival of the locally scarce orchid *Dactylorhiza praetermissa*.

In the 2015 survey plots, some grass species (especially *H. lanatus*) remained dominant, but legumes (Fabaceae), especially *Viccia cracca*, *V. sativa*, and *Trifolium dubium*, had a greater percentage contribution to the quadrats (Fig. 4). Although overall grass cover declined in the quadrats between 2011 and 2015, the latter year saw the arrival of three new grass species, namely *Phleum pratense*, *Lolium multiflorum*, and *Schedonorus pratensis*, as well as the locally scarce sedge *Carex flacca*.

The percentage cover of grasses in the quadrats showed a further substantial decrease by 2017 (2011–2017 decline from 93 to 64.7%; Fig. 4), reflecting sharp declines of *Elymus repens* and *P. trivialis*, while *H. lanatus* maintained a relatively stable

Table 1. Overall changes in the flora of Sayer's Old Meadow 2011–2022 detailing the arrival of new species, species losses and the numbers of species present that are scarce in the wider countryside.

Year of survey (no. of years since abandonment)	*Total no. species in flora*	*No. species new to flora*	*Species permanently lost from the flora (not seen subsequently)*	*Number and identity of locally scarce species*
2011 (6)	63	—	—	0
2013 (8)	67	19	8	1: *Dactylorhiza praetermissa*
2015 (10)	77	17	6	2: *Carex flacca*, *D. praetermissa*
2017 (12)	82	18	8	9: *C. flacca*, *C. muricata* subsp. *pairae*, *Centaurium erythraea*, *Cynosaurus cristatus*, *D. praetermissa*, *Daucus carota*, *Isolepis setacea*, *Rhinanthus minor*, *Trifolium arvense*
2019 (14)	79	6	10	8: *C. flacca*, *C. muricata* subsp. *pairae*, *C. cristatus*, *D. praetermissa*, *D. carota*, *Holcus mollis*, *Luzula campestris*, *R. minor*
2022 (17)	86	8	8	11: *C. flacca*, *C. divulsa* subsp. *leersii*, *C. obtrubae*, *C. muricata* subsp. *pairae*, *C. paniculata*, *C. erythraea*, *C. cristatus*, *D. praetermissa*, *D. carota*, *H. mollis*, *R. minor*

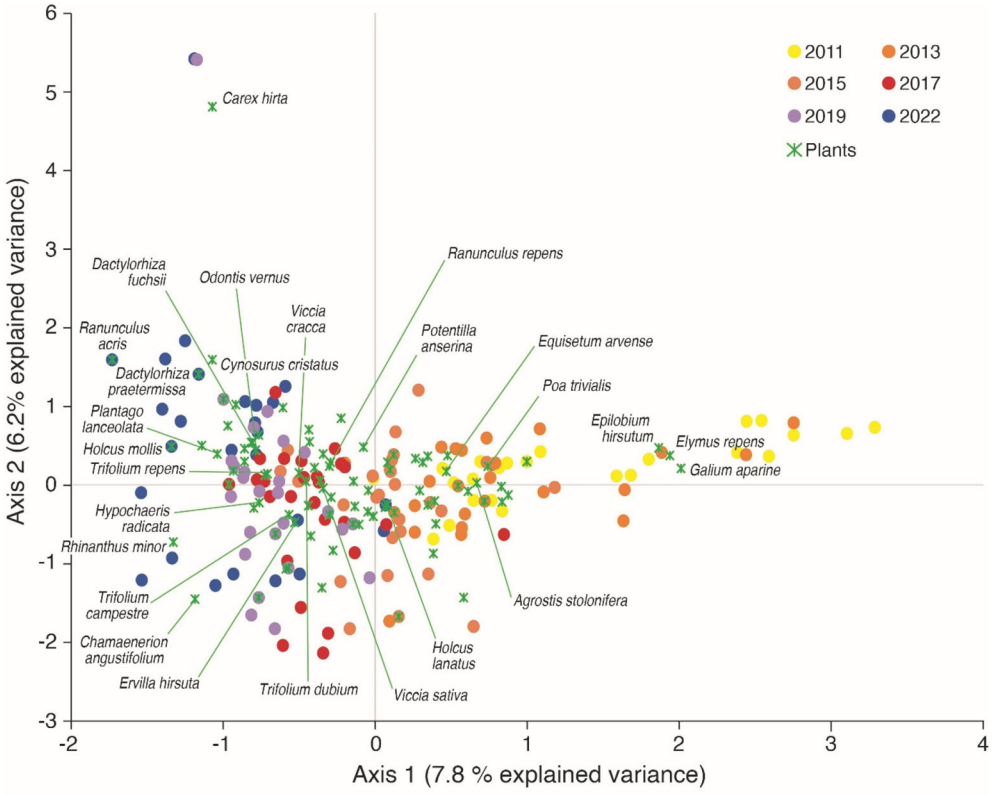


Figure 3. Correspondence analysis of Sayer's Old Meadow vegetation quadrats over 2011–2022, with stars indicating the modeled center of each plant species' maximum abundance / maximum occurrence likelihood, and the colored points marking the modeled centers for each plot in relation to its plant community composition.

cover at around 39%. The 2017 quadrats also exhibited a continued shift toward legume-dominance (with an average cover of 52.7%; Fig. 4), with additional legume species becoming abundant, including *T. repens*, *T. campestre*, and *Ervilla hirsuta* (Table S1). Both *Ranunculus repens* and *Hypochaeris radicata* also became more abundant in 2017, which saw the arrival of eight additional locally scarce species: *C. muricata* subsp. *pairae*, *Centaurium erythraea*, *Daucus carota*, *Isolepis setacea*, *Lotus corniculatus*, *Rhinanthus minor*, *Trifolium arvense*, and *Cynosurus cristatus* (Table 1).

While the 2019 quadrats show high ordination space overlap with the 2017 samples (Fig. 3), there are some important underlying compositional changes occurring, including a reduction in the dominance of legumes (Fig. 4), as well as an increase in the hemiparasitic *Odontites vernus* (first recorded in 2017 at 0.4%) to 4.2%. New arrivals of locally scarce species in this year included the locally scarce *Luzula campestris*, as well as *H. mollis* (Table 1). After 2017, grasses generally stabilized in terms of quadrat cover.

