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Identifying time lags in the restoration of grassland butterfly communities: A multi-site assessment

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Abstract

Although grasslands are crucial habitats for European butterflies, large-scale declines in quality and area have devastated many species. Grassland restoration can contribute to the recovery of butterfly populations, although there is a paucity of information on the long-term effects of management. Using eight UK data sets (9-21 years), we investigate changes in restoration success for (1) arable reversion sites, were grassland was established on bare ground using seed mixtures, and (2) grassland enhancement sites, where degraded grasslands are restored by scrub removal followed by the re-instigation of cutting/grazing. We also assessed the importance of individual butterfly traits and ecological characteristics in determining colonisation times. Consistent increases in restoration success over time were seen for arable reversion sites, with the most rapid rates of increase in restoration success seen over the first 10 years. For grasslands enhancement there were no consistent increases in restoration success over time. Butterfly colonisation times were fastest for species with widespread host plants or where host plants established well during restoration. Low mobility butterfly species took longer to colonise. We show that arable reversion is an effective tool for the management of butterfly communities. We suggest that as restoration takes time to achieve, its use as a mitigation tool against future environmental change (i.e. by decreasing isolation in fragmented landscapes) needs to take into account such time lags.

Highlights

- We assessed limiting factors for butterflies during grassland restoration.

- For arable reversion restoration success increased to a plateau over time.
- Restoration success did not change over time under grassland enhancement.
- Restoration is promoted by rapid host-plants establishment.
- Dispersal and the national distribution of host plants limit colonisation.

Keywords

Arable reversion; Calcareous; Grassland Enhancement; Mesotrophic; Functional traits; Recreation

1. Introduction

Across Europe, the wide-scale loss and degradation of species-rich grassland has created a pressing need to augment remaining areas using grassland restoration (Bakker and Berendse, 1999, Blackstock *et al.*, 1999, Pywell *et al.*, 2003 and van Swaay, 2002). Grasslands are an important habitat not just for plants, but are also crucial to the conservation of UK and European butterflies (Brereton, 2004 and van Swaay, 2002), providing breeding and foraging habitat for more than 90% of UK species (Brereton, 2004). By restoring grasslands there is the potential to mitigate against extinction debts caused by long-term habitat fragmentation (Kuussaari *et al.*, 2009), while increasing functional connectivity essential for climate change adaptation policies (Hodgson *et al.*, 2009).

Agri-environmental schemes represent the principal mechanism in Europe by which financial incentives are provided to restore grasslands (Critchley *et al.*, 2003). For plants, the success achieved during restoration is often variable, with recruitment processes, competitive interactions and underlying abiotic factors limiting success (Bakker and Berendse, 1999, Bischoff, 2002, Fagan *et al.*, 2008 and Pywell *et al.*, 2003). Where restoration is on existing grasslands that have become degraded as a result of infrequent or absent management, restoration typically involves the removal of scrub and the re-instigation of extensive grazing and cutting regimes (Crofts and Jefferson, 1999 and Redhead *et al.*, 2012). Overcoming dispersal limitation by sowing seeds is also an important approach used during grassland restoration, although is most often applied to sites that have been used for alternative land uses, such as arable agricultural (Bakker and Berendse, 1999, Bischoff, 2002, Edwards *et al.*, 2007 and Öster *et al.*, 2009). Host-plant establishment during restoration is crucial for phytophagous invertebrate assemblages (Bakker and Berendse, 1999, Edwards *et al.*, 2007, Pöyry *et al.*, 2004, Woodcock *et al.*, 2012 and Woodcock *et al.*, 2010). This is particularly important as the artificial introduction of invertebrates during restoration is often too expensive to be widely used, and colonisation by invertebrates is therefore usually by natural immigration only (Littlewood *et al.*, 2012 and Woodcock *et al.*, 2010).

The high cost of grassland restoration means that quantification of its success is of fundamental importance to policy makers and conservationists alike (Matthews *et al.*, 2009).

Grasslands are defined on the basis of their vegetation, and restoration success has generally been valued on the basis of plant species' establishment (Bakker and Berendse, 1999, Edwards *et al.*, 2007, Matthews *et al.*, 2009 and Rodwell, 1992). In contrast, quantification of restoration success for invertebrates, which tend to be more speciose than plants (Tscharntke and Greiler, 1995), has been largely ignored (Fagan *et al.*, 2010, Littlewood *et al.*, 2012, Pöyry *et al.*, 2004 and Woodcock *et al.*, 2010). This reflects the often limited information about what species are expected to establish, as well as a fundamental lack of knowledge about their expected relative abundances in target communities (Pöyry *et al.*, 2004 and Woodcock *et al.*, 2010). Assessments of long-term community level responses are vital to address this paucity of data and will allow us to understand which factors limit invertebrate restoration. Long-term data sets (>10 years) linked with restoration studies, while rare for plants, are almost entirely lacking for invertebrates. Butterflies represent one of the best recorded invertebrate taxa, and have well characterised life-histories and plant feeding associations (Asher *et al.*, 2001). Their charismatic appearance and ecological suitability as indicator species also makes them a useful flagship group for promoting management in grasslands (Asher *et al.*, 2001, New *et al.*, 1995 and Thomas *et al.*, 2009). Butterflies therefore represent a useful model for understanding, with the aim of overcoming, factors that limit restoration success for grassland invertebrates.

