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1
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Limiting factors in the restoration of UK grassland beetle assemblages

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Abstract

Grasslands restoration is a key management tool contributing to the long-term maintenance of insect populations, providing functional connectivity and mitigating against extinction debt across landscapes. As knowledge of grassland insect communities is limited, the lag between the initiation of restoration and the ability of these new habitats to contribute to such processes is unclear. Using ten data sets, ranging from 3 – 14 years, we investigate the lag between restoration and the establishment of phytophagous beetle assemblages typical of species rich grasslands. We used traits and ecological characteristics to determine factors limiting beetle colonisation, and also considered how food-web structure changed during restoration. For sites where seed addition of host-plants occurred the success in replicating beetle assemblages increased over time following a negative exponential function. Extrapolation beyond the existing data set tentatively suggested that success would plateau after 20 years, representing a *c.* 60% increase in assemblage similarity to target grasslands. In the absence of seed addition, similarity to the target grasslands showed no increase over time. Where seed addition was used the connectance of plant-herbivore food webs decreased over time, approaching values typical of species rich grasslands after *c.* 7 years. This trend was, however, dependent on the inclusion of a single site containing data in excess of 6 years of restoration management. Beetles not capable of flight, those showing high degrees of host-plant specialisation and species feeding on nationally rare host plants take between 1- 3 years longer to colonise. Successful grassland restoration is underpinned by the establishment of host-plants, although individual species traits compound the effects of poor host-plant establishment to slow colonisation. The use of pro-active grassland restoration to mitigate against future environmental change should account for lag periods in excess of 10 years if the value of these habitats is to be fully realised.

Key-words: Calcareous; Mesotrophic; lowland grassland; functional traits; recreation; food web; meta-analysis.

1. Introduction

Grasslands represent a vital and diverse habitat for a wide range of insects, including beetles (Batary, et al., 2007; Fadda, et al., 2007; Woodcock, et al., 2008), butterflies (van Swaay, 2002) and grasshoppers (Knop, et al., 2011). Insects play a functionally important role within grasslands, characterised by complex trophic interactions with other species (Albrecht, et al., 2007), an important role in the delivery of ecosystem services like pollination (Otieno, et al., 2011) and a direct effect on plant succession (De Deyn, et al., 2004). However, both the area and quality of grasslands has shown wide scale declines in Europe, with European Union member states showing a 12.8% reduction in area between 1990-2003 (FAO, 2006). This decline is the result of conversion to alternate land uses (e.g. arable agriculture) combined with continued management intensification (inorganic fertilisers, drainage, reseeding, and intensive cutting and grazing regimes) (Stoate, et al., 2009). Such losses are significant because species-rich grasslands can mitigate against extinction debt resulting from long-term habitat fragmentation (Schtickzelle, et al., 2005), while also providing functional connectivity crucial to climate change adaptation (Lawton, et al., 2010). Where species-rich grassland was a typical or former component of landscapes restoring species rich grasslands will be important to any large scale management polices intended to conserve biodiversity and maintain ecosystem service delivery. Within Europe, grassland restoration is largely implemented through agri-environmental schemes, which offer farmers financial incentives to both manage extensively and create habitats (Critchley, et al., 2003; Kohler, et al., 2007). The period between policy implementation (i.e. the decision to restore grasslands) and the time taken for grasslands to establish may potentially be considerable. If this is the case, then the time required for restoration to support landscapes capable of delivering high levels of biodiversity may be far longer than anticipated by policy makers.

The restoration of insect assemblages, particularly in the case of phytophagous taxa, is linked to the establishment of floral communities (Woodcock, et al., 2008; Woodcock, et al., 2010). Success in restoring plant communities is variable, with recruitment processes, competitive interactions and underlying abiotic factors limiting success (Bakker and Berendse, 1999; Willems, 2001). Overcoming dispersal limitation and influencing successional trajectories, typically by sowing seeds, is an economically viable approach often used for floral restoration (Bakker and Berendse, 1999; Edwards, et al., 2007; Pywell, et al., 2003). Dispersal limitation is also a problem for insects, which often travel only moderate distances and cannot persist in unfavourable habitats as plants do within seed banks (Bakker and Berendse, 1999; Woodcock, et al., 2010). Although single insect species have been introduced artificially (e.g. Thomas, et al., 2009) doing so for whole communities is impractical or prohibitively expensive, and as such colonisation during restoration is invariably by natural immigration only (Woodcock, et al., 2010). Understanding which individual species traits and ecological characteristics (e.g. host-plant establishment characteristics or distributional range) predict insect establishment may help to identify species susceptible to population decline within modern agricultural environments and assess the limits of restoration success.