Between 2019 and 2022, the plots showed greater variation along CA axis 2, suggesting a potential heterogenization of the meadow flora (Fig. 3). Between these years, *C. cristatus*, *R. minor* (Fig. 1D), and *Plantago lanceolata* showed major abundance increases, while legumes continued a strong decline (Fig. 4), especially for the species *T. repens* and *E. hirsuta*. Three new locally scarce sedge (Cyperaceae) species were found in the walk-over survey in 2022: *Carex obtrubae*, *C. divulsa*, and *C. paniculata* (Fig. 1E). *Calamagrostis epigejos* was also found for the first time in this year. In this later period, ruderal species (e.g. *E. repens*), abundant in the early years post-mowing, had declined to become only very minor components of quadrat percentage cover.

The CA based on the NVC system (Fig. 5) again showed a strong shift along the first ordination axis (21.6% explained variance) from high to low values over time. In the early years post land abandonment, vegetation components representing open vegetation and ruderal communities dominate, interspersed with some early succession grassland assemblages. As time progresses, there is a phase of apparent relative stability in terms of plant classes, followed by a distinct shift and diversification of grassland vegetation types in the final two surveys in 2019 and 2022. In this timespan, vegetation elements representing British NVC communities MG8 (mesotrophic grassland *C. cristatus–Caltha palustris* grassland), MG5 (unimproved neutral grassland *C. cristatus–Centaurea nigra* grassland) and MG4c (mesotrophic grassland *Alopecurus pratensis–Sanguisorba officinalis* grassland) become increasingly important, showing that grassland communities of high conservation

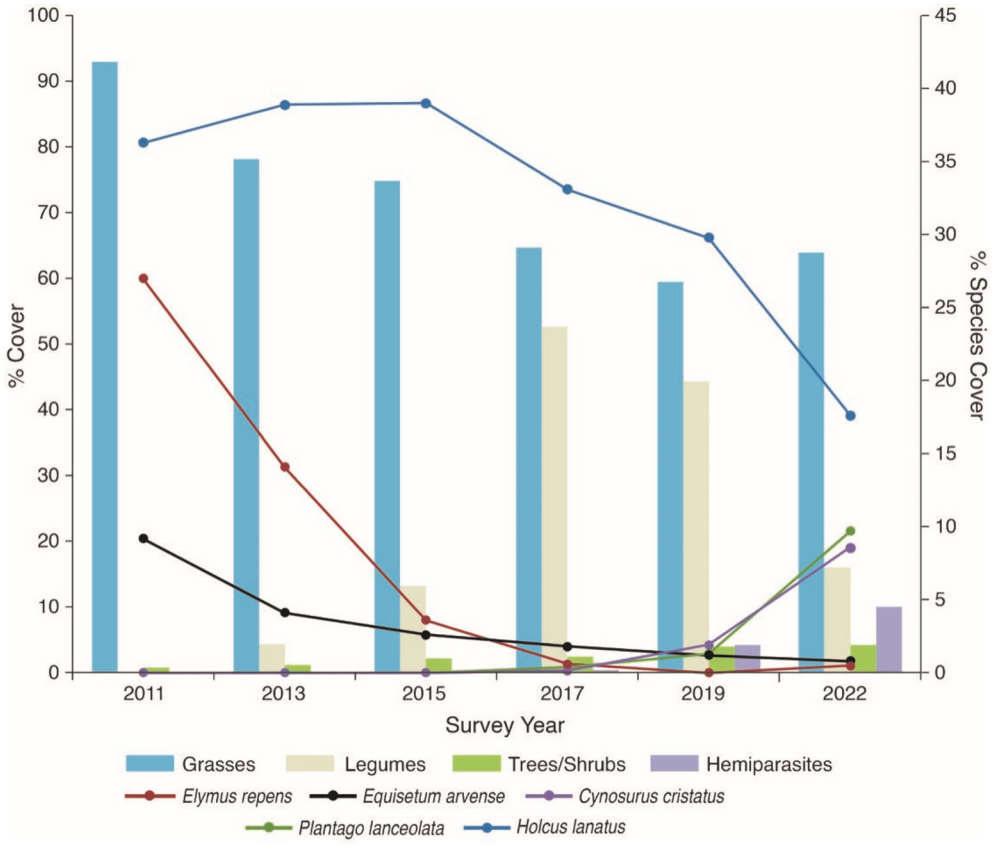


Figure 4. Percentage contribution of key plant groups and five key species to quadrat cover in Sayer's Old Meadow over 2011–2022. *Elymus repens* and *Equisetum arvense* were selected as dominant ruderal species. *Holcus lanatus* was selected as a dominant grass species. *Cynosurus cristatus* was selected as an indicator of mesotrophic grassland. *Plantago lanceolata* was selected as a species less vulnerable to parasitism by *Rhinanthus minor*.

interest are emerging as potential restoration endpoints in the hay meadow succession.

Colonization Patterns for *D. fuchsii*, *D. praetermissa* and *R. minor*

Both *D. fuchsii* and *D. praetermissa* were first recorded in 2013, some 8 years after the last harvest of the field and 2 years following the first hay cut. In 2013 *D. praetermissa* was restricted to a single spike in the south-west corner, with 12 spikes of *D. fuchsii* found in the south-west corner and central meadow area (Fig. 6). By 2014 both orchid species had spread considerably (especially *D. fuchsii*) in these areas, but with an expansion of *D. fuchsii* into eastern and western central areas. In 2015, the number of *D. fuchsii* spikes had increased considerably, with a distinct filling in of gaps between previous orchid-dominated patches. In addition, *D. praetermissa* was recorded in the eastern central area for the first time. *D. fuchsii* was occupying large areas of the field by 2016, with colonization of the north-west corner. Following 2016, the abundance of *D. fuchsii*, was so high (compare Fig. 1B & 1C) that mapping of this species was impractical. By 2022, *D. fuchsii* was found, often at high density, in all areas of the meadow with *D. praetermissa* also widely distributed, but with major concentrations in the north-east and north-west corners.