Here we assess the success with which butterfly communities re-establish during the restoration of calcareous and mesotrophic grasslands. We compare two forms of management applied to restore grasslands, representing the complete re-establishment of grasslands on land previously under different land uses, and the enhancement of degraded grasslands that have been poorly managed. To achieve this we use data sets describing the development of butterfly populations over time in response to grassland restoration. We aim to identify time lags between the start of restoration and the establishment of butterfly communities typical of species-rich grasslands (Pöyry *et al.*, 2004 and Woodcock *et al.*, 2010). While the development of butterfly communities is our principal measure of restoration success, understanding factors that limit colonisation rates for individual species has important implications, for example by identifying species unable to disperse in response to climate change (Hodgson *et al.*, 2009). We use a combination of species' traits and ecological characteristics to determine which factors decrease the mean time taken to colonise. We predict that: (1) mobile species will be the first to colonise; (2) butterflies feeding on host-plants that readily establish or are able to persist well during restoration will have a better chance of establishing early; (3) butterflies feeding on widely distributed host plants, or those butterflies that are widely distributed themselves, will be more likely to have source populations in the vicinity of restoration sites, and so more likely to colonise rapidly.

2. Materials and methods

We collected eight unpublished UK data sets, ranging in length from 9 to 21 years. Each data set records the establishment of butterfly communities during the restoration of either lowland mesotrophic hay meadows (three sites) or calcareous (five sites) grasslands (Table

1). The bias towards calcareous grasslands reflects their high importance as habitats for European butterflies (van Swaay, 2002). The restoration of these sites fell into two main categories: (1) Four sites were restored from bare soil using seed addition in the first year to overcome plant dispersal limitation (Bakker and Berendse, 1999 and Edwards *et al.*, 2007). We refer to this as ‘arable reversion‘ for consistency with published literature (Littlewood *et al.*, 2012), however, the bare soil in this study originated from ex-arable (two sites), ex-landfill (one site) and landscaping associated with road construction (one site). Arable reversion involves seed addition, as without this the impoverished seed banks would be unable to limit the establishment of weedy species (Bakker and Berendse, 1999 and Edwards *et al.*, 2007). (2) Four sites were managed as ‘grassland enhancement‘. These were floristically species poor and dominated by competitive or shade tolerant species, with some level of scrub encroachment resulting from the cessation of historic management practices (Crofts and Jefferson, 1999 and Redhead *et al.*, 2012). Enhancement involved scrub removal followed by the re-instigation of extensive cutting or grazing regimes. Long-term management differed among sites, reflecting historical management practices typical for a particular region and underlying soil type (see Table 1 for additional information). However, in all cases either grazing alone, or cutting combined with grazing were applied yearly. In no situation would inorganic fertilisers be applied to the restoration sites. Arable reversion and grassland enhancement represent two of the main forms of restoration currently undertaken to benefit butterflies in the UK (Brereton, 2004 and Crofts and Jefferson, 1999).

The availability of semi-natural grassland in the landscapes surrounding these arable reversion and grassland enhancement sites could play a role in determining restoration success by promoting connectance to source populations of butterflies (Maes and Bonte, 2006, Shepherd and Debinski, 2005 and Woodcock *et al.*, 2010). However, the data sets used in this study are long-term (up to 21 years) and as such year by year changes in landscape structure are not available over their duration. As such detailed analyses of the effects of landscape structure are not practical. However, based on the 2000 UK Land Cover Map (Fuller *et al.*, 2002) the proportions of semi-natural grassland at radii of 0.5 km, 1.0 km and 2 km surrounding the restoration sites were determined (Table 1). Semi-natural grassland excluded all grasslands that had been agriculturally improved by the use of inorganic fertilisers. There were no significant differences in the proportion of semi-natural grassland between the grassland enhancement and arable reversion sites (Anova: 0.5 km: $F_{1,6} = 1.49$, $p = 0.24$; 1.0 km: $F_{1,6} = 1.46$, $p = 0.27$; 2 km: $F_{1,8} = 0.34$, $p = 0.57$).

Table 1. Restoration site characteristics and management practices for the eight long-term data sets. Grassland habitat codes refer to those described by Rodwell (1992). Proportion of semi-natural grassland is derived from the 2000 UK Land Cover Map.

