Effects of initial site management on the Coleoptera assemblages colonising newly established chalk grassland on ex-arable land

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Abstract

Large areas of chalk grassland in north-western Europe have been lost as a result of changes in land use, and the remaining areas have become increasingly fragmented. Consequently, one of the major constraints on chalk grassland restoration is the availability of sources of potential colonists in the landscape. This paper describes a study of the impact of different restoration management techniques on the colonization of new chalk grasslands by Coleoptera. Plots sown with seed mixtures of different diversity were compared with plots undergoing natural plant colonization. A second treatment involved the use of small-scale turf and soil translocation as a means of overcoming dispersal limitation. Significant differences in the Coleoptera assemblages were found in response to the experimental treatments. However, these significant differences were the result of differences in the abundance of a small number of common eurytopic grassland species. Four years after the initiation of the restoration management, the experimental plots supported very different assemblages in comparison with those found on two established chalk grassland sites in the immediate vicinity of the experimental site. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Ecological theory suggests a strong correlation between the diversity of plants and the diversity of higher trophic levels (Hutchinson, 1959; Southwood, 1978). Diversity in the range of food available to consumers provides opportunities for niche differentiation amongst primary consumers and other trophic levels. The relationship between plant and insect diversity has been the subject of many studies. Observational and experimental studies have identified linkages between plant diversity and insect diversity (Murdoch et al., 1972; Southwood et al., 1979; Siemann, 1998), and these have been supported by the results of modelling approaches (Tilman, 1986; Rosenzweig, 1995). However, the relationship between plant and insect diversity may be weak if the appearance of host plant species to their associated insects is limited, especially when the plant species occurs in diverse mixtures (Siemann et al., 1998), or if the host plant patch is small or isolated (Davis and Jones, 1986). The latter is to be expected in early successional situations, such as those associated with habitat creation on ex-arable land.

The chalk grasslands of north-western Europe support a diverse insect fauna (McLean, 1990). The insect assemblages present in chalk grassland are determined not only by the plant species composition, but also by the vertical canopy and horizontal spatial structure of the vegetation (Brown et al., 1990; Mortimer et al., 1998). Some high profile conservation species occur in such grasslands, such as the large blue butterfly (Maculinea arion; Thomas, 1991), and the wart-biter cricket (Decticus verrucivorus; Cherrill and Brown, 1990). However, in spite of this, there is a paucity of work on the factors controlling the diversity of insects within chalk grasslands, notable exceptions being the studies of Morris and his co-workers (e.g. Morris and Rispin, 1987, 1988). Coleoptera contribute significantly to the diversity of the chalk grassland fauna as a result of the high species number and wide range of ecological types within the order (Morris and Rispin, 1988).

Large areas of chalk grassland have been lost in recent years, primarily as a result of agricultural intensification (Keymer and Leach, 1990). In most areas, the remaining chalk grassland fragments occur as islands in a sea of intensively farmed land. Dispersal of species
between these fragments depends on the dispersal ability of the species concerned, the degree of isolation and the nature of the surrounding land use. Little information exists on the dispersal ability of insects associated with chalk grasslands (but see Thomas and Harrison, 1992; Thomas et al., 1992).

A considerable amount of information exists on the restoration management of chalk grasslands (Smith, 1980; Hillier et al., 1990). Until recently, much of this work had focussed on the restoration of grasslands after the abandonment or relaxation of grazing, within the context of nature reserves or protected areas (Jones-Walters, 1990). Recent policy changes, such as the EU Agri-environment Regulation, the Habitats Directive and the Convention on Biological Diversity, have encouraged schemes to recreate chalk grassland on ex-arable land (Mitchell, 1997). A major constraint on the restoration of degraded habitats, or the establishment of new areas of species-rich habitat, is the availability of potential colonists (Mortimer et al., 1998; Poschlod et al., 1998). This is particularly the case for the restoration of species-rich communities associated with traditional agricultural practices, such as the chalk grasslands of north-western Europe (Londo, 1990; Mortimer et al., 1998). It is, however, possible to manipulate the colonisation of restoration sites by plant species through sowing (Stevenson et al., 1995, 1997), though it is not always possible to obtain seed of local provenance. Natural colonisation is therefore the preferred option for sites adjacent to remnant patches of chalk grassland, in order to avoid contamination of local genotypes (Jones and Hayes, 1999). Natural colonisation is a slower process, but can be successful if appropriate sources of colonists are present near the restoration site, and appropriate management regimes are adopted (Gibson and Brown, 1992).