Beetles represent one of the most diverse taxa of insects within grasslands (Woodcock, et al., 2008). Their great diversity and variety of ecological niches makes them a useful model taxon for looking at factors limiting restoration of insects as a whole (Woodcock, et al., 2008). Here we take a meta-analysis approach to investigate the time scales over which phytophagous beetles respond to temperate grassland restoration. We predict that 1) seed addition will promote the rapid colonisation of beetle communities by increasing the establishment of larval host-plants, thus increasing the rate at which target grassland communities are replicated (Woodcock, et al., 2010). While the matching of beetle communities to targets is our principal measure of restoration success, we also consider factors that limit colonisation of individual beetle species by taking a trait based approach. We predict that: 2) mobile species will be the first to colonise; and that 3) beetles feeding on widely distributed host-plants, or beetles widely distributed themselves, will colonise rapidly as they have source populations in the vicinity of restoration sites. By applying a food web analysis to identify underlying structural differences in trophic interactions, we predict that 4) restoration success will be linked with an increase in the linkage density and connectance between host-plants and beetle species (Albrecht, et al., 2007).

2. Methods

2.1 Data sources

Long-term monitoring of biological communities is relatively rare, and data sets on the establishment of beetle communities under grassland restoration are scarce. However, we collected ten UK data sets, ranging from 3 to 14 years, recording the establishment of phytophagous beetles (Curculionidae, Apionidae and Chrysomelidae) during calcareous (6 sites, Table 1a) and mesotrophic (4 sites, Table 1b) grassland restoration. Prior to the instigation of restoration management, these sites were either on intensively managed arable land (6 sites) or were agriculturally improved grasslands, receiving inorganic fertiliser combined with high intensity grazing and cutting regimes (4 sites). Proximity of individual sites to existing areas of species rich grassland (i.e. potential source populations for colonising beetles) varied from *c.* 0.5 to 1.5 km.

For nine of the restoration sites (excluding M3 compensation area) the use of alternative experimental treatments meant that restoration without seed addition could be compared to restoration with seed addition (Table 1a & b). Seed addition was either in the form of a seed mix containing species typical of the target grassland or was from seeds within green hay collected from local species rich grassland and then spread on the experimental plots (all other sites) (for more detail see Woodcock, et al., 2010). For each site these two treatments were replicated in either four or five blocks, with individual experimental plots 10 × 10 m in dimension and separated by 10 m. It is always possible in replicated block experiments that some degree of cross-contamination between adjacent plots may occur, i.e. as a result of beetle moving between different plots. Beetles are on the whole less mobile than many insects (e.g. bees) reducing the extent to which such a problem may occur. In addition, the association of phytophagous species within experimental plots is largely dictated by the presence of their host plants (Woodcock, et al., 2008). As such differences in plant establishment between seed addition treatments would be expected to limit movement between plots. All our analyses were based on average beetle abundances per treatment per site. This would also reduce the influence of colonisation times resulting from non-resident beetle temporarily moving through a particular plot. The M3 compensation area received seed addition, although there was no paired no-seed control at this site (Table 1a). At all sites seed addition was applied once, in the first year of restoration. Long-term management differed on a site by site basis, reflecting historical grazing and cutting management practices typical for a particular grassland type.

2.2 Beetle monitoring

All sites were sampled by vacuum sampling, either by D-vac (Rincon Insectary, California) (M3 compensation area) or Vortis (Burkard Ltd, London) suction sampler (all other sites), both of which are suited to the quantitative collection of sward active insects in grasslands (Brook, et al., 2008). Each experimental plot was sampled three times a year (May, July and September), with the sampler placed in 15 positions for a duration of 10 s on each occasion. In all cases, local species rich grasslands were used as target communities, with which restoration success in the experimental plots could be compared (Table 1a & b). These target communities were examples of the kind of grassland that was being aimed at by the restoration, as determined by underlying soil type and historical management practices. In all cases they were sampled with the same suction sampler and at the same intensity as their paired restoration experiment. This yearly monitoring of the restoration sites occurred for between 3 and 14 years depending on site (Table 1a & b). For the target grassland community, beetle sampling occurred in only one year, typically the first year during which restoration management was applied at the experimental site. From these samples all weevils (Curculionidae), seed weevils (Apionidae) and leaf beetles (Chrysomelidae, including the Bruchidae) were identified to species (see Electronic Appendix A).

2.3 Similarity to target grasslands

Restoration success was assessed by calculating the Euclidean distance between the summed abundance of beetle communities at each site for a particular year, and their respective target grassland communities. Individual species abundance within a particular site and for a particular year was expressed as a proportion of the total beetle abundance in that year. This proportional abundance corrected for different numbers of beetle observations at different sites. Euclidean distance was defined as:

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

Where: ED_{jk} = Euclidean distance between samples j and k; X_{ij} = proportional abundance of species i in sample j; There is an inverse relationship between the Euclidean distance and the similarity of samples. As the Euclidean distance between restoration sites and their respective target communities can scale in an unpredictable manner depending on how many species are present, it was decided to scale it relative to the distance achieved after the first year of restoration at an individual site. Thus, $ED_S = 1-(ED_{tn}/ED_{t1})$, where ED_{t1} = Euclidean distance between restoration site and target community in the initial year of restoration; ED_{tn} = Euclidean distance between restoration site and target community in the n^{th} year after the start of restoration. ED_S reaches a value of 1 when the restoration site and target communities share the same species with the same proportional abundances. It should be pointed out that achieving an ED_S of 1 is an unrealistic target for restoration. However, as a conservative estimate values of $ED_S > 0.7$ would be likely to represent high degrees of restoration success.