Tables

Site	Grassland type	Pre-restoration conditions	Restoration management	Duration	Proportion of semi-natural grassland surrounding site		
Grassland enhancement					0.5 km	1.0 km	2.0 km
Yew Hill, Hampshire (51°02′11.44″N 01°21′06″W)	CG2/CG3 calcareous	Scrubbed up grassland that had received no grazing or cutting.	Scrub removal followed by long-term re-instigation of low intensity sheep grazing.	19 years	0.052	0.057	0.357
Magdalene Hill Down Original, Hampshire (51°03′40″N 01°16′43″W)	CG2/CG3 calcareous	Scrubbed up grassland that had received no grazing or cutting.	Scrub removal followed by long-term re-instigation of low intensity sheep grazing.	21 years	0.000	0.017	0.242
Bentley Station Meadow, Hampshire (51°10′47″N 00°51′47″W)	MG5 Lowland Hay meadow	Meadow had become overgrown with scrub and was infrequently managed.	Scrub clearance followed by long-term re-instigation of cutting management and aftermath cattle / sheep grazing.	18 years	0.084	0.038	0.354
Millhoppers pasture, Hertfordshire (51°49′45″N 00°42′01″W)	MG5 Lowland Hay meadow	Rank grassland that had received no management for at least 5 years.	Some scrub clearance followed by long-term re-instigation of cutting management and aftermath cattle / sheep grazing.	12 years	0.133	0.105	0.532
Arable reversion							
Magdalene Hill Down Ext., Hampshire (51°02′58″N 01°17′14″W)	CG2/CG3 calcareous	Ex-arable land.	Re-seeding with local provenance seed mix with plugs of horseshoe vetch and common rock-rose in chalk scrapes. Long term sheep grazing.	11 years	0.051	0.022	0.191
A33 compensation area, Hampshire (51°02′54″N 01°18′45″W)	CG2/CG3 calcareous	An abandoned road covered with top soil.	Sown with a seed mixture derived from species rich calcareous grassland swards. Long term sheep grazing management.	9 years	0.253	0.174	0.359
M3 compensation area, Hampshire (51°02′27″N 01°18′53″W)	CG2/CG3 calcareous	Ex-arable land	Sown with a seed mixture derived from species rich calcareous grassland swards. Long term sheep grazing management.	11 years	0.195	0.170	0.426
Ryton Wood Meadows, Warick. (52°21′08″N 01°26′44″W)	MG5 Lowland Hay meadow	Ex-landfill site covered with top soil.	Sown with a principally grass seed mixture with some key forbs butterfly host plants. Long term cutting and sheep / cattle grazing management.	21 years	0.065	0.059	0.327

Table 1. Restoration site characteristics and management practices for the eight long-term datasets. Grassland habitat codes refer to those described by Rodwell (1992). Proportion of semi-natural grassland is derived from the 2000 UK Land Cover Map.

2.1. Butterfly monitoring

Data on butterfly abundance were collected following the standard transect based recording methodology described in Pollard and Yates (1993). The length of transects varied on the basis of individual site area and within site habitat variability. Transects were typically c. 2 km in length, and were always 5 m wide. Each year transects were walked from the beginning of April until the end of September (a maximum of 26 transects a year). Transect walks were undertaken between 10.45 am and 3.45 pm under dry conditions (>13 °C) with wind speeds less than a Beaufort scale 5. To account for differences in the number of individuals sampled at sites and between years, butterfly species richness was rarefied to the lowest common number of individuals (75) using the VEGAN package (Dixon, 2003) in the R statistical environment (R Core Development Team, 2008).

2.2. Similarity to target grasslands

To assess restoration success, extant examples of species-rich grassland were used to define target butterfly communities. Different target communities were used for lowland mesotrophic hay meadows and calcareous grasslands, reflecting differences in the butterfly communities that may be expected to establish (Asher *et al.*, 2001). Each target community (mesotrophic and calcareous) was created by averaging the abundance of butterfly species from three sites, representing examples of good quality species rich grassland from the same region. Targets for the calcareous grassland were Holtspur Bottom 51°36′22′′N 00°40′35′′W, St. Catherine′s Hill 51°02′39′′N 01°18′36′′W and Catherington Down 50°55′31′′N, 1°0′57′′W. Targets for mesotrophic hay-meadows were Wendleholme 50°51′48′′N 01°17′55′′W, Ashford Hill Woods and Meadows 51°21′10′′N 01°11′37′′W, Bubbenhall Meadow 52°20′33′′N 01°27′16′′W. There was no significant difference in the distance from restoration sites to respective target grasslands between arable reversion and grassland enhancement sites (Anova: $F_{1,22} = 0.16$, $p = 0.69$; mean distance between grassland enhancement and each target grasslands = 56.3 km SE ± 12.1; mean distance between arable reversion and each target grasslands = 48.6 km ± 15.3). Butterflies at these sites were recorded in the same way as the restored sites.

Restoration success was assessed by calculating the Euclidean distance between the summed abundance of butterfly populations present at a restoration site for a particular year and the target grassland communities. The target community was based on an average across multiple years at the target sites. While a year by year comparison would have been preferable there was insufficient data from the target communities to make this possible. Euclidean distance has been used in previous studies to measure successional trajectories relative to target communities for both plants and insects (Fagan *et al.*, 2008 and Woodcock *et al.*, 2010). Individual species abundance within a particular site and for a particular year was expressed as a proportion of the summed yearly abundance at that site. This proportional abundance corrected for different numbers of butterfly observations from transects of different lengths. Euclidean distance was defined as:

(1) $$ED_{jk} = \sqrt{\sum_{i=1}^{n} \left(X_{ij} - X_{ik} \right)^2}$$

where ED_{jk} is the Euclidean distance between sites j and k, X_{ij} is the proportional abundance of species i in sample j, and n is the number of butterfly species. There is an inverse relationship between the Euclidean distance and the similarity of samples. As the Euclidean distance between different restoration sites and their respective target communities often varied reflecting differences in the species numbers present at different sites, we used a scaled measure of Euclidean distance (ED_S) to define restoration success for the butterflies (Woodcock *et al.*, 2012).