It is far more difficult to manipulate colonisation of restoration sites by invertebrates (Keening and Wratten, 1998). Reintroduction programmes have been successfully adopted for a small number of ‘flagship’ species (see Thomas, 1991), but this approach is clearly not feasible for the total complement of species typical of the insect fauna of chalk grasslands. Community translocation may facilitate colonisation of new sites by some invertebrate species, but most studies show high levels of dissimilarity between the translocated areas and the target communities (Bullock, 1998). However, small-scale translocation may provide focal points for the colonisation of new sites on ex-arable land, and thereby overcome problems of dispersal limitation.

The aim of this study was to investigate the impact of restoration management practices on the Coleoptera assemblages colonising newly established chalk grassland on ex-arable land, and to compare these with the Coleoptera assemblages of established chalk grassland. The study involved comparison of the efficacy of two types of restoration management: the sowing of chalk grassland seed mixtures, and the use of soil translocation and turf transplantation. In particular, the experimental design allowed comparison of the Coleoptera assemblages in plots of similar plant diversity, but with different plant species composition, and plots with similar plant species composition, but different levels of plant diversity. Here, we describe the results for the fourth year of the experiment, since at this stage the treatments are well-established and restoration potential can be realistically assessed. Two hypotheses were tested by examining the Coleoptera assemblages collected using suction sampling from the different treatment plots. Firstly, that sowing seed of late-successional chalk grassland plants accelerated the development of Coleoptera assemblages typical of established chalk grassland in comparison to allowing natural plant colonisation. Secondly, that there is a positive correlation between plant diversity and the diversity of the Coleoptera assemblages.

2. Study site and methods

2.1. Site attributes

The study was carried out on the Bradenham Estate in the Chiltern Hills (51° 40’ N, 0° 48’ W), 50 km northwest of London, on land owned by the National Trust. Parts of the estate comprising woodland and species-rich calcareous grassland are managed as a nature reserve by the Trust; this area is currently designated a Site of Special Scientific Interest and is a candidate Special Area of Conservation. The remainder of the estate is managed by a tenant farmer and comprises arable land and permanent pasture. Several areas of arable land have been taken out of cultivation over the last 30 years and are being managed for the re-establishment of calcareous grassland.

The field experiment was set up along the upper edge of an arable field (National Grid reference SU 828974) in an area measuring ca. 230×35 m. The site is bounded on the east by an open plantation of Fagus sylvatica that was planted about 30 years ago, to the south by an improved permanent pasture and the north and west by arable land. The site is fenced on three sides, the boundary with the rest of the field is unfenced. The soil is a grey rendzina over Cretaceous Chalk bed rock. The average annual precipitation is about 750 mm. The area was sown to winter barley in 1994 and was harvested in August 1995. The site was cultivated in the autumn of 1995 and harrowed in March 1996 before the start of the experiment.

Two areas of existing chalk grassland on the Bradenham Estate were sampled in order to allow comparison of the plant and insect assemblages typical of the ‘target’...
community. Small Dean Bank is an area of calcareous grassland situated 1.5 km north of the experimental plots (National Grid reference SU 824990). The site has no history of agricultural improvement and the tussocky vegetation is dominated by Festuca rubra, with abundant Arrhenatherum elatius and tall forbs such as Origanum vulgare. The second site, Butterfly Bank, lies 200 m north-east of the experimental plots (National Grid reference SU 976829). This site was cultivated for a short period ca. 30 years ago, and supports a more open vegetation with Festuca rubra, Leontodon hispidus and Lotus corniculatus. Both sites fall into the Arrhenatherum elatius grassland (MG1) of the National Vegetation Classification (Rodwell, 1992). The sites are lightly grazed by sheep for short periods each year. In addition, Butterfly Bank is occasionally mown.