R. minor was first recorded in 2016 in the north-west corner (2 m^2 patch) of the field and by 2017 a second patch was present in the western central area (Fig. 7). By 2018 there had been a rapid expansion of *R. minor* with seven small patches (made up of a few individual plants) recorded in the western part of the meadow and with a new patch found in the south-eastern corner. Expansion of *R. minor* continued in 2019 with further patches recorded in the western area and with two additional sites found in the eastern central area. In 2021, the original *R. minor* patch (of 2016) had resulted in spread of the plant throughout almost all of the north-west part of the meadow (black block in Fig. 7) with many new plants and patches found in central and eastern areas and in the south-western corner. By 2022 (Fig. 1D), the plant was so frequent (attaining 8.8% in the quadrats) that mapping became impractical.

Discussion

In many parts of the world (Cramer et al. 2008) and especially in Eastern and Central Europe (Valkó et al. 2016), there has been a recent trend for taking farmed land out of agricultural production. Similarly, in the United Kingdom, there is a current push toward large-scale landscape recovery projects that necessitate the restoration and re-vegetation of ex-arable land (Defra 2023).

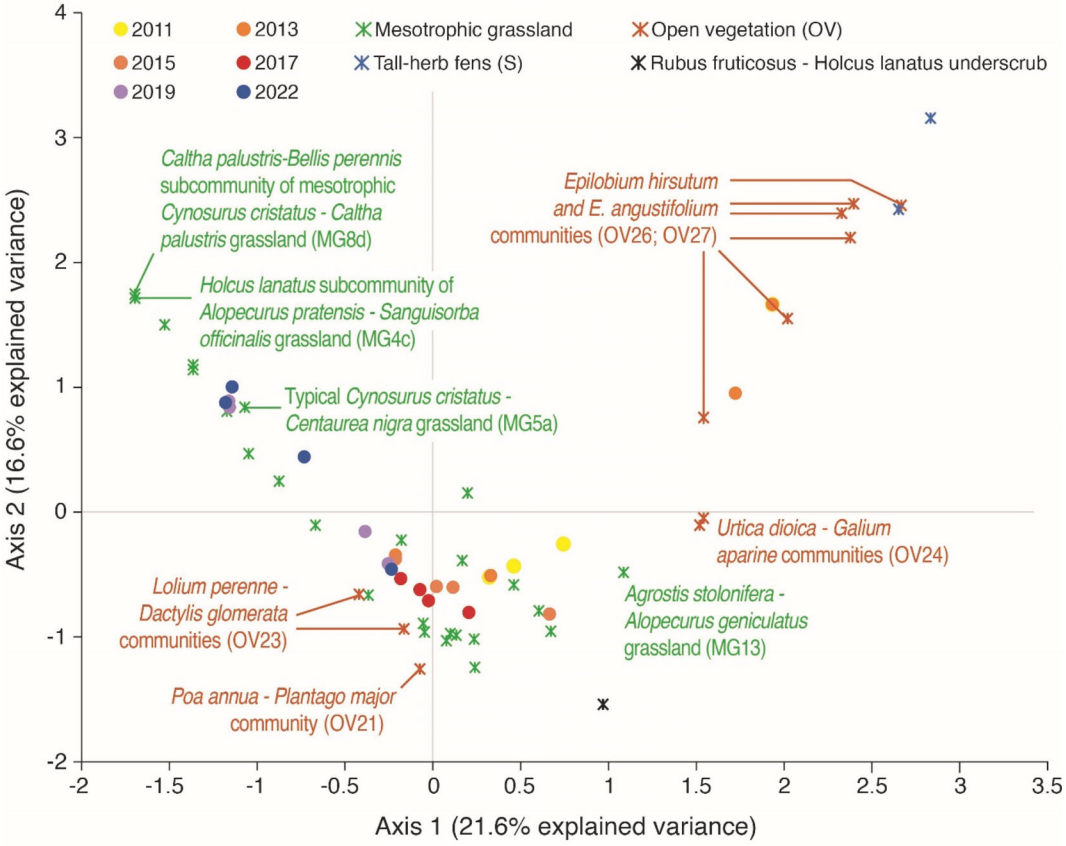


Figure 5. Correspondence Analysis of Sayers Old Meadow vegetation quadrats 2011–2022 showing the relative vegetation contributions of different British National Vegetation Classification (NVC) grassland types. The dots represent the vegetation data of the four annual data points forming the basis of the MAVIS-based classification (see main text), while the stars represent NVC-based plant communities associated with the respective vegetation data.

This trend opens up the opportunity for restoring species-rich grasslands, but the degree to which this might be achieved spontaneously, at scale, without active introduction of seeds (of commercial or local origin) is relatively poorly understood. A still prevalent view is that, due to hostile soil conditions, impoverished and short-lived seedbanks, dominance by persistent arable weeds and the long-time scales deemed necessary for success, seeding is preferable in grassland restoration. As a consequence, seed introduction has been the favored choice for restoring species-rich meadows in agri-environment schemes and many conservation projects (Conrad & Tischew 2011; Kiss et al. 2022).

Contradicting the prevailing view on a need for seeding, Old Meadow shows a highly positive outcome from spontaneous grassland restoration under a mowing regime. There are caveats in that Old Meadow is just one site with the survey restricted to two transects on the western side of the meadow. Nevertheless, the findings from Old Meadow are replicated across many other ex-arable grasslands in continental Europe (Csecserits & Rédei 2001; Lencová & Prach 2011; Sojneková & Chytrý 2015). Following the commencement of mowing in 2011, it took around 4 years to emerge from a ruderal plant-dominated phase, with formerly abundant species such as *Equisetum arvense* and *Elymus repens* undergoing major declines in dominance by 2015. High ruderal cover in the early years after arable abandonment was likely due to the persistence of weedy arable-associated species in the field's seedbank (Török et al. 2010). The decline of ruderal species in Old Meadow can probably be explained by increasing competition from perennial plants, especially legumes, whose cover peaked in 2017.