(2) $$ED_S = 1-(ED_{tn}/ED_{Max})$$

where ED_{Max} is the maximum recorded Euclidean distance between the butterfly communities of a restoration site and that of the target community. Typically this was found in the first year of restoration; ED_{tn} is the Euclidean distance between the restoration site and its target community in the nth year after the start of restoration. ED_S ranges from 0 to 1, with this highest score being achieved if the restoration site and target communities share the same species with the same proportional abundances. Achieving an ED_S of 1 is biologically unrealistic as complete replication of target communities is unlikely. Note, the presence of species within restoration sites that were not common to the target community would reduce ED_S, even if restoration sites and target grasslands otherwise shared the same species with similar relative abundances. However, as a conservative estimate we suggest that $ED_S > 0.7$ represents a high degree of restoration success.

2.3. Butterfly ecological characteristics and traits

The time taken for butterfly species to colonise each site (i.e. the time to the first record at the site) was recorded in years, and then averaged for each species across all sites that the species colonised. This average colonisation time was related to individual species traits and ecological characteristics. Following Reich *et al.* (2003), traits represent species characteristics that have evolved in response to competitive interactions and abiotic environmental conditions, and are defined as any attribute likely to influence establishment, survival or fitness. For butterflies we used the following traits. (1) Mobility, based on published values in Cowley *et al.* (2001) which used expert opinion to rank butterflies from low to high mobility. This scoring was square root transformed. Ideally mobility would have been assessed on the basis of mark recapture experiments (Stevens *et al.*, 2010), however, such information was only available for a sub-set of the species considered and so this preferred approach was rejected as impractical. (2) Host-plant specialisation, by which species were defined as monophagous, strict oligophagous (feeding within a single plant genus), loose oligophagous (feeding within the same plant family), and polyphagous (BRC, 2009). In the case of host plants we focused on species that represent the main established feeding relationships of individual species. (3) Voltinism, with butterflies defined as having either single or multiple generations per year (Asher *et al.*, 2001 and Cowley *et al.*, 2001).

Ecological characteristics of butterflies describe aspects of individual species distribution or attributes of their host-plants. We used the following characteristics. (1) The number of 10 km squares in England and Wales in which the butterfly species had been recorded (Asher *et al.*, 2001). (2) The number of 10 km squares in England and Wales in which the most common of a butterfly species main host plants had been recorded (Preston *et al.*, 2002). (3) Host-plant regeneration strategy, defined as reproducing by seeds only, or reproducing at least in part clonally (Hill *et al.*, 2004). Where multiple principal host plants were present, a butterfly was considered to feed on a clonal plant if at least one of its food plants was clonal; (4) Annual or perennial host-plants (Hill *et al.*, 2004). (5) The competitive ability of the host plants, based on Grime *et al.* 's (1988) 'C' index (Dennis *et al.*, 2004). Where multiple host plants were present, we use the 'C' index for the most competitive of the principal food plants. (6) Success of establishment of main host plant. This was based on Pywell *et al.* (2003), which considered the success of plant establishment over the initial 4 years of grassland restoration, and represents a corrected index derived from multiple sites and grassland types. Success of establishment uses the corrected mean population size (N_c) of the host-plant in the first year of restoration. Based on this, species are classified as either (i) not being a target for grassland restoration (e.g. ubiquitous plants or pernicious weeds), or targets for restoration that have either (ii) good ($N_c > 0.5$), (iii) neutral ($N_c = 0.1\text{-}0.5$) or (iv) bad ($N_c < 0.1$) establishment in year one. (7) Persistence of main host plant following restoration. This is also based on the Pywell *et al.* (2003) data and uses a regression showing the trend in population growth over the first 4 years of restoration for the main host plant. As before, this is derived for multiple sites and grassland types. Main host plants are classified as being either (i) not a target for restoration, or either (ii) increasing (slope > 0.1), (iii) remaining constant (slope between -0.1 and 0.1) or (iv) declining (slope < -0.1) in cover following establishment. Note that for both success of establishment and persistence of host plant, thresholds used to define the categories above were based on expert opinion, and as such are arbitrary.

2.4. Data analysis

Following Matthews *et al.* (2009), the response of rarefied butterfly species richness (SR) and restoration success (ED_S) to the number of years of restoration were tested against three competing models. These were: (1) a null model, which assumed that species richness or restoration success did not change in response to the number of years of restoration, (SR or EDs = α); (2) a negative exponential function, which predicted that the temporal change in either species richness or restoration success would increase over time until an asymptote, where it would thereafter remain (SR or $ED_S = \alpha(1\text{-exp.}^{-\beta\cdot year})$); (3) a double exponential function, which predicted that species richness or restoration success would increase initially over time, but would then decline (SR or $ED_S = \alpha(\text{exp.}^{-c\cdot year} - \text{exp.}^{-\beta\cdot year})$). The fit of these three models to the data was assessed using non-linear mixed models (Proc NLMIXED) in SAS 9.01. Restoration site was included as a subject classification within the random effects to account for the repeated measures over time. Differentiation between the best fit models (i.e. the null model, negative exponential or double exponential) for either species richness or restoration success was achieved using Akaike's Information Criterion (AIC), which allows the comparison of models with different numbers of parameters. Separate analyses were run for the arable reversion and grassland enhancement sites. The duration over which butterfly communities were recorded differed between sites, ranging from 9 to 21 years (Table 1). To confirm the validity of parameter estimates for the tested models we repeated the analysis for a temporally reduced data set, restricted to a sampling period of less than 10 years of butterfly monitoring.