2.2. Experimental treatments

Two types of initial site management were compared in the experiment. One set of treatments compared plots sown with seed mixtures of different diversity. In addition, the efficacy of soil translocation and turf transplantation, a means of accelerating the colonisation of the site by local genotypes of calcareous grassland species, was tested. This method, whilst impractical over large areas, may provide effective focal-points for colonization of some calcareous grassland species on ex-arable land.

2.2.1. Sowing treatments

Two sowing treatments were used in the experiment, plots sown with high diversity (HD) and low diversity (LD) seed mixtures were compared with those on which spontaneous vegetation development occurred (natural colonisation, NC). The HD plots were sown with a seed mixture comprising five grass species, five legume species and five other forb species. All of the species chosen occur with high frequency in calcareous grasslands in the vicinity of the experimental site. The seeds were sown at a rate of 500 seeds m$^{-2}$ for the grass species and 100 seeds m$^{-2}$ for the forb species. The low diversity seed mixtures consisted of two grass species, one legume and one other forb species. The seeds were sown at a rate of 1250 seeds m$^{-2}$ for the grass species and 500 seeds m$^{-2}$ for forb species. The low diversity mixtures were selected by random allocation of the five species in each functional group used in the HD mixture (Table 1). The species composition of the LD mixtures therefore varied between replicate blocks, in order to avoid confounding of any effects of diversity with the effects of species choice (Huston, 1997).

2.2.2. ‘Stepping stone’ treatment

For the soil translocation, 150 l of soil were collected from Butterfly Bank, from evenly spaced points on a grid in the centre of the field. At each point, the top 1 cm of soil was removed and an area measuring 22×22 cm was excavated, giving 10 l of soil. The soil from each sampling point was kept separately and each sample randomly allocated to one of the stepping stone (SS) treatment plots. Before application of the soil to the SS plots, the top 5 cm of soil in each 2×2 m plot was temporarily removed. The 10 l of soil was then spread evenly over the area of the plot and the top layer then replaced. The topsoil was also removed from the plots with no SS treatment and then replaced, in order to mimic the disturbance caused by this treatment.

The turf transplantation consisted of taking 60 turves measuring 25×25 cm from points on an evenly spaced grid in the centre of Butterfly Bank. The turves were randomly allocated to the SS treatment plots. Four turves were placed in each of the stepping stone plots at the corners of the central 1 m$^2$ sampling area, being buried so that the top of each turf was level with the level of the surrounding soil.

2.2.3. Experimental design and site management

The experiment consisted of a fully factorial combination of the three sowing treatments and two stepping stone treatments, and adopted a randomised block design. In each block six plots measuring 2×2 m were marked out and treatment combinations randomly allocated. The plots were separated by 2-m wide paths. The sets of plots in each block were separated by 30 m, and were interspersed with plots of a second experiment sharing the same block structure (van der Putten et al., 2000; Leps et al., 2001).

The soil translocation was carried out in April 1996 and the plots sown shortly afterwards. The turf transplantation was carried out in the following November,
in order to minimize the potential for the turves to dry out. The experimental plots were mown to a height of 8 cm in late September or early October each year and the cuttings removed from the site. The paths between the experimental plots were mown to a height of 5 cm at ca. 8-week intervals between May and September each year.

2.3. Sample collection

2.3.1. Vegetation

The composition of the vegetation in the experimental plots was sampled in July–August. The abundance (estimated percentage cover) of each species of vascular plant was recorded in a permanently marked 1 m² quadrat in the centre of each experimental plot.

2.3.2. Coleoptera

Coleoptera assemblages were sampled by the suction method, using a Vortis sampler (Burkhard Manufacturing, Rickmansworth, UK). This method provides more efficient sampling than the more widely used D-Vac suction sampler, as the collected material does not impede the air flow, thus allowing a greater speed of enclosure and a greater likelihood of trapping actively flying species (Arnold, 1994). The method is considered to be effective in dry, upright vegetation less than 15 cm tall (Southwood and Henderson, 2000).