2.4 Beetle ecological characteristics and traits

The time taken for beetles to colonise each site was recorded in years, and then averaged for each species across sites where that species was present. This colonisation time was then related to individual species traits and ecological characteristics of the beetles and their associated host plants. Following Reich *et al.*(2003), traits represent species characteristics that have evolved in response to competitive interactions and abiotic environmental conditions, and were defined to be any attribute that would be likely to influence establishment, survival or fitness. For the beetles this was represented by: 1) flight, as determined by the presence of fully developed wings or reduced / absent (brachypterous / apterous) wings; 2) host-plant specialisation, where species were defined as monophagous, strict oligophagous (feeding within a single plant genus), loose oligophagous (feeding within the same plant family) or polyphagous (BRC, 2009). In the case of host-plants we focused on species that represent the main established feeding relationships of individual species.

The following ecological characteristics of beetles were used to describe aspects of individual species distribution or attributes of their host-plants. 1) Number of 10 km squares in England and Wales where the beetle species has been recorded (Cox, 2007; NBN, 2011). 2) Number of 10 km squares in England and Wales where the most common host-plant of a beetle species was 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 beetle was considered to feed on a clonal plant if at least one of its hosts was clonal. 4) The inter-specific competitive ability of the host-plants, based on Grime et al's (1988) 'CSR' life history classification. Where multiple host-plants were present, we use the 'C' index for the most competitive of the principal host-plants. 5) Success of establishment of main host plant. This is based on Pywell et al. (2003) which considered the success of plant establishment over the initial 4 years of grassland restoration, and is 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) moderate (N_c =0.1- 0.5) or (iv) bad ($N_c < 0.1$) establishment in year one. Note that these thresholds are arbitrary.

2.5 Food web complexity

Using known larval host-plant feeding associations (BRC, 2009) bipartite interaction networks (i.e. interaction networks showing feeding associations between the two trophic levels of plants and beetle) were constructed for each restoration site for each year, as well as for the target communities. Phytophagous beetles present within a restoration plot were assumed to feed only on those host-plants that had become established during restoration at a site. From these networks the Bipartate package (Dormann, et al., 2008) of the R statistical environment (R Core Development Team, 2008) was used to derive three food web descriptive statistics: 1) Connectance, representing the realised proportion of all possible trophic links between phytophagous beetles and host-plants (Dunne, et al., 2002); 2) Linkage density, representing the mean number of interactions per species (Tylianakis, et al., 2007); 3) Mean number of shared hosts, representing a simple measure of similarity in host preference (Stone and Roberts, 1992). All of these food web statistics are based on un-weighted links between species.

2.6 Data analysis

Following Matthews et al. (2009) the change in similarity of the beetle communities to the target grasslands (ED_S) in response to the number of years of restoration was tested against two competing models, the negative exponent function and the double exponential function. This was done using non-linear mixed models (Proc NLMIXED) in SAS 9.01. The negative exponential describes a scenario whereby the similarity of beetle assemblages to the grassland target for restoration increases in a predictable and orderly fashion during restoration. Thus this would fit data where ED_S increases to an asymptote as described by the function $ED_S = a(1\text{-exp.}^{-b\cdot \text{year}})$. The alternative scenario represented by the double exponential function is similar; however, while similarity to the target grassland initially increases with time, it ultimately declines indicating a long term failing of restoration. The double exponential function has the form $ED_S = a(\text{exp.}^{-c\cdot \text{year}} - \text{exp.}^{-b\cdot \text{year}})$. Both of these functions were tested against the null model that ED_S did not change with time ($ED_S = a$), i.e. restoration management had no effect. Restoration site was included as a subject classification within the random effects to account for the repeated measures over time from individual sites. A normal error structure was used for both the fixed and random effects. Separate models were run for sites where plant establishment was by natural colonisation only and those that received artificial introduction of seeds (Table 1a & b). Differentiation between the best fit models for the response of ED_S to year, i.e. either the null model, negative exponential or double exponential, was achieved using Akaike’s Information Criterion (AIC) which allows the comparison of models with different numbers of parameters (Burnham and Anderson, 1998).

Typically individual 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 have biologically meaningful relationships with colonisation time when considered as individual factors. However, minimum adequate model selection based on stepwise deletion or addition may well result in biologically relevant explanatory variables being deleted (Burnham and Anderson, 1998). To account for this we selected models using Akaike's Information Criterion (Burnham and Anderson, 1998). Applying this model selection approach, general linear models (GLM) in SAS 9.01 were used to assess responses of mean colonisation time to the seven explanatory traits and ecological characteristics described above. Individual models were created for all combinations of the fixed effects, ranging from the inclusion of single terms, up to a model containing all seven fixed effects (127 models in total). No interaction terms were considered. For each model AIC was calculated. As AIC is a model selection index that corrects for the number of parameters it allows direct comparison of the fit of models of different structure (Burnham and Anderson, 1998). The AIC difference (Δ_i) was derived to assess the relative support for each model as $\Delta_i = AIC_i - AIC_{min}$, where AIC_{min} represented the lowest recorded value for any model (the model with the best fit to the data), and AIC_i is the model specific AIC value. From the Δ_i index Akaike Weights (w_i) (Burnham and Anderson, 1998) were calculated:

$$w_i = \frac{\exp\left[-\frac{1}{2}\Delta_i\right]}{\sum_{r=1}^{R}\exp\left[-\frac{1}{2}\Delta_r\right]}$$