Typically, species‘ traits and ecological characteristics will show correlations and trade-offs as a result of biophysical limitations on structure and function (Weiher *et al.*, 1999). Such inter-correlated traits and ecological characteristics may individually have biological meaningful relationships with colonisation time. To fully explore relationships univariate responses of mean butterfly colonisation times to each of the 10 traits and ecological characteristics were performed. This was achieved using either simple regressions or ANOVA models, depending on whether explanatory variables where continuous or categorical. This was used as a sifting process to exclude traits or ecological characteristics that did not have a significant effect on mean butterfly colonisation time. Of those traits/ecological characteristics that were retained, a subsequent set of general linear models were run containing all possible combinations of these fixed effects, excluding interaction terms. This included models containing single explanatory variables up to one containing all retained traits and ecological characteristics. These models were again ranked using AIC to identify the single best model that explained butterfly colonisation times.

3. Results

A total of 277,175 individual butterflies were recorded using transect walks, representing 36 of the UK resident and regular migrant species (Asher *et al.*, 2001). As many UK butterflies are not grassland specialists this list represents a large proportion of species that might be expected to colonise during grassland restoration.

3.1. Species richness

Rarefied species richness of butterflies was not shown to change with the number of years of restoration for either the arable reversion or grassland enhancement sites. In both cases mean rarefied species richness was similar at c. 12-14 butterfly species. This lack of a response to year was indicated by the null model ($SR = \alpha$) having a better fit to the data (arable reversion: $AIC = 208.1$, $\alpha = 12.4$; enhancement: $AIC = 296.1$, $\langle = 13.1$) than either the negative exponential (arable reversion: $AIC = 214.7$; enhancement: $AIC = 325.6$) or double negative exponential functions (arable reversion: $AIC = 216.2$; enhancement: $AIC = 348.8$). When the analysis was repeated using the restricted data set limited to sampling points from less than 10 years (a sampling period common to all sites), the null models remained the best fit to the data for both seed addition and no-seed addition sites (arable reversion: $\alpha = 12.3$; enhancement: $\alpha = 13.7$). The results presented her are for the scaled Euclidean distance

(ED_S), reflecting the need to correct for differences in the numbers of species between restoration sites. However, see Electronic Appendix S1 for trends over time for raw Euclidean distances.

3.2. Similarity to target grasslands

Where arable reversion was used to restore the grasslands, the success of restoration in the butterflies increased to an asymptote, following the form of a negative exponential function ($ED_S = 0.72 \times (1\text{-exp}^{-0.24\times\text{year}})$; Fig. 1a). Restoration success tended to show a sharp increase within an initial 10 years of arable reversion. The asymptote for EDS was at *c.* 0.72 and indicates a relatively high degree of similarity to the target butterfly communities under arable reversion. The negative exponential function (AIC = 4.0) had a better fit to the data than either the null hypothesis (AIC = 9.4) or the double exponential function (AIC = 21.8). When the data set was restricted to data collected under 10 years, the negative exponential model remained the best fit to the data and retained parameter estimates comparable to those derived from the model based on longer term data set ($ED_S = 0.73 \times (1\text{-exp}^{-0.30\times\text{year}})$).

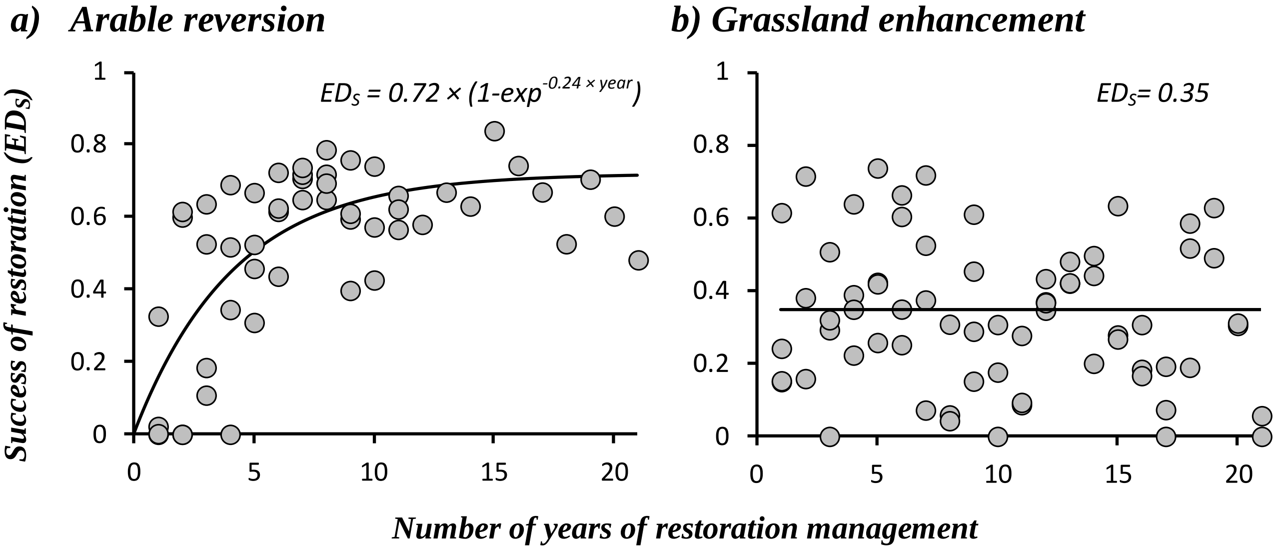


Fig. 1. Success in restoring butterfly communities typical of species-rich grasslands during grassland restoration by either arable reversion (a) or grassland enhancement (b). For arable reversion sites the negative exponential functions for the change in restoration success with years since the start of restoration management has been fitted. For the grassland enhancement sites there was no change in restoration success with year.