Suction sampling was chosen for three reasons. Firstly, it offers a rapid, non-destructive method, making it suitable for long-term studies of replicated field experiments. Secondly, it overcomes the problems associated with pitfall trapping, a method that tends to reflect levels of activity on the soil surface rather than abundance. Finally, one of the main aspects for investigation in this long-term study was the colonization dynamics of phytophagous insects in relation to colonization of the site by their host plants. Suction methods are particularly good for sampling canopy-dwelling phytophagous beetles, such as those in the families Apionidae, Chrysomelidae and Curculionidae (Standen, 1999). The Monte Carlo permutation tests involved running 1000 random permutations of plots within blocks.

The total sampler aperture area of 0.155 m² per sample. Placed in eight positions in each plot, corresponding to the total sampler aperture area of 0.155 m² per sample. The total area over which insects were captured is likely to be greater than the total aperture area, as insects may have been drawn into the sampler as it was lowered down over the turf. However, the same sampling procedure was employed for every sample, so differences found between the samples are likely to reflect differences in Coleoptera assemblages. In addition, five samples were collected using the same procedure from the ‘target’ established grassland sites of Butterfly Bank and Small Dean Bank, the five sample locations being evenly spaced across each field. Adult Coleoptera were extracted from the samples and the specimens stored in alcohol prior to identification to species.

2.4. Data analysis

2.4.1. Plant diversity

The number of species and Shannon diversity ($H'$), Shannon evenness ($H/E$) and Berger–Parker dominance ($N$) indices were calculated for the vegetation in each plot. Differences between treatments were tested, with analyses of variance (ANOVAs), using the General Linear Model module of SPSS.

2.4.2. Coleoptera diversity

The data for the three sampling dates were combined for the analysis, providing an indication of the Coleoptera assemblages in the plots. The number of individuals, number of species and Shannon diversity ($H'$), Shannon evenness ($H/E$) and Berger–Parker dominance ($N$) indices were calculated for the samples. Values were calculated for all Coleoptera species, and for certain families with good representation in the samples. Differences between treatments were tested, with analyses of variance (ANOVAs), using the General Linear Model module of SPSS. Data on numbers of individuals were log ($n + 1$) transformed prior to analysis.

2.4.3. Coleoptera assemblages

Multivariate analysis techniques were used to explore the relationship between the Coleoptera assemblages of the experimental plots and the two target calcareous grassland sites. The data for the three sample dates were combined and log ($n + 1$) transformed prior to analysis. Firstly, the assemblages in the experimental plots were compared with those of the two target sites by detrended correspondence analysis (DCA) using the CANOCO package (ter Braak and Smilauer, 1998). Secondly, redundancy analysis (RDA) was used to assess the significance of treatment effects using only data from the experimental plots. Redundancy analysis was used because the DCA showed the species composition of the experimental plots to be homogenous and the explanatory variables were categorical. Using various combinations of explanatory variables and covariables, together with the appropriate permutation scheme in the Monte Carlo tests in CANOCO, allows testing of treatment effects in a manner analogous to ANOVA. Separate analyses were carried out to test each main effect and the interaction of the treatments, following the methods adopted by van Dobben et al. (1999). The Monte Carlo permutation tests involved running 1000 random permutations of plots within blocks.
3. Results

3.1. Plant diversity

The sowing and the stepping stone treatments had significant effects on the plant diversity of the experimental plots. Both species richness and Shannon diversity were lower in the LD sowing treatment than the NC or HD treatments (Fig. 1). The plant assemblages in the LD plots were also characterized by higher values of the dominance index and lower values of evenness. Whilst the NC and HD plots had similar values for plant diversity, the vegetation differed in the characteristics of the constituent plant species. The NC plots consisted of early successional ruderal species, the most abundant being *Poa pratensis* and *Crepis capillaris*. The HD plots consisted mainly of the sown chalk grassland species, with few unsown species in the sward. The most abundant sown species were *Centaurea nigra*, *Festuca rubra* and *Lotus corniculatus*.

Plots with the SS treatment had significantly higher values of plant species richness and Shannon diversity than the corresponding plots without the treatment (Fig. 1). The treatment led to an increase in plant species richness of around 3–6 species per sample. Species colonising the plots as a result of the SS treatment included *Galium mollugo*, *Hypericum perforatum*, *Ori- ganum vulgare* and *Veronica chamaedrys*.