The most recent successional phase (post-2019) in Old Meadow would appear to be at least partly driven by the hemiparasitic action of the expanding *Rhinanthus minor* population. In Old Meadow this mechanism seems a likely explanation for the decline of *Holcus lanatus* and legumes over 2017–2022, as well as the increasing dominance of *Plantago lanceolata* between 2019 and 2022 (1.3–9.7%), a species known to be less vulnerable to *R. minor* parasitism (Cameron & Seel 2007). In the future, in accordance with the "rock-paper-scissors" population dynamics model developed by Cameron et al. (2009), once the *R. minor* invasion and consequent high parasitism has peaked, a new more stable co-dominance of forbs and grasses should develop. Future site surveys will provide an opportunity to evaluate the applicability of this model, including the nature and stability of meadow community composition in the context of regenerating ex-arable land.

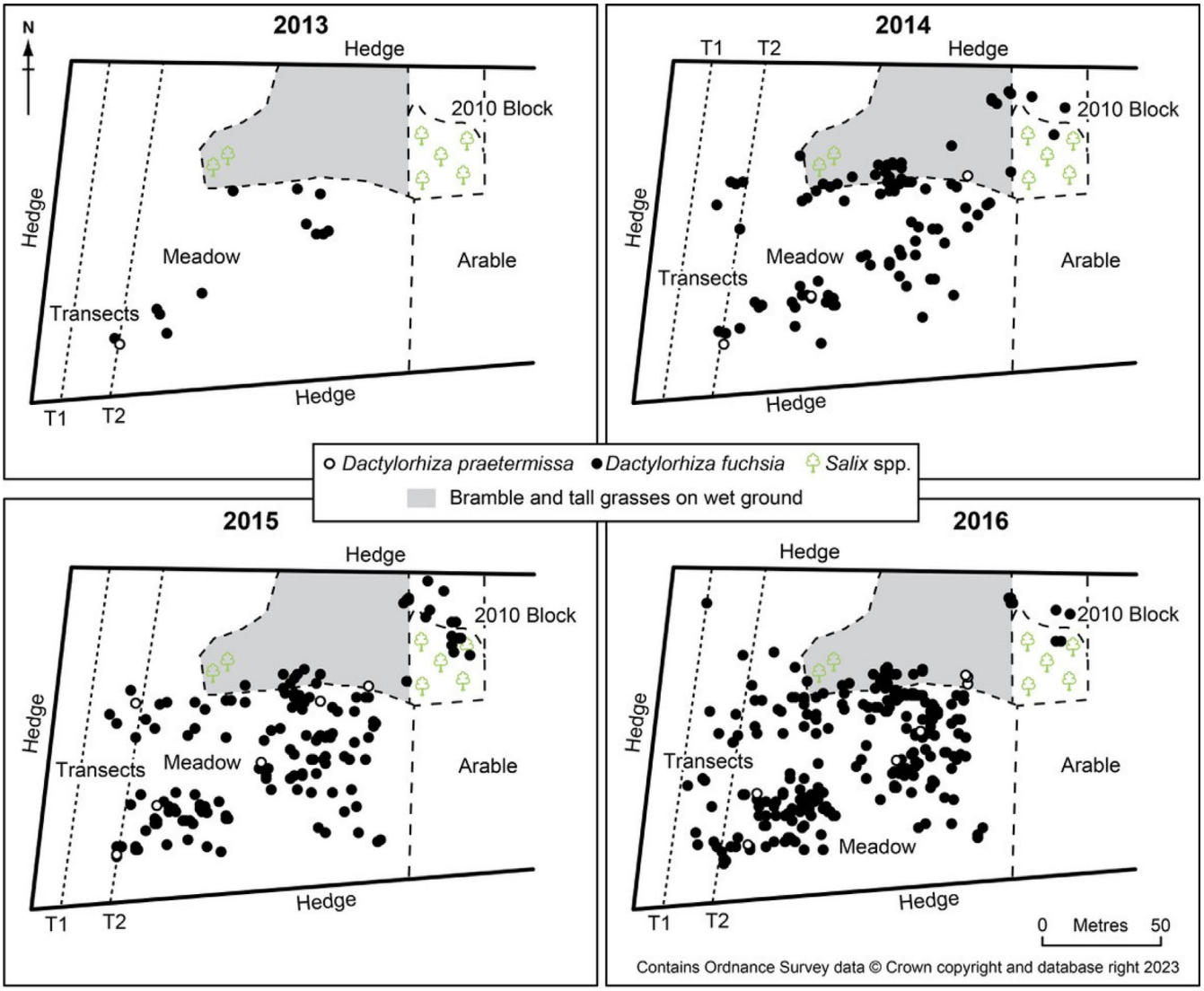


Figure 6. Distribution and spread of *Dactylorhiza praetermissa* (open circles) and *D. fuchsii* (closed black circles) in Sayer's Old Meadow over 2013–2016.

It is clear from the progressive shifts in vegetation composition in the ordination analysis that Old Meadow is still undergoing substantial species turnover. However, just 17 years post-abandonment and 11 years post-mowing, there has been a major desired decline in highly competitive grasses (especially of *H. lanatus*) and emergence of a species-rich community supporting a number of locally uncommon "target" grassland species largely absent from the wider farmed countryside. Other studies of spontaneous succession in former arable fields have shown similar results, with the timescales for grassland recovery varying between 10 and 20 years (Lencová & Prach 2011; Albert et al. 2014; Prach et al. 2014) and less commonly 20–40 years (Boecker et al. 2015; Sojneková & Chytrý 2015). Thus, Old Meadow appears to be following a comparable restoration pathway to grasslands elsewhere. This is significant, as research on grassland recovery in ex-arable land is widely lacking in the United Kingdom. Ordination analysis of the Old Meadow transect data in the context of British NVC communities MG4, MG5, and MG8 shows that these mesotrophic grassland types, all of which are highly valued from a conservation perspective in the United Kingdom, may afford realistic targets for the site in the future. That the meadow is clearly moving in the direction of these grassland types is hence a highly positive restoration outcome.