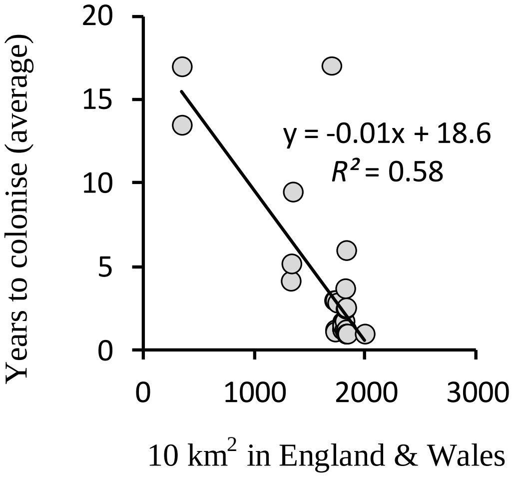
In contrast, restoration by grassland enhancement showed no evidence of an increase in restoration success over time, so that the null model gave the best fit to the data ($ED_S = 0.35$, AIC = -25.2) (Fig. 1b). The null model was superior to either the negative exponential function (AIC = -6.5) or the double exponential function (failed to converge in its parameter estimates). Restoration success was highly variable, and while restoration success was comparable to values seen under arable reversion in some years it did not remain consistently high. Using the restricted temporal data set (<10 years) the null model remained the best fit to the data ($ED_S = 0.36$).

3.3. Colonisation times for butterfly species

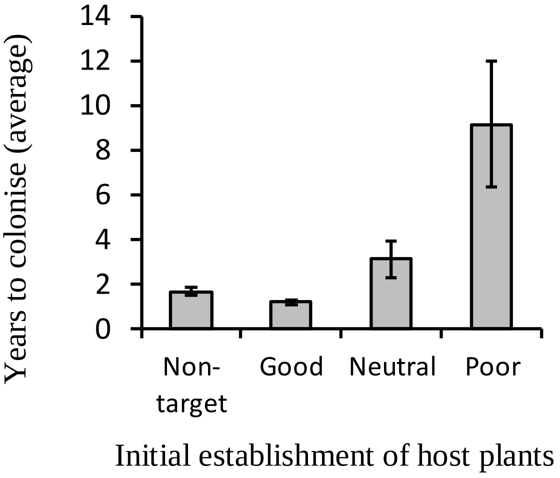
Initial univariate tests were undertaken to identify which of the explanatory traits and ecological characteristics showed significant correlations with butterfly mean colonisation times. Colonisation time reduced linearly in response to increasing national frequency of the butterflies host-plants ($F_{1,31} = 43.9$, $p < 0.001$; Fig. 2a). Butterfly colonisation was fastest where host-plants were either not actively encouraged during restoration (i.e. widespread species) or were characterised by good initial establishment or positive population growth following this establishment period. However, where host plants had poor initial establishment or showed negative population growth, colonisation times were slower. Both these responses were demonstrated by significant responses to both the establishment success of host-plants ($F_{2,30} = 8.86$, $p < 0.001$; Fig. 2b) and their subsequent trends in population growth during restoration ($F_{3,29} = 5.92$, $p < 0.01$; Fig. 2c). Colonisation times were lowest for the butterflies feeding on host plants that were not dependent on seed production, but could reproduce clonally ($F_{1,31} = 7.12$, $p < 0.01$; Fig. 2d). Finally, as butterfly mobility/dispersal decreased so did the mean colonisation times ($F_{1,31} = 7.57$, $p < 0.01$; Fig. 2e). None of the remaining traits or ecological characteristic were significantly correlated with mean colonisation times ($p > 0.05$). After testing all possible model combinations of the five traits and ecological characteristics identified as significant in the univariate tests, a model containing both the national frequency of host plants and host plant establishment success had the best fit to the data (AIC = 163.6).

Fig. 2. Effect of butterfly traits and ecological characteristics in predicting the mean colonisation times of butterflies during grassland restoration. In univariate tests colonisation time responded significantly to all the presented traits, however, the best fit model based on AIC includes ‘national frequency of host-plants‘ and ‘Host plant establishment success‘ only.