3.2. Coleoptera abundance

A total of 1744 adult Coleoptera were collected on the three sampling dates, comprising individuals of 119 species in 20 families (Table 2). The most abundant families in the experimental plots were the Staphylinidae, Chrysomelidae and Curculionidae. The same families were abundant in the established ‘target’ chalk grassland sites, although at these sites the Apionidae was the second most abundant family. In addition, the target chalk grassland sites were characterized by a greater abundance of Coccinellidae and Ptiliidae.

Significant treatment effects on the abundance of some families were found (Table 2). Nitrilulidae were more abundant in the NC plots than the sown plots, largely the result of high numbers of *Meligethesa aeneus* feeding on the pollen of the many yellow-flowered ruderals in these plots. Members of the Apionidae were more abundant in the HD plots than the LD plots, relating to differences in the abundance of *Apion loti*, a phytophagous species feeding on the most abundant sown legume species, *Lotus corniculatus*. Chrysomelidae were more abundant in the plots without the SS treatment. This is

![Fig. 1. Mean values (± one S.E.M.) of (a) species richness, (b) Shannon diversity index *H*, (c) Shannon evenness index *H/E* and (d) Berger-Parker dominance index *N* for the plant assemblages in the six treatment combinations. NC, natural colonization; LD, low diversity sowing; HD, high diversity sowing; SS, stepping stone treatment. The significance levels from analysis of variance are shown (ns, non-significant; *** *P* < 0.001), sowing treatments sharing the same letter are not significantly different (Tukey test, *P* > 0.05).](image-url)
related to patterns of abundance of *Longitarsus pratensis*, and its host plant, *Plantago lanceolata*, which were both more abundant in the plots without the SS treatment.

### 3.3. Coleoptera diversity

Species diversity was similar in the experimental plots and the target chalk grasslands (Table 3). In contrast to the significant treatment effects on beetle abundance, few significant effects on diversity were found. Differences in diversity were analyzed for total Coleoptera assemblages, and for families for which greater than 10 species were found, namely the Staphylinidae, Chrysomelidae and the super-family Curculionoidea. The dominant families in the latter, the Apionidae and Curculionidae, were combined for this analysis in order to ensure that all samples contained individuals of this group. Few significant differences in species richness, diversity, evenness or dominance were found (Fig. 2). The SS treatment plots had higher Shannon diversity indices for total Coleoptera assemblages. A positive relationship was found between the Shannon index of the plant and Coleoptera assemblages ($r=0.380$, $P=0.038$, Fig. 3). No significant correlations were found between the diversity indices of the plant community and those of phytophagous beetle families (Chrysomelidae, Curculionoidea).

### 3.4. Coleoptera assemblages

#### 3.4.1. Comparison with target sites

DCA was used in a preliminary analysis to explore the similarity of the Coleoptera assemblages in the various treatment plots with those of the two target chalk grassland sites. All sample dates were combined for the analysis and the data were log ($n+1$) transformed. The sample plot from the DCA (Fig. 4) showed clear separation of the samples from the target chalk grassland sites and those from the experimental plots along the first ordination axis (eigenvalue = 0.39). Slight separation of the different sowing treatments (NC, LD, HD) occurred along the second axis (eigenvalue = 0.16).

The species found only in the target chalk grassland sites, or showing a greater affinity for those sites, are shown in Table 4. The most abundant species showing a preference are *Acrotrichus atomaria* (Ptilidae), *Longitarsus parvulus* (Chrysomelidae) and *Subecoccinella 24-punctata* (Coccinellidae). Species contributing significantly to the assemblages found in the experimental plots, but largely absent from the target sites included...
Amischa soror and Stenus ossium (Staphylinidae), and two species associated with flowers, Meligethes aeneus (Nitidulidae) and Olibrus liquidus (Phalacridae).