Origins of Meadow Vegetation Diversification

The relatively rapid transition from an intensively farmed arable field to a species-rich hay meadow supporting a number of locally uncommon plants is not easily explained. A number of studies have shown that seedbanks on land that becomes arable are short-lived, rendering them unlikely to drive grassland recovery (Török et al. 2010). While the arrival and rapid spread of the two *Dactylorhiza* spp. orchids observed in this study can

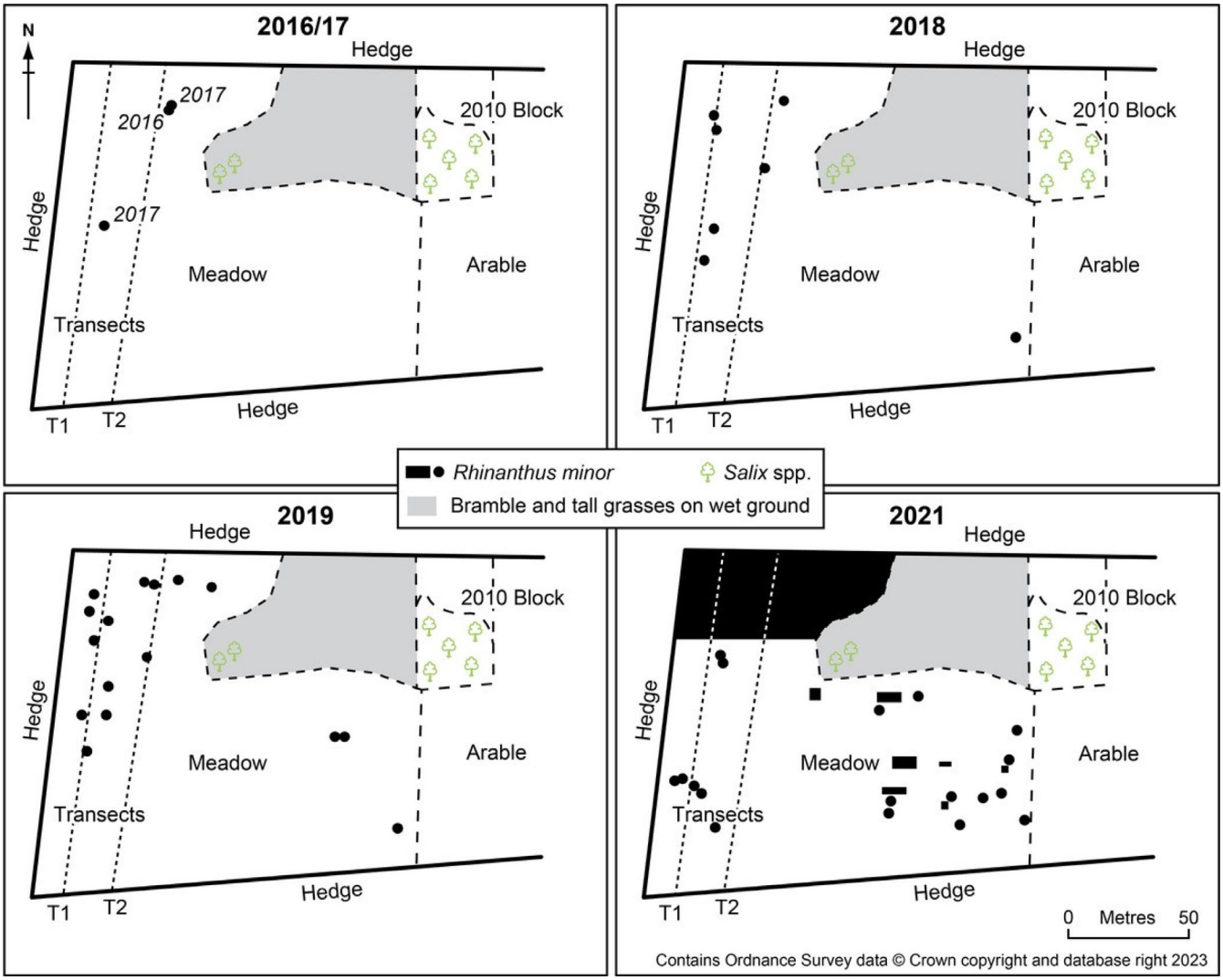


Figure 7. Distribution and spread of *Rhinanthus minor* in Sayer's Old Meadow over 2016–2021. Black dots are one *R. minor* plant or a few plant individuals and black blocks approximate substantial *R. minor*-dominated patches.

be readily attributed to wind dispersal, due to their very small and light-weight "dust seeds" (Harrap & Harrap 2005), the same cannot be said of most other species. Given this, it might be reasonably concluded that long-distance animal dispersal or inadvertent human-dispersal (e.g. on clothing, boots, or machinery) was key to plant arrival in Old Meadow. Many studies of spontaneous succession have emphasized the importance of proximal (perhaps <500 m) seed sources for scarcer, often specialist plants due to dispersal limitation (Török et al. 2011; Sojneková & Chytrý 2015). For example, in Romanian old fields, Ruprecht (2006) showed that propagule pressure, assessed as the area of potential seed sources in a 500 m radius buffer, had a significant influence on grassland recovery. As typical of English lowland farmland, however, Old Meadow is relatively isolated from remnant patches of high-quality grassland. The nearest fragment of old species-rich grassland is a churchyard (13th Century church in Bodham) 0.9 km distant but, with the exception of *Luzula campestris*, all other locally scarce plants that colonized Old Meadow are absent from this site. There are four additional semi-natural valley fen grasslands between 3.4 and 4.7 km away which, in combination, do support all of the locally scarce species present in the study meadow. However, the arable agricultural matrix between the meadow and these more distant sites likely greatly reduces animal dispersal potential. Further, arrival of propagules via machinery is unlikely as the contractor who cuts and bales the meadow otherwise works in species-poor commercial grasslands. Thus, the mechanism via which rarer plants assembled so quickly in Old Meadow is obscure.

No species is more puzzling in terms of its appearance in the meadow than *R. minor*. This plant first occurred in 2016, with its nearest other known location being some 3.4 km distant. *R. minor* is an annual species with seeds not thought to enter dormancy, hence largely ruling out a seed bank source

(Westbury 2004). Further, its seeds are large, which is thought to reduce dispersal via wind or animals to between a few meters of parent plants (Coulson et al. 2002; Bullock et al. 2003). Hence, the rapid spread and rise to dominance of *R. minor* over 2016–2022 is hard to explain, perhaps indicating more effective seed dispersal by animals or people than hitherto thought. In this respect, deer-mediated dispersal seems most likely (Albert et al. 2015). Non-native Muntjac deer *Muntiacus reevesi* and native Roe deer *Capreolus capreolus* and Red deer *Cervus elaphus* are all common in the area, with the former two species especially abundant.