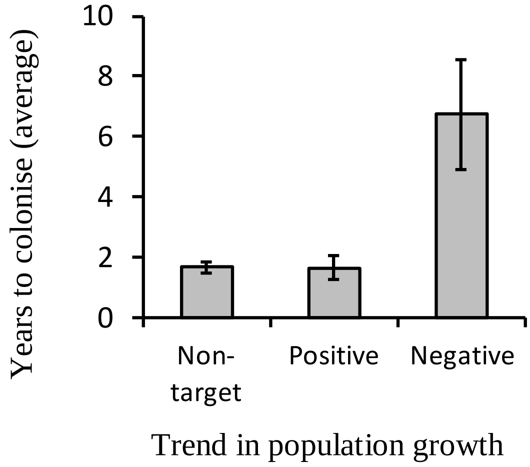
a) National frequency of host-plants



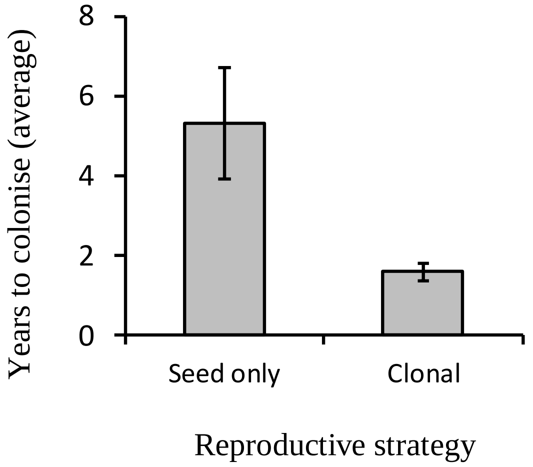
b) Host plant establishment success



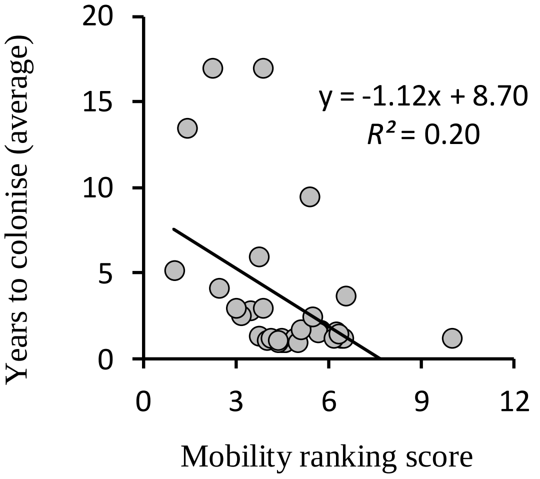
c) Host plant population growth



d) Host plant reproductive strategy



e) Adult mobility / dispersal



4. Discussion

4.1. Species richness

Quantification of grassland restoration success is crucial to the development of management practices that will benefit declining butterfly populations and inform policy makers on how to maximise biodiversity gains from financially limited resources (Benayas *et al.*, 2009 and Matthews *et al.*, 2009). While species richness represents a fundamental measure of the complexity of a community, it is of questionable value as an indicator of restoration success (Fagan *et al.*, 2010 and Woodcock *et al.*, 2012). For any site undergoing restoration, some of the species that become established will not be characteristic of the target habitat type, and their use in the valuation of restoration success is potentially misleading. It would be possible to restrict measures of species richness to butterflies known to be indicator of high quality semi-natural grasslands. However, such an approach requires a priori knowledge of what these indicator species are; information which may vary according to local species pools and is not necessarily available in all regions. Such an approach that uses a sub-set of target species could be used to improve the resolution of the restoration success metric (i.e. EDs). However, in the case off the current study the numerical dominance of grassland specialist species made such an approach unwarranted. Species richness also takes no account of the relative abundance of a particular species and so does not distinguish between those with a robust population size and those on the edge of local extinction (Hanski and Singer, 2001). Finally, we found no suggestion that rarefied butterfly species richness change in response to the number of years of restoration for either the arable reversion or grassland enhancement sites.

4.2. Similarity to target grasslands

The measure of restoration success used (ED_S) quantified changes in similarity between restoration sites and target grasslands in terms of both species composition and relative abundances of individuals. For the arable reversion sites, restoration success increased rapidly over the first 5-10 years, while grassland enhancement showed no change in restoration success with time. Rapid increases in restoration success for the arable reversion sites could in part be linked to these communities being established on bare ground, with no existing butterfly species. In contrast grassland enhancement sites started as grasslands, albeit of low quality, and so would have contained some grassland butterfly species. However, these species would have been principally ubiquitous grassland species that were typically present in the first year of arable reversion.

An alternative possibility is that a rapid increase in restoration success for arable reversion sites was linked to the establishment of target plant communities resulting from seed addition. There are, however, multiple confounding factors between the management of arable reversion and grassland enhancement sites, so it is not possible to isolate seed addition as the factor driving restoration success. The establishment of butterflies, or any phytophagous insects, will require the presence of host-plants for larval development (Maccherini *et al.*, 2009, Pöyry *et al.*, 2004, Tscharntke and Greiler, 1995, van Swaay, 2002 and Woodcock *et* *al.*, 2010). For this reason, seed addition combined with scarification to create germination niches, warrants further consideration as an approach for introducing butterfly host-plants during grassland enhancement (Edwards *et al.*, 2007). Host-plant occurrence is not the only limiting factor that must be overcome by establishing butterflies, for example larvae of many species exploit only a sub-set of their food plant(s), being limited to specific microhabitats or particular management regimes (Asher *et al.*, 2001, New *et al.*, 1995, Pöyry *et al.*, 2004, Thomas *et al.*, 2009 and van Swaay, 2002). Indeed this may be a key difference between restoration successes achieved under arable reversion as opposed to grassland enhancement. For example, where competitively dominant grasses persist during enhancement, their shading of the ground may affect microclimate conditions required for larval development. Without appropriate host-plants present in the sward the achievement of other environmental requirements, such as microclimate, is likely, however, to be of secondary importance (New *et al.*, 1995 and van Swaay, 2002). Responsive management intended to promote the establishment and persistence of plants could be used to benefit butterfly restoration on a site by site basis, for example, by using multiple sward cuts to reduce the dominance of some plant species (Crofts and Jefferson, 1999). While useful in promoting plant establishment, such intensive practices could have a catastrophic effect on butterfly and other invertebrate assemblages already established (Humbert *et al.*, 2009 and New *et al.*, 1995). Rotational management should be considered as a tool to promote multi-taxa restoration, where species differ in sensitivity to management (Crofts and Jefferson, 1999 and New *et al.*, 1995).