3.4.2. Effects of treatments

Redundancy analysis was used to investigate the effects of the experimental restoration treatments. Monte Carlo permutation tests showed that both sowing treatment \((P = 0.001)\) and SS treatment \((P = 0.039)\) had significant effects on the Coleoptera assemblages. Axis 1 (eigenvalue = 0.10) separates the samples according to the sowing treatments and axis 2 (eigenvalue = 0.06) generally separates those plots with and without the SS treatment (Fig. 5). The diagram explains 83% of the variance of the fitted abundance values of the full model (sum of unconstrained eigenvalues = 0.829; sum of canonical eigenvalues = 0.232). Fig. 6 shows the distribution of the most abundant species along the first two axes of the ordination. Differences between the treatments are the result of significant differences between the treatment plots in the abundance of a small number of beetle species (Table 4). The NC plots have greater numbers of Meligethes aeneus (Nitidulidae) and Tychius junceus (Curculionidae), whilst the HD plots have significantly more Apion loti (Apionidae) and Gymnetron pascuorum (Curculionidae), both associated with sown chalk grassland plant species (Lotus corniculatus and Plantago lanceolata, respectively).

4. Discussion

4.1. Efficacy of sampling method

There has been much debate about the most effective method of sampling invertebrates in grasslands. The efficiency of capture of different methods varies between different groups of invertebrates. Destructive sampling by turf removal and heat extraction is considered to be the most effective method (Morris and Rispin, 1987). The study reported here is part of a long-term replicated plot experiment, so methods that rely on removing turf or involve significant depletion of invertebrates within the plots (e.g. placing barriers around the plots and using repeated pitfall trapping) were considered inappropriate. A recent comparative study in grasslands similar to those used in this study has shown that suction sampling and pitfall trapping sampled different subsets of the total Coleoptera fauna present at a site (Standen, 2000). Suction sampling was chosen for this study as it provides a rapid, repeatable, non-destructive method suitable for short grassland swads.

The study of Standen (2000) concluded that suction sampling and sweep netting provided effective means of characterizing assemblages of herbivorous Coleoptera in grasslands. However, certain Coleoptera species are only effectively sampled with other methods, such as taking soil cores or pitfall trapping. It is likely that ground-dwelling and nocturnal species, most notably
members of the Carabidae, were significantly under-represented using the adopted sampling method. In addition, care needs to be taken in using such methods to provide absolute estimates of population densities (Southwood and Henderson, 2000). In this study, a standard sampling procedure was employed in plots of similar vegetation height and canopy structure, so differences identified between samples are likely to reflect actual differences in population densities.

4.2. Effects of restoration treatments on plant assemblages

Both the sowing and the SS treatments had significant effects on the various measures of plant diversity. The sowing of low or high diversity mixtures of chalk grassland plants resulted in suppression of many of the unsown weed species colonising the plots from the seed bank or seed rain. Whilst the NC plots had a mean of ca. 16 species m⁻² in the fourth summer after establishment of the plots, the LD and HD plots were composed predominantly of sown species, with only a few unsown species able to persist in the sward (see also van der Putten et al., 2000). The effect of the SS treatment was to increase plant species richness by between three and six species per plot. This increase in diversity is the result of colonisation of the plots by a number of chalk grassland species which had persistent seed banks in the soil translocated from the established grassland site at Butterfly Bank. The enhancement of colonization was greatest in the NC plots and lowest in the HD plots, although there was no significant interaction between sowing and SS treatments.

The low diversity mixtures, which were composed of random allocations (within functional groups) of the species used in the high diversity mixture, showed great variability between replicates. They were generally characterized by higher values of the dominance index and lower values of the evenness index compared with the NC and HD plots. Studies of the same treatments in a second experiment at the same site have shown that the performance of each species in the HD plots
provides a good indicator of the performance of that species in the LD plots. This suggests that the variability between the LD replicates reflects the probability of including a good performing species in the mixture (Leps et al., 2001).

4.3. Effects of restoration treatments on Coleoptera assemblages

The nature of the Coleoptera assemblages varied significantly between the restoration treatments. The differences could be attributed in part to between-plot differences in the abundance of particular host plants and their associated insects. For other non-phytophagous insect groups, differences in abundance between treatments may be caused by differences in microclimate or the amount of litter. Both of these factors are related to the primary productivity of the vegetation. In spite of differences in the composition of the Coleoptera fauna, the restoration treatments had no clear effects on their diversity. There was a small but significant increase in Shannon diversity index with the SS treatment. However, neither comparison of plots of similar plant composition but different plant diversity (LD vs. HD), nor of plots with the same plant diversity but different life histories (NC vs. HD), demonstrated any significant effects on overall Coleoptera diversity, although a significant correlation between Shannon indices for plant and Coleoptera assemblages was found.