Prior to abandonment, Old Meadow was subject to fertilizer application, but this was probably not as intensive as for many United Kingdom farmed fields due to the small-scale nature of the Sayer family farming operation. This, in conjunction with free-draining soils in the study field that readily leach nutrients, may have quickly reduced the nutrient-enrichment constraint (Janssens et al. 1998) acting as a key facilitating factor of grassland recovery. The importance of soil conditions to meadow secondary succession is suggested in a number of studies showing relatively rapid grassland recovery for free-draining nutrient-poor soils (Csecserits & Rédei 2001; Ruprecht 2005, 2006). In addition, seepage of calcium-rich water through the soils of the field could also have been critical due to phosphorus co-precipitation with calcite rendering it unavailable for plant growth (Boyer & Wheeler 1989). Changing nutrient status over the course of the successional process is unknown for our study site, however. Equally, the quality of the seedbank prior to abandonment in Old Meadow was not studied so further work is necessary in this direction.

Natural Unassisted Grassland Recovery

Introductions of locally or commercially collected seeds dominate meadow restoration practice (Conrad & Tischew 2011; Lencová & Prach 2011). In particular, use of commercial seed mixes is popular in agri-environment schemes looking to turn former arable land into conservation grassland due to ease of availability and the speed at which high ground cover is usually achieved (Conrad & Tischew 2011). However, sowing can sometimes introduce non-local species and genotypes which are not well placed to cope with local conditions (Lencová & Prach 2011), which can also homogenize plant communities at the landscape scale (Mudrák et al. 2022). In addition, some studies have shown that seeded fields do not always progress toward regionally typical remnant species-rich grassland (Conrad & Tischew 2011). This may be because introduction of competitively dominant and high seed-producing species reduces the successful immigration of local plants into grasslands (Walker et al. 2014), but more work is needed to test this idea. The vast majority of seeded agri-environment grasslands and field margins in the study region are dominated by *Leucanthemum vulgare*, *Centaurea debauxii*, and *Lotus corniculatus*, all of which are present but rare in the meadow. Hence, in supporting a different potentially more locally characteristic grassland community, including a good number of locally scarce species, Old Meadow is making an important contribution to local wild plant conservation. As the site is owned by the family of the first author, its sustainable management is guaranteed. However, given its relative isolation from other species-rich grasslands, the degree to which species diversity will continue to increase and mesotrophic grassland types MG4, MG5, and MG8 are achieved is unknown, with the possibility that additional management and/or targeted future species translocations will be beneficial.

As advocated by Prach et al. (2001), to help understand the conditions that permit natural recovery (or not) of target grassland communities, we encourage scientists and conservationists to undertake more real-time studies of plant compositional patterns and soil structure, chemistry and biology changes following the abandonment of arable land. We suspect that free-draining soils may be an important prerequisite for rapidly achieving species-rich grassland on ex-arable land, but more studies will be needed here. There is potential to save money with a natural regeneration approach, which in turn more easily enables large landscape-scale grassland recovery. With ever increasing recognition of the importance of working at large spatial scales in nature recovery projects that encompass grassland restoration, we pose the question: should we be employing patience over seed packet more often?

Acknowledgments

We thank the late and brilliant Steve Henson of Norfolk Wildlife Trust and River Glaven Conservation Group for good early advice on meadow management. Thanks also to Miles Irving for drawing the figures, Suki Pryce for survey assistance and encouragement, Will and Richard Amies and Tom Youngman for undertaking hay meadow management and Diane, Callum, and JP Ringer for assistance with Common ragwort *Senecio jacobaea* removal and much general support. Finally, we thank three reviewers and the Restoration Ecology editorial team for some very useful comments that have much improved the clarity of this paper. We dedicate this paper to Herbert Breese who wandered the fields of the area with CDS and who inspired a life loving nature in the study patch.

LITERATURE CITED

Albert A-J, Auffret AG, Cosyns E, Cousins SAO, D'hondt B, Eichberg AE, Heinken T, et al. (2015) Seed dispersal by ungulates as an ecological filter: a trait-based meta-analysis. Oikos 124:1109–1120. https://doi.org/10.1111/oik.02512

Albert A-J, Kelemen A, Valkó O, Miglécz T, Csecserits A, Rédei T, Deák B, Tóthmérész B, Török P (2014) Secondary succession in sandy old-fields: a promising example of spontaneous grassland recovery. Applied Vegetation Science 17:214–224. https://doi.org/10.1111/avsc.12068

Albert A-J, Mudrák O, Jongepierová I, Fajmon K, Frei I, Ševčíková M, Klimešová J, Doležal J (2019) Grassland restoration on ex-arable land by transfer of brush-harvested propagules and green hay. Agriculture, Ecosystems and Environment 272:74–82. https://doi.org/10.1016/j.agee.2018.11.008

Baasch A, Engst K, Schmiede R, May K, Tischew S (2016) Enhancing success in grassland restoration by adding regionally propagated target species. Ecological Engineering 94:583–591. https://doi.org/10.1016/j.ecoleng.2016.06.062

Bardgett RD, Bullock JM, Lavorel S, Manning P, Schaffner U, Ostle N, et al. (2021) Combatting global grassland degradation. Nature Reviews Earth & Environment 2:720–735. https://doi.org/10.1038/s43017-021-00207-2

Bekker RM, Verweij GL, Smith REN, Reine R, Bakker JP, Schneider S (1997) Soil seed banks in European grasslands: does land use affect regeneration perspectives? Journal of Applied Ecology 34:1293–1310. https://doi.org/10.2307/2405239

Boecker D, Centeri C, Welp G, Möseler BM (2015) Parallels of secondary grassland succession and soil regeneration in a chronosequence of central-Hungarian old fields. Folia Geobotanica 50:91–106. https://doi.org/10.1007/s12224-015-9210-3

Boyer MLH, Wheeler BD (1989) Vegetation patterns in spring-fed calcareous fens: calcite precipitation and constraints on fertility. Journal of Ecology 77:597–609. https://doi.org/10.2307/2260772

Bullock JM, Moy IL, Coulson SJ, Clarke RT (2003) Habitat-specific dispersal: environmental effects on the mechanisms and patterns of seed movement in a grassland herb *Rhinanthus minor*. Ecography 26:692–704. https://doi.org/10.1034/j.1600-0587.2003.03525.x