Where w_i represents the probability that model i would be selected as the best fitting model if the data were collected again under identical conditions. Therefore w_i represents a variable selection approach which allows all models to be considered, while weighting them for their plausibility (Burnham and Anderson, 1998). As the w_i of all considered models sums to 1, this provides a basis for selecting a set of models for which there is a 95 % confidence that the most appropriate model for the data is contained within. The w_i can also be summed across all models that contain a particular fixed effect (within this 95 % confidence set) to assess the probability that a particular trait or ecological characteristic would affect colonization times if the experiment were repeated. The summed w_i for a particular fixed effect will range between 0 and 0.95 (for models within the 95% confidence set) depending on the importance of this parameter in explaining colonization times.

For the analyses of food web parameters (connectance, linkage density and mean number of shared hosts) preliminary investigation suggested that their responses to year were best described by an exponential function; therefore all three parameters were log_e transformed. Each of these response variables was then correlated against the number of years of restoration within a standard general linear model. Again separate analyses were run for those sites receiving seed addition and the control sites without seed addition.

3. Results

3.1 Restoration success for whole beetle communities

Where restored grasslands were managed by sowing seeds to overcome plant dispersal limitation, success of restoration for the beetles (ED_S) increased over time in a predictable manner. This was best described by the negative exponential function ($ED_S=0.64\times(1-\exp^{-0.20\times year})$). Restoration success was predicted to asymptote after *c.* 20 years, although this is an extrapolation beyond the current time scale of the data and should be treated with caution. Beetle restoration success tended to show a relatively sharp increase within the first 10 years (Fig. 1a), suggesting that this is the minimum time scale over which restoration can be considered to be effective. As ED_S has a predicted asymptote of *c.* 0.65 a high level of success in the replication of the target communities was achieved. The fit of the negative exponential function (AIC = 11.1) was superior to either the null model, where ED_S showed no response to time (AIC = -0.8), or the double exponential function, which failed to converge in its parameter estimates. For those sites receiving seed addition data was available for a 14 year period, a time scale greater than that of the control sites (≤ 6 years). To confirm that these trends were not unduly affected by this longer time series the analysis was re-run ignoring all data points above 6 years. Even with this reduced data set parameter estimates remained comparable to the original analysis (ED_S=0.67× (1-exp$^{-0.24\times\text{year}}$)). The AIC value was lower (-5.1), but superior to competing models. The inclusion of the 14 year data set is therefore likely to have added greater resolution to the predictions rather than created a bias.

In contrast, where the colonisation of plants was by natural immigration only (controls receiving no seed addition) there was no evidence that restoration success changed over time, i.e. the null model gave the best fit (ED_S = 0.15, AIC = 11.7) (Fig. 1b). The superiority of the null model to either the negative exponential function (AIC = 12.9) or the double exponential function (failed to converge in its parameter estimates) indicated that seed addition was necessary for successful restoration of the phytophagous beetle assemblages over the time scales considered in this study.

3.2 Colonisation times for beetle species

The Information Theoretic approach assessed the fit of all 127 tested models to define a subset where there was 95.0 % confidence that the most appropriate model for the data was included. Thirty-three of these models were included within this 95 % confidence set. Within these models all 7 of the traits and environmental characteristics were represented at least once, although only three of these consistently had summed w_i above 0.80, i.e. a greater than 0.80 probability that this explanatory variable would affect colonization times of the beetles if the experiments were repeated. As these three traits and environmental characteristics have high support as explanatory variable that affect colonisation times we focus on these in this paper (see Electronic Appendix B for the responses of the remaining traits). Of these four remaining environmental characteristics, the summed w_i ranged between 0.27 (host-plants competitive ability) to 0.47 (establishment success of main host-plant), while none appear in more than 46 % of the models within the 95 % confidence set.

For phytophagous beetles, mean colonisation time was shown to be greatest for species unable to fly. However, this difference was relatively minor, with flightless beetles taking *c.* 1 year longer to colonise than beetles capable of flight (summed w_i = 0.81, percentage representation within 95% confidence set = 66.7 %) (Fig 2a). Beetle host-plant specialisation was also an important trait in determining colonisation times (summed w_i = 0.91, percentage representation within 95.0% confidence set = 81.8 %). The general pattern was characterised by longer colonisation times where beetles were more specific in the range of host plants that they fed on. Typically, polyphagous beetles tended to colonise *c.* 2 years before monophagous species (Fig. 2b). Finally, mean colonisation time was negatively correlated with the national frequency of the most common host-plant (summed w_i = 0.95, percentage representation within 95% confidence set = 100 %). Over the range of 10 km^2 occupancy values that described host-plant frequency in England and Wales (ranging from *c.* 250 – 2200 records), beetles with the most common food sources would be expected to colonise *c.* 3 years faster than species with the rarest host-plants (Fig. 2c).