4.4. Similarity of Coleoptera assemblages to target sites

The Coleoptera assemblages of the experimental plots were distinct from those of the target chalk grassland sites. The data collected provide no evidence that any of the restoration treatments resulted in Coleoptera assemblages that resembled the target sites more closely than any other treatments. The significant differences in
Coleoptera assemblages between the restoration treatments are the result of differences in the abundance of a small number of eurytopic grassland species. A number of species, including herbivores, fungivores, detritivores and predators, were found exclusively on the target chalk grasslands sites.

Unlike certain insect taxa (e.g. Lepidoptera, Orthoptera, Carabidae), knowledge of the habitat affinities of many of the grassland Coleoptera species sampled in this study is limited. It is not known how many of the species present in greater abundance on the target chalk grassland sites are stenotopic (i.e. show a high fidelity to that habitat). The failure of many of these species to colonize the experimental plots could be the result of poor dispersal ability or unsuitable conditions in the plots (e.g. absence of host plants, paucity of litter). Studies on the Carabidae assemblages of heathlands has demonstrated the importance of dispersal ability in allowing the survival of stenotopic species in fragmented habitats (Turin and den Boer, 1988; den Boer, 1990; de Vries et al., 1996). Dispersal ability is likely to be a key factor determining the recolonization dynamics of insects in newly-created habitat patches (Mortimer et al., 1998).

4.5. Implications for restoration of chalk grasslands

The study has shown that, whilst both the sowing and the stepping stone treatments enhanced the colonization of the experimental plots by plant species typical of chalk grassland, this was not the case for the Coleoptera. The data suggest that the early stages of establishment of newly created grasslands on ex-arable land are characterized by a limited species pool of Coleoptera species. Two factors may promote the rapid colonization of new grasslands by these species. Firstly, colonization may occur by species that possess traits that allow dispersal. Comparison of the distribution of wing-form
Table 4
Affinities of the most abundant Coleoptera species found in the experimental plots and the target chalk grassland sites

<table>
<thead>
<tr>
<th>Species found only in established grasslands</th>
<th>Target sites</th>
<th>Sowing treatments</th>
<th>Stepping stone treatments</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>NC</td>
<td>LD</td>
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<tr>
<td>Staphylinidae Falagria thoracica</td>
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<td>Stenus flavipes</td>
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<td>Stenus ochropus</td>
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<tr>
<td>Coccinellidae Subcoccinella 24-punctata</td>
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<td>1.3</td>
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<td>Apionidae Apion flavimanum</td>
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<td>Species occurring with greater abundance in established grasslands than experimental plots (ratio &gt; 3:1)</td>
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<tr>
<td>Ptiliidae Acrotrichus atomaria</td>
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<td>Staphylinidae Drusilla canaliculata</td>
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<td>Species with similar abundances in established grassland and experimental plots</td>
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<td>0.6</td>
</tr>
<tr>
<td>Latridiidae Corticarina gibbosa</td>
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<td>1.5</td>
<td>3.2</td>
</tr>
<tr>
<td>Chrysomelidae Longitarsus pratensis</td>
<td></td>
<td>1.7</td>
<td>3.3</td>
</tr>
<tr>
<td>Apionidae Apion loit</td>
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<td>2.4</td>
<td>0.9a</td>
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<tr>
<td>Curculionidae Orthochaetes setiger</td>
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<td>0.4</td>
</tr>
<tr>
<td>Sitona lineatus</td>
<td></td>
<td>1.8</td>
<td>2.4</td>
</tr>
<tr>
<td>Tychius meliloti</td>
<td></td>
<td>1.5</td>
<td>0.7</td>
</tr>
<tr>
<td>Species occurring with greater abundance in experimental plots than established grasslands (ratio &gt; 3:1)</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Staphylinidae Amischa soror</td>
<td></td>
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<td>3.9</td>
</tr>
<tr>
<td>Atheta (Mocyta) fungi</td>
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<td>0.3</td>
</tr>
<tr>
<td>Stenus brunnipes</td>
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<tr>
<td>Stenus ossium</td>
<td></td>
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<td>1.0a</td>
</tr>
<tr>
<td>Nitidulidae Meligethes aeneus</td>
<td></td>
<td>0.1</td>
<td>8.6a</td>
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<tr>
<td>Phalacridae Olibrus liquidus</td>
<td></td>
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<td>2.6</td>
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<td>Sibillus testaceus</td>
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<td>0.9a</td>
</tr>
<tr>
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<td>1.1</td>
</tr>
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<tr>
<td>Curculionidae Trichosirocalus trochodytes</td>
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<td>0.6</td>
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<tr>
<td>Tychius junece</td>
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<td>3.1a</td>
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<tr>
<td>Species found only in experimental plots</td>
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<td>Staphylinidae Stenus fulvicornis</td>
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<td>Tachyporus solutus</td>
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<td>Curculionidae Gymnetron pascuorum</td>
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<td>0.5a</td>
<td>0.0a</td>
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<tr>
<td>Sitona humeralis</td>
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</tr>
</tbody>
</table>