Cameron DD, Seel WE (2007) Functional anatomy of haustoria formed by *Rhinanthus minor*: linking evidence from histology and isotope tracing. New Phytologist 174:412–419. https://doi.org/10.1111/j.1469-8137.2007.02013.x

Cameron DD, White A, Antonovics J (2009) Parasite-grass-forb interactions and rock-paper-scissor dynamics: predicting the effects of the parasitic plant *Rhinanthus minor* on host plant communities. Journal of Ecology 97:1311–1319. https://doi.org/10.1111/j.1365-2745.2009.01568.x

CEH (UK Centre for Ecology & Hydrology) (2016) Modular analysis of vegetation information system (MAVIS). UK Centre for Ecology & Hydrology, Wallingford, United Kingdom. https://www.ceh.ac.uk/form/software-request-form

Conrad MK, Tischew S (2011) Grassland restoration in practice: do we achieve the targets? A case study from Saxony-Anhalt/Germany. Ecological Engineering 37:1149–1157. https://doi.org/10.1016/j.ecoleng.2011.02.010

Coulson SJ, Bullock JM, Stevenson MJ, Pywell RF (2002) Colonization of grassland by sown species: dispersal versus microsite limitation in response to management. Journal of Applied Ecology 38:204–216. https://doi.org/10.1046/j.1365-2664.2001.00585.x

Cramer VA, Hobbs RJ, Standish RJ (2008) What's new about old fields? Land abandonment and ecosystems assembly. Trends in Ecology & Evolution 23:104–112. https://doi.org/10.1016/j.tree.2007.10.005

Csecserits A, Rédei T (2001) Secondary succession on sandy old-fields in Hungary. Applied Vegetation Science 4:63–74. https://doi.org/10.1111/j.1654-109X.2001.tb00235.x

Defra (Department for Environment, Food & Rural Affairs) (2023) Landscape recovery: round 1. https://www.gov.uk/government/publications/landscape-recovery-more-information-on-how-the-scheme-will-work/landscape-recovery-more-information-on-how-the-scheme-will-work (accessed 8 Aug 2025)

Dengler J, Janišová H, Török P, Wellstein C (2014) Biodiversity of palaearctic grasslands: a synthesis. Agriculture, Ecosystems & Environment 182:1–14. https://doi.org/10.1016/j.agee.2013.12.015

Donath TW, Bissels S, Hölzel N, Otte A (2007) Large scale application of diaspore transfer with plant material in restoration practice – impact of seed and microsite limitation. Biological Conservation 138:224–234. https://doi.org/10.1016/j.biocon.2007.04.020

Feltwell J (1992) Meadows: a history and natural history. Sutton Publishing, Stroud, Gloucestershire, United Kingdom

Habel JC, Samways MJ, Schmitt T (2019) Mitigating the precipitous decline of terrestrial European insects: requirements for a new strategy. Biodiversity and Conservation 28:1343–1360. https://doi.org/10.1007/s10531-019-01741-8

Harrap A, Harrap S (2005) Orchids of Britain and Ireland. A&C Black, London, United Kingdom

Hedberg P, Kotowski W (2010) New nature by sowing? The current state of species introduction in grassland restoration, and the road ahead. Journal for Nature Conservation 18:304–308. https://doi.org/10.1016/j.jnc.2010.01.003

Janssens F, Peeters A, Tallowin JRB, Bakker JP, Bekker RM, Fillat F, Oomes MJM (1998) Relationship between soil chemical factors and grassland diversity. Plant and Soil 202:69–78. https://doi.org/10.1023/A:1004389614865

Jost L (2006) Entropy and diversity. Oikos 113:363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Kiss R, Deák B, Tóth K, Lukács K, Rádai Z, Kelemen A, Miglécz T, Tóth A, Godó L, Valkó O (2022) Co-seeding grasses and forbs supports species-rich grasslands and improves weed control in ex-arable land. Scientific Reports 12:21239. https://doi.org/10.1038/s41598-022-25837-4

Kiss RT, Tóthmeresz B, Valkó O, Török P (2016) Seedbank research in central-European grasslands – an overview. Pages 1–33. In: Murphy J (ed) Seed banks: types, roles and research. Nova Scientific Publishers, New York

Klimbowska A, Diggelen RV, Bakker JP, AbP G (2007) Wet meadow restoration in Western Europe: a quantitative assessment of the effectiveness of several techniques. Biological Conservation 140:318–328. https://doi.org/10.1016/j.biocon.2007.08.024

Knappová J, Hemrová L, Münzbergová Z (2012) Colonization of central European abandoned fields by dry grassland species depends on the species-richness of source habitats: a new approach for measuring habitat isolation. Landscape Ecology 27:97–108. https://doi.org/10.1007/s10980-011-9680-5

Kuhn T, Görzen E, Sohrabi M, Donath TW, Ruprecht E (2025) Seed bank as a source for the spontaneous regeneration of dry grasslands on former arable fields in an agro-pastoral landscape. Restoration Ecology 33:e70112. https://doi.org/10.1111/rec.70112

LandIS® (2024) LandIS: the land information system. https://www.landis.org.uk/soilsguide/wrb.cfm?wrbc=RG (accessed 8 Feb 2024)

Lencová K, Prach K (2011) Restoration of hay meadows on ex-arable land: commercial seed mixes vs. spontaneous succession. Grass and Forage Science 66:265–271. https://doi.org/10.1111/j.1365-2494.2011.00786.x

MetOffice (2024) UK climate maps and data. https://www.metoffice.gov.uk/research/climate/maps-and-data/uk-climate-averages/u127sby66 (accessed 8 Feb 2024)

Mudrák O, Hrabovský A, Dvorský M, Liancourt P, Albert A-J, Doležal J, Čierniková M, Hölzel N, Májeková M (2022) Grassland restoration on former arable land: fine-scale grass accumulation and damaged soil conditions limit species establishment. Applied Vegetation Science 25:e12665. https://doi.org/10.1111/avsc.12665