3.3 Food web complexity

Where seed addition was used to overcome plant dispersal limitation, food web connectance declined following an exponential function ($F_{1,41}$=5.00, p=0.03; Fig. 3). Within *c.* 7 years the realised proportion of all possible trophic links between beetles and host-plants (i.e. connectance) declined to values comparable to those of the target species-rich grasslands (mean = 0.09; SE ± 0.01). The significance of this response was dependent on the inclusion of data in excess of 6 years ($F_{1,37}$=0.91, p<0.05). Without further data from sites with long term monitoring in excess of six years this reduction in connectance over time should be treated with caution. For the control plots, connectance did not change in response to the number of years of restoration ($F_{1,33}$=2.72, p>0.05) and was on average higher than recorded from the target grasslands (mean=0.21; SE ± 0.02). For both the control and seed addition sites, linkage density (control: $F_{1,33}$=1.31, p>0.05; seed addition: $F_{1,41}$=0.12, p>0.05) and mean number of shared host-plants (control: $F_{1,33}$=0.66, p>0.05; seed addition: $F_{1,41}$=5.00, p>0.05) showed no change with the number of years of restoration. In addition their mean values remained higher in the restoration sites (linkage density = 2.58, SE± 0.30; shared host-plants = 0.49, SE± 0.13) than those values observed for the target grasslands (linkage density = 1.94, SE± 0.35; shared host-plants = 0.21, SE± 0.03).

4. Discussion

For phytophagous beetles, grassland restoration success was largely dependent on the use of seed addition practices in the initial years. Such practices have received wide attention as tools used to overcome dispersal limitation in plant communities, particularly where potential seed banks are no longer viable (Bakker and Berendse, 1999; Edwards, et al., 2007; Jones, et al., 1999). Seed addition during restoration is normally in the form of commercially available seed mixes or alternatively as green hay originating from local examples of the target grassland type (Edwards, et al., 2007; Jones, et al., 1999). Given the fragility of many insects, transfer within cut hay is possible, but is thought to be an unlikely mechanism of dispersal as the mechanical process of cutting results in high levels of mortality (Humbert, et al., 2009). In addition, for phytophagous insects colonisation within hay would be likely to precede the establishment of their host plants (Woodcock, et al., 2008). Seed addition as a component of green hay has been considered to be preferable, as it introduces plants of local provenance and so helps maintain local genetic diversity (Jones, et al., 1999). Such local provenance plants are also potentially important for phytophagous insects, as there is some evidence that larval survival is greatest where host-plants are of local genetic stock (Ballabeni, et al., 2003).

In this study beetle colonisation times were also influenced by the occurrence of their host-plants at a national scale. The importance of this is likely to be underpinned by the increased availability of source populations from which beetles can colonise. Previous studies have shown that for beetles, snails and grasshoppers, their similarity to target communities increased where species-rich grasslands were present as source populations in the local landscape (Knop, et al., 2011; Woodcock, et al., 2010). This was seen to be particularly important for low mobility species, such as snails (Knop, et al., 2011). Individual species mobility is likely to compound the consequences of a lack of source populations from which to colonise, with low mobility species colonising restored sites in highly fragmented landscapes at a much slower rate (Knop, et al., 2011). However, for relatively mobile species, including some butterflies, it is the availability of suitable habitats within the landscape, rather than their ability to move between them, that will determine population persistence (Wood and Pullin, 2002). It is interesting to note that the national occurrence of host-plants was a better predictor of beetle colonisation times than that of the national occurrence of the beetles themselves. Distribution maps for plants are typically more comprehensive and so may well have acted as a surrogate for previously unrecorded beetle populations.

Perhaps the most surprising failure of grassland restoration, at least for the phytophagous beetles, was where no seeds were added during the first year of management. Note that this difference between sites where seeds were and were not added was maintained even when the analysis of the restoration success was restricted to comparable length time series for both treatments. The reduction in availability of host-plants under such management regimes seems to prevent the development of communities towards those of the target grassland types. Based on an extrapolation from the existing data, we predicted that it would take *c.* 20 years under seed addition management for similarity to target grasslands to reach its maximum. It should be noted that as with any extrapolation this is dependent on the current trends continuing, and as such can only be considered an indication of what may happen. This contrasts with where no seed addition was applied, as at such sites there was no evidence of restoration success increasing over time although it did show a high degree of variability. Priority effects may play a role here, whereby the order of beetle species colonisation determined by which plants establish first may dictate long term community structure (Young, et al., 2001). Where seed addition was not used to introduce host plants, beetles able to colonise the few host plants present (e.g. polyphagous species) may have subsequently competitively dominated the community. However, experimental evidence for such priority effects for grassland insects is absent.