ns, not significant.

* Only species with a mean abundance greater than 0.5 per sample in either the experimental site or the target chalk grassland sites are included. The results of analysis of treatment effects using ANOVA are shown where statistically significant.

b Post-hoc comparisons of the sowing treatments were carried out using the Tukey test, treatments sharing the same letter are not significantly different (P > 0.05).

c P < 0.05.

d P < 0.01.

e P < 0.001.
variants has shown that macropterous forms are better able to colonize newly created grasslands and that micropterous forms are restricted to stable habitats (Hollier et al., 1997). Secondly, early colonization of newly created grasslands may be limited to eurytopic species with wide habitat affinities or those which are associated with common grassland plants. Several of the most abundant phytophagous species found in the experimental plots are associated with host plants that, whilst occurring in chalk grasslands, also occur in mesotrophic grasslands, banks and hedgerows (e.g. Plantago lanceolata, Medicago lupulina, Trifolium spp.). Therefore, colonization of the plots by such species could have been the result of local dispersal from the field edge.

Although several correlative studies have shown the importance of dispersal ability for the persistence of stenotopic species in fragmented habitats (Davis and Jones, 1986; Turin and den Boer, 1988; den Boer, 1990; de Vries et al., 1996), few studies have followed the recolonization of restoration sites by invertebrate groups. Of those that have been published, most are concerned with land reclamation after mining operations (e.g. Majer et al., 1984; Holl, 1995). However, similar results have been found for other insect groups in studies of newly created grasslands on ex-arable land (e.g. van Dijk, 1987; de Goede and van Dijk, 1998). The studies of Morris (1990) on the Hemiptera fauna of newly created chalk grasslands showed that, for this group of insects, the early stages of succession were dominated by opportunists and inhabitants of agricultural habitats.

The results of this study suggest that, whilst initial site management practices have the potential to significantly accelerate the development of vegetation which resembles the plant communities typical of chalk grassland, colonization by associated invertebrate assemblages may be a much slower process. Many components of the Coleoptera assemblages characteristic of established chalk grasslands are associated with plant species which are rare and restricted in their distribution to chalk grasslands. Colonization of newly created grasslands on ex-arable land by these species will take time. These rarer chalk grassland plant species, by their very nature, have low apparency, so colonization of new populations by their associated insects will be a slow process. The presence of a new population of the host plant may not, in itself, be enough to facilitate colonization. The age-structure, physiology and spatial patterning of the population of the host plant are also important factors in determining patch suitability for the associated fauna (Mortimer et al., 1998).

The results highlight the importance of considering the spatial arrangement of landscape elements, as well as site management practices, when implementing habitat re-creation or restoration schemes. The colonization of new sites by species with limited powers of dispersal is likely to be a slow process, often driven by stochastic events. Whilst it is comparatively easy to enhance the colonization of a new site by plant species, through seed sowing or turf/soil translocation, assisting the colonization of new sites by insect species is more difficult. The targeting of restoration schemes on land adjacent to existing areas of the desired target community, or creating corridors or linkages between remnant patches of such habitat, are likely to result in more rapid colonization of new sites by stenotopic invertebrates.

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References