Öster M, Ask K, Römermann C, Tackenberg O, Eriksson O (2009) Plant colonisation of ex-arable fields from adjacent species-rich grasslands: the importance of dispersal vs. recruitment ability. Agriculture, Ecosystems & Environment 130:93–99. https://doi.org/10.1016/j.agee.2008.12.005

Prach K, Bartha S, Jorce CB, Pyšek P, van Diggelin R, Gerhard W (2001) The role of spontaneous vegetation succession in ecosystems restoration: a perspective. Applied Vegetation Science 4:111–114. https://doi.org/10.1111/j.1654-109X.2001.tb00241.x

Prach K, Jongepierovác I, Řehounková K, Fajmon K (2014) Restoration of grasslands on ex-arable land using regional and commercial seed mixtures and spontaneous succession: successional trajectories and changes in species richness. Agriculture, Ecosystems & Environment 182:131–136. https://doi.org/10.1016/j.agee.2013.06.003

Pywell RF, Bullock JM, Hopkins A, Walker KJ, Sparks TH, Burkes MJW, Peel J (2002) Restoration of species rich grassland on arable land: assessing the limiting processes using a multi-site experiment. Journal of Applied Ecology 39:294–309. https://doi.org/10.1046/j.1365-2664.2002.00718.x

Resch MC, Schütz M, Graf U, Wagenaar R, van der Putten WH, Risch AC (2019) Does topsoil removal in grassland restoration benefit both soil nematode and plant communities? Journal of Applied Ecology 56:1782–1793. https://doi.org/10.1111/1365-2664.13400

Rodwell JS (1992) British plant communities volume 3 – grasslands and montane communities. Cambridge University Press, Cambridge, United Kingdom

Ruprecht E (2005) Secondary succession in old-fields in the Transylvanian lowland (Romania). Preslia 77:145–157. https://www.preslia.cz/article/340

Ruprecht E (2006) Successfully recovered grassland: a promising example from Romanian old fields. Restoration Ecology 14:473–480. https://doi.org/10.1111/j.1526-100X.2006.00155.x

Sojneková M, Chytrý M (2015) From arable land to species-rich semi-natural grasslands: succession in abandoned fields in a dry region of central Europe. Ecological Engineering 77:373–381. https://doi.org/10.1016/j.ecoleng.2015.01.042

Stace C (2024) New flora of the British Isles. 4th ed. C & M Floristics, Southend-On-Sea, United Kingdom

Stroh PA, Hughe FMR, Sparks TH, Mountford OJ (2012) The influence of time on the soil seedbank and vegetation across a landscape-scale wetland restoration project. Restoration Ecology 20:103–112. https://doi.org/10.1111/j.1526-100X.2010.00740.x

ter Braak C, Šmilauer P (2010) Canoco reference manual and user's guide: software for ordination (version 5.0). Microcomputer Power, Ithaca, New York

Török P, Brudvig LA, Kollmann J, Price JN, Tóthmérész B (2021) The present and future of grassland restoration. Restoration Ecology 29:1–6. https://doi.org/10.1111/rec.13378

Török P, Deák B, Vida E, Valkó O, Lengyel S, Tóthmérész B (2010) Restoring grassland biodiversity: sowing low-diversity seed mixtures can lead to rapid favourable changes. Biodiversity and Conservation 143:806–812. https://doi.org/10.1016/j.biocon.2009.12.024

Török P, Kelemen A, Valkó O, Miglécz T, Tóth K, Tóth E, et al. (2018) Succession in soil seed banks and its implications for restoration of calcareous sand grasslands. Restoration Ecology 26:S134–S140. https://doi.org/10.1111/rec.12611

Török P, Vida E, Deák B, Lengyel S, Tóthmérész B (2011) Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. Biodiversity and Conservation 20:2311–2332. https://doi.org/10.1007/s10531-011-9992-4

Valkó O, Deák B, Török P, Kelemen A, Miglécz T, Tóth K, Tóthmérész B (2016) Abandonment of croplands: problem or chance for grassland restoration? Case studies from Hungary. Ecosystem Health and Sustainability 2: e01208. https://doi.org/10.1002/ehs2.1208

van Dijk G (1991) The status of semi-natural grasslands in Europe. Pages 15–36. In: Goriup PD, Batten LA, Norton JA (eds) The conservation of lowland dry grassland birds in Europe. JNCC, Newbury, United Kingdom

Vécrin MP, van Diggelen R, Grevilliot F, Muller S (2002) Restoration of species-rich flood-plain meadows from abandoned arable fields in NE France. Applied Vegetation Science 5:263–270. https://doi.org/10.1111/j.1654-109X.2002.tb00556.x

Veen P, Jefferson R, de Smidt J, van der Straaten J (2009) Grasslands in Europe of high nature value. KNNV Publishing, Zeist, Netherlands. https://doi.org/10.1163/9789004278103

Wagner M, Hulmes S, Hulmes L, Redhead JW, Nowakowski M, Pywell RF (2021) Green hay transfer for grassland restoration: species capture and establishment. Restoration Ecology 29:e13259. https://doi.org/10.1111/rec.13259

Wagner M, Walker KJ, Pywell RJ (2017) Seed bank dynamics in restored grasslands following the sowing of high- and low-diversity seed mixtures. Restoration Ecology 26:S189–S199. https://doi.org/10.1111/rec.12616

Walker KJ, Stevens PA, Stevens DP, Mountford OJ, Manchester SJ, Pywell RF (2014) The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. Biological Conservation 119:1–18. https://doi.org/10.1016/j.biocon.2003.10.020

Wesche K, Krause B, Culmsee H, Leuschner C (2012) Fifty years of change in central European grassland vegetation: large losses in species richness and animal-pollinated plants. Biological Conservation 150:76–85. https://doi.org/10.1016/j.biocon.2012.02.015

Westbury DB (2004) *Rhinanthus minor* L. Journal of Ecology 93:906–927. https://doi.org/10.1111/j.0022-0477.2004.00929.x

Supporting Information

The following information may be found in the online version of this article:

Table S1. Species lists for each of the six years of survey (2011, 2013, 2015, 2017, 2019, 2022) in Sayers Old Meadow.

Coordinating Editor: Leonardo Teixeira

Received: 20 November, 2025; First decision: 7 January, 2026; Revised: 1 May, 2026; Accepted: 15 June, 2026