During restoration, there was evidence that food web connectance (i.e. the proportion of realised trophic interactions) decreased to levels typical of target species-rich grasslands, but only where seed addition management was used. Food webs have been shown to be more robust to the random removal of species where there is a high degree of connectance (Dunne, et al., 2002). This suggests that as succession progresses these restored grasslands may become increasingly more sensitive to disturbance as food web connectance declines. Independent of this, the loss of any plant species on which many beetles species feed (e.g. due to over grazing) would be likely to results in a large loss of beetle species through secondary extinctions (Dunne, et al., 2002). The direction of this change in connectance contrasted with our prediction which were based on the findings of Albrecht et al. (2007). Albrecht et al.'s study considered predator or parasitoid interactions with prey, and showed a tendency for the number of trophic interactions to increase over time. It seems that there are fundamental differences in how food webs develop during restoration among different trophic levels (i.e. predator- prey or plant-herbivore). The reduction in connectance observed for the food webs in this study is principally due to beetles with higher levels of host plant specialisation colonising later on during restoration. This seems to have been dependent on seed addition introducing these host plants. Such specialist beetle species have comparatively few trophic interactions, and result in a net decrease in overall web connectance. This slower rate of colonisation by monophagous species was also demonstrated within this study, which provides additional support for this proposed mechanism. Investigation of food webs that consider all species within a site (e.g. plants, herbivores, predators and parasitoids) may be more informative than the sub-set approaches used both here and by Albrecht et al. (2007), but such webs would be hard to construct. This reduction in food web connectance was dependent on the inclusion of long term data in excess of 6 years. The trend therefore has limited support until it is confirmed with data sets from comparable periods. This is an inherent problem with this kind of restoration meta-analysis, where short term studies outweigh long-term monitoring. Even with this caveat the potential reduction in connectance provides at least an indication of community trends during restoration that warrant further investigation.

Connectance was very variable in the initial years of restoration, ranging from values comparable to those of the target species-rich grasslands, to far higher levels. This variability suggests that for some sites food web structure, at least in terms of connectance, came to match that of the target community rapidly during grassland restoration (even within the first 1-2 years), but for many sites it differs considerably from that of the target. Despite this high initial variability, within *c.* 7 years sites had approached levels comparable to that of target grasslands. This contrasts with species composition in terms of community similarities, which took 13 years longer to reach a plateau. Within the constraints of the caveats described above, this may imply that functionally equivalent assemblages, at least in terms of connectance, are relatively easy to replicate during restoration for phytophagous beetles, although the establishment of a specific fauna would take far longer to achieve. However, as linkage density and mean number of shared hosts at the restoration sites have greater mean values than seen at the target grasslands, evidence of restoration of these other aspects of food web complexity is absent.

5. Conclusions

The high economic cost of grassland restoration means that quantification of success, normally defined by whether specific communities establish or whether ecosystem functions are enhanced, is of fundamental importance to policy makers and conservationists alike (Benayas, et al., 2009; Matthews, et al., 2009). Indeed, measures of restoration success may eventually be incorporated into the valuation of payments to farmers for agri-environmental schemes (Gibbons, et al., 2011). Such measures of success also provide information about the likely time lags between the implementation of grassland restoration and its value being realised at a landscape scale. For example, if grassland restoration is used as a mitigation measure against climate change by increasing connectivity at a landscape scale (Lawton, et al., 2010), its impact in achieving this will not be instantaneous. For the beetles at least, such time lags are likely to be in excess of 10 years and as high as 20 years. Given the dependence of many insects on grasslands (Batary, et al., 2007; van Swaay, 2002; Woodcock, et al., 2008), their contribution to ecosystem service provision (Otieno, et al., 2011), and an often declining population status (e.g. van Swaay, 2002), restoration methodologies need to consider the needs of insects as well as plants. Logistically, the disparate nature of research into the restoration of grassland insects has meant that for the majority of taxa data remains absent or sparse. For this reason, management choices are often by necessity extrapolated from those taxa where data are available, e.g. beetles and butterflies (Maccherini, et al., 2009; van Swaay, 2002; Woodcock, et al., 2010). Such extrapolations are fraught with potential problems (Maccherini, et al., 2009), but serve as a starting place for the development of future grassland management strategies.

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Electronic Appendix A. The presence or absence of each species for the restoration sites and their rarity.

Electronic Appendix B. Summary graphs and tables detailing the response of beetle colonisation times to the effect of beetle traits and host plant characteristics for variables that summed low summed w_i (< 0.47) and percentage representation (< 40 %) across models within the 95 % confidence set.