4.3. Colonisation times for butterfly species

Understanding the factors that determine the time scales over which individual species colonise provides a knowledge-base for the development of strategies that target high risk butterfly species establishing poorly during restoration. For butterflies, responses to landscape scale changes in habitat structure are well known, in particular the negative effects of isolation and fragmentation on population establishment and persistence (e.g. Hanski *et al.*, 1994, Öckinger *et al.*, 2010, Steffan-Dewenter and Tscharntke, 2000 and Thomas, 2000). It is therefore unsurprising that colonisation during grassland restoration was slowest for low mobility species. To counteract such effects, a landscape scale perspective should be considered during restoration, whereby sites are strategically positioned close to existing grasslands to minimise isolation (Öckinger *et al.*, 2010, Steffan-Dewenter and Tscharntke, 2000 and Woodcock *et al.*, 2010). An alternative approach for more isolated sites could involve the artificial introduction of butterflies, however, this is expensive and would not ensure the survival of species persisting as metapopulations (New *et al.*, 1995 and Steffan-Dewenter and Tscharntke, 2000; but see Thomas *et al.*, 2009).

Dispersal ability was the only butterfly trait that had strong support as a factor limiting colonisation times. However, other aspects of the biology and distribution of host-plants were also identified as limiting factors. Species utilising nationally widespread food plants colonised more rapidly, probably because they were more likely to have source populations in the vicinity of restoration sites. The importance of this is likely to interact with the dispersal abilities of individual species (Cowley *et al.*, 2001, New *et al.*, 1995 and Steffan-Dewenter and Tscharntke, 2000). It is not clear why the national frequency of the butterflies themselves was not a better predictor of colonisation times, although this may in part be due to some under-recording of butterflies relative to plants (Asher *et al.*, 2001 and Preston *et al.*, 2002). It is also possible that the spatial scale at which distribution maps record butterfly occupancy (i.e. presence or absence within 10 km2) represents too large an area relative to the distances travelled by low mobility species to predict colonisation rates effectively.

The ability of host-plants to establish and persist dictates whether or not a larval food resource will be present during restoration (Bakker and Berendse, 1999, Littlewood *et al.*, 2012, Pywell *et al.*, 2003 and Woodcock *et al.*, 2010). We show that faster butterfly colonisation times are to be found where host-plants establish well and/or show positive population growth during restoration. Similarly, butterfly colonisation times are lower where host plants reproduce clonally, and so are likely to be better adapted to persisting in closed and competitive sward than species dependent on seeds for reproduction (Edwards *et al.*, 2007, Pywell *et al.*, 2003 and Woodcock *et al.*, 2011). All three factors point to the need to establish and maintain host-plants populations during restoration if butterflies are to colonise rapidly. While the sowing of seeds represents an obvious method to introduce host-plants, this approach typically only occurs in the initial year of management (Edwards *et al.*, 2007). It may be necessity to consider incorporating subsequent sowing events or to use plug plants to get hard to establish species into restoration sites (Pywell *et al.*, 2003). The importance of host-plants may also extend beyond their immediate value as food. For example, butterfly traits that could affect colonisation times have been linked to aspects of host-plant biology, specifically the competitive ability of the plant. Dennis *et al.* (2004) showed that butterflies feeding on competitive host plants tended to be more mobile, have longer flight periods and be characterised by rapid larval development. While this highlights the often inter-correlated nature of traits (Weiher *et al.*, 1999), it does point to the need to consider host-plant biology when identifying butterfly species likely to be poor colonisers during restoration.

5. Conclusions

Given the dependence of many insects on grasslands (Tscharntke and Greiler, 1995 and van Swaay, 2002), their often declining population status (e.g. van Swaay, 2002) and their role in ecosystem service provision (Losey and Vaughn, 2006), invertebrates need to be considered during development of grassland restoration methodologies. However, long term data sets detailing invertebrate restoration are absent from the literature for most groups, and as such butterflies make an important model system on which to make inferences about the consequences of grassland restoration. While a period of 10 years between recreation and its subsequent utility as a habitat for butterflies is not unexpectedly large, policy makers still need to incorporate these time lags into strategic planning. For example, if grassland recreation is to promote functional connectivity to mitigate against climate change, then at least a 10 year delay between the implementation of restoration and its realised value for butterflies needs to be accounted for (Hodgson *et al.*, 2009). While butterflies are used as a model group to give an idea of potential time lags between the start of management and successful restoration, for other invertebrate taxa with very low mobility (e.g. snails) such time periods could be much longer (Knop *et al.*, 2011 and Woodcock *et al.*, 2012). For such groups, wide scale grassland restoration may simply occur too late to have any tangible benefits to be of value as a mitigation measure against future environmental change.

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