Tables 1a

Calcareous grassland restoration sites	**Grassland type**	**Pre-restoration conditions**	**Restoration management**	**Seed addition**	**Data set length**	**Restoration target**
M3 compensation area, Hampshire (51°21′10″N 01°18′30.66″W)	CG2 calcareous grassland	Ex-arable land	Sown with a seed mixture derived from species rich calcareous grassland swards.	Yes	14 years	St. Catherine's Hill (51°02′39″N 001°18′36″W)
Brush Hill, Buckinghamshire (51˚43'27" N, 0˚48'46" W)	CG2/MG1	Agriculturally improved grassland	1) Natural regeneration only; 2) Sown with green hay combined with scarification. In both cases followed by sheep grazing from May until sward 4-7 cm	Both	6 years	Gomms Wood, Buckinghamshire (51˚37'43"N, 0˚42'30"W)
Aston Rowant, Oxfordshire (51°39'47" N, 0°57'14" W)	CG2	Ex-arable land	1) Natural regeneration only; 2) Sown with green hay. For subsequent management see Brush Hill	Both	3 years	Aston Rowant NNR, Oxfordshire (51˚'39"55N, 0˚57'01"W)
Cold Blow Farm (pasture), Kent (51˚09'42" N, 0˚59'00" E)	CG2/MG1	Agriculturally improved grassland	1) Natural regeneration only; 2) Sown with green hay combined with scarification. For subsequent management see Brush Hill	Both	6 years	Wye and Crundale Downs NNR, Kent (51˚10'10"N, 0˚57'56"E)
Cold Blow Farm (arable), Kent (51˚09'52" N, 0˚58'41" E)	CG2/MG1	Ex-arable land	1) Natural regeneration only; 2) Sown with green hay. For subsequent management see Brush Hill	Both	6 years	Wye and Crundale Downs NNR, Kent
Dancers End, Buckinghamshire (51˚46'37" N, 0˚42'15"W)	CG2/MG1	Agriculturally improved grassland	1) Natural regeneration only; 2) Sown with green hay combined with scarification. For subsequent management see Brush Hill	Both	4 years	Butterfly Bank, Buckinghamshire (51˚40'13"N, 0˚48'04"W)

Table 1a & b. Summary habitat and restoration management practices for the calcareous (1a) and mesotrophic (1b) grassland data sets used in the analysis. Where grazing management occurred it was at a low rate at c.1.5 to 2.5 livestock units ha-1 yr-1. All codes for grassland types refer to those defined under the UK National Vegetation Classification (NVC) (Rodwell, 1992).

Table 1b

Mesotrophic grassland restoration sites	Grassland type	Pre-restoration conditions	Restoration management	Seed addition	Data set length	Restoration target
Chimney Meadows, Oxfordshire (51˚42'08" N, 1˚29'15" W)	MG4/5 Mesotrophic grassland	Ex-arable land	Sown with green hay. Long term management of , a cut for hay in July/August followed by aftermath grazing by sheep and cattle	Yes	5 years	Chimney Meadows NNR, Oxfordshire (51˚41'52" N, 1˚29'27"W).
Kemhide, East Sussex (50˚55'31" N, 0˚26'15" E)	MG5 lowland hay meadow	Ex-arable land	1) Natural regeneration only; 2) Sown with green hay. Spring grazing (March - April) by sheep and cattle, a July hay cut and aftermath grazing.	Both	3 years	Coach Road, East Sussex (50˚55'24"N, 0˚22'46"E).
Rocks Farm, East Sussex (50˚55'56" N, 0˚24'13" E)	MG5 lowland hay meadow	Agriculturally improved grassland	1) Natural regeneration only; 2) Sown with green hay combined with scarification. Spring grazing (March - April) by cattle, a July hay cut and aftermath grazing.	Both	4 years	Coach Road, East Sussex
Little Sprays, East Sussex (50˚56'28" N, 0˚24'41" E)	MG5 lowland hay meadow	Ex-arable land	1) Natural regeneration only; 2) Sown with green hay. Spring grazing (March - April) by sheep, a July hay cut and aftermath grazing.	Both	4 years	Coach Road, East Sussex

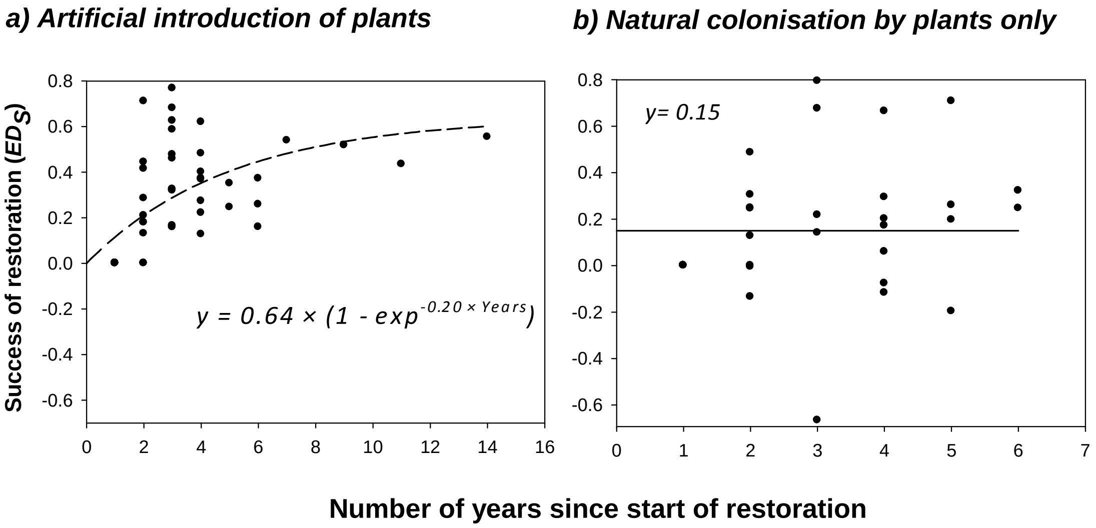
Figure legends

Fig. 1 Success in restoring beetle communities typical of species-rich grasslands during grassland restoration. Separate responses have been fitted for sites which were sown with (a) seeds to overcome host-plant dispersal limitation (negative exponential functions) and (b) those where colonisation by host-plants was by natural immigration only (intercept only).

Fig. 2 Effect of beetle traits and ecological characteristics in predicting the mean colonisation times of beetles during grassland restoration (±SE). Based on the information theoretic selection approach only explanatory variables with a summed w_i of greater than 0.80 are presented.

Fig. 3 Change in food-web connectance for plant feeding beetles with the number of years of restoration management for sites receiving seeds to overcome host-plant dispersal limitation. Solid circles represent restored grasslands, while crosses represent connectance values for the target species-rich grasslands (arbitrarily placed at 20 years).

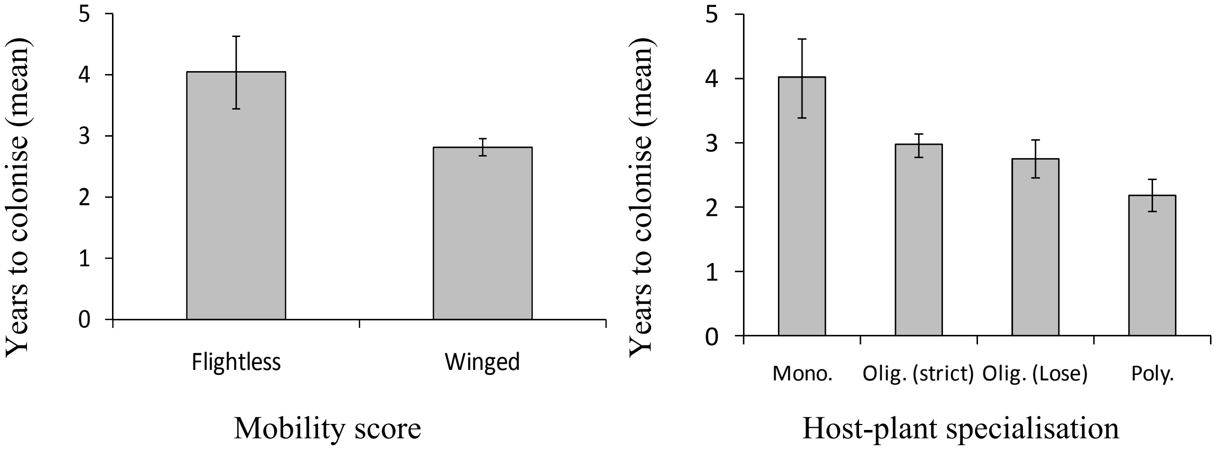
Fig.1



a) Artificial introduction of plants

b) Natural colonisation by plants only

Fig. 2



a) Beetle flight

b) Host-plant specialisation

c) Frequency of host-plant in 10 km^2 in England & Wales

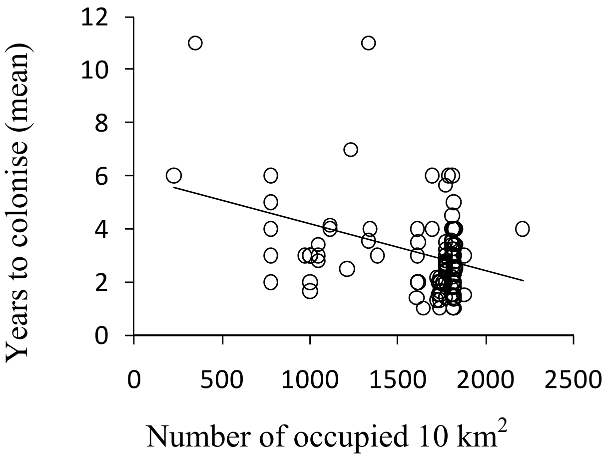
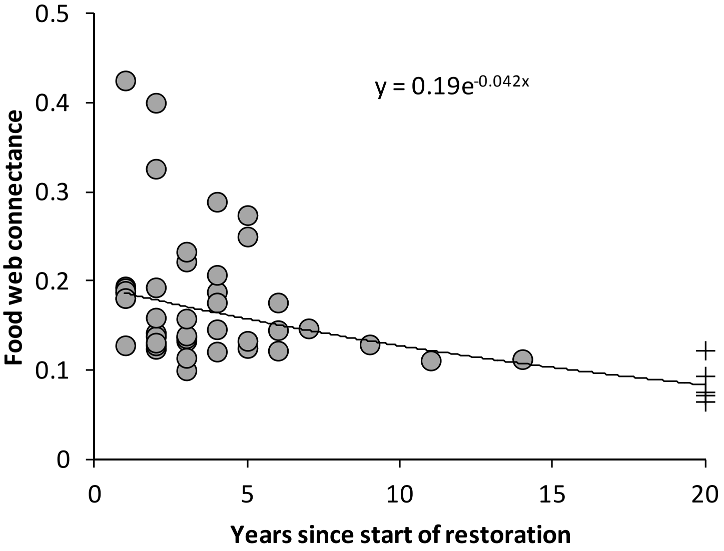


Fig 3


y = 0.19e^-0.042x
Food web connectance
0.5
0.4
0.3
0.2
0.1
0
0
5
10
15
20
Years since start of restoration