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The potential of grass field margin management for enhancing beetle diversity in intensive livestock farms

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Summary

1. Declining populations of UK grassland flora and fauna have been attributed to intensification of agricultural management practices, including changes in cutting, fertilizer, grazing and drainage regimes. We aimed to develop field margin management practices that could reverse declines in intensively managed grassland biodiversity that would have application in the UK and Europe. Here we focus on one aspect of grassland biodiversity, the beetles.

2. In four intensively managed livestock farms in south-west England, 10-m wide field margins in existing grasslands were managed to create seven treatments of increasing sward architectural complexity. This was achieved through combinations of inorganic (NPK) fertilizer, cattle grazing, and timing and height of cutting. To examine the potential influence of complexity on faunal diversity, beetles were identified to species level from suction samples taken between 2003 and 2005, and their assemblage structure was related to margin management, floral assemblages and sward architecture.

3. Beetle abundance, and species richness and evenness were influenced by margin management treatment and its interaction with year. Correlations with sward architecture and the percentage cover of dominant forbs and grasses were also found. Functional groups of the beetles showed different responses to the management treatments. In particular, higher proportional abundances of seed/flower-feeding guilds were found in treatments not receiving NPK fertilizer.

4. The assemblage structure was shown to respond to margin management treatments, sward architecture and the percentage cover of dominant forbs and grasses. The most extensively managed treatments were characterized by distinct successional trajectories from the control treatment.

5. *Synthesis and applications.* This study provides management options suitable for use within agri-environment schemes intended to improve faunal diversity associated with intensively managed lowland grasslands. Field margins receiving either no management or a single July silage cut were shown to support greater abundances and species richness of beetles, although subtler modifications of conventional management may also be beneficial, for example the absence of NPK fertilizer while maintaining grazing and silage cutting systems.

Key-words: agri-environment scheme, beetle diversity, cutting, functional group, grazing, inorganic fertilizer, intensive grassland management, silage

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Introduction

Alternative management of field margins has been used extensively in arable cropping systems to improve the nature conservation value of farmland (Marshall & Moonen 2002; Meek *et al.* 2002; Woodcock *et al.* 2005b) as well as to increase densities of beneficial invertebrates (Thomas *et al.* 2001). However, to date such field margin management has rarely been used in grasslands (but see Haysom *et al.* 1999). In England and Wales, permanent (> 5 years) and temporary (< 5 years) grassland covers 40% of all agricultural land (Defra 2004), of which a large proportion has been modified by intensive agricultural management (Duffey *et al.* 1974; Blackstock *et al.* 1999). Intensive grassland management normally involves the use of inorganic fertilizers (NPK), improved drainage, reseeding with one or two grass species/varieties and the replacement of hay with silage cutting as the principal conserved forage (Frame 2000). Technological developments in silage production have enabled greater flexibility in the timing and frequency of cutting as higher grass water contents are tolerated (Vickery *et al.* 2001). Increased productivity has also allowed higher stocking densities to be supported. The increased levels of disturbance associated with these changes in management have had a major impact on the composition and structure of agricultural grassland (Duffey *et al.* 1974; Blackstock *et al.* 1999; Vickery *et al.* 2001), leading to species-poor and structurally uniform grasslands of low nature conservation value (Duffey *et al.* 1974). Declines in populations of higher plants (Blackstock *et al.* 1999), farmland birds (Vickery *et al.* 2001) and invertebrates (Duffey *et al.* 1974; Morris 1978; Asher *et al.* 2001) have all been attributed to this intensification of grassland management.

Invertebrates represent a key functional component of agricultural grassland systems (Woodcock *et al.* 2005a, 2006) and have importance as pests (Norris 1994) and food resources for farmland birds (Vickery *et al.* 2001) and their own innate conservation value (Asher *et al.* 2001). Invertebrates also contribute to key ecosystem functions, such as nutrient cycling, biocontrol and pollination (Norris 1994). The causes of declines in invertebrate populations in response to improved grassland management are primarily driven by changes in the plant community as they respond to intensification in the form of cutting, grazing, fertilizer application and reseeding regimes (Duffey *et al.* 1974; Vickery *et al.* 2001). The direction of invertebrate responses to cutting has been related to the interaction between the insects' lifecycles and the phenological development of the vegetation in the period since it was last cut (Duffey *et al.* 1974; Morris 1978; Asher *et al.* 2001). Increased stocking densities have negative impacts resulting from the disturbance caused by destruction of the sward canopy (Duffey *et al.* 1974; Morris 1978). Inorganic fertilization (Fenner & Palmer 1998) and residues of anti-helminth drugs in dung (Hutton & Giller 2003)

have also been shown to have negative impacts on invertebrate populations.

An increased complexity of the above-ground vegetation structure (often referred to as sward 'architecture') is of key importance to both the abundance and diversity of invertebrates (Gibson, Hambler & Brown 1992; Dennis, Young & Gordon 1998; Morris 2000). The presence and availability of structures, such as flowers, seed heads, stems and leaves, have been shown to be important for many phytophagous and predatory invertebrates, as well as insect parasitoids (Gibson, Hambler & Brown 1992; Dennis, Young & Gordon 1998; Finke & Denno 2002). The intensification of grassland management, in particular multiple silage cuts and grazing, has been associated with reduced sward architectural complexity (Gibson, Hambler & Brown 1992; Morris 2000). This reduction in sward architecture would normally result in a reduced availability of reproductive plant structures, many of which represent key resources for phytophagous invertebrates (Morris 2000; Woodcock *et al.* 2005a). The strong temporal component of sward architecture would also impact on grassland invertebrates (Morris 2000).

The present study aimed to establish whether the beetle assemblages of intensively managed lowland grassland can be enhanced by modifying field margin management. The impacts of combinations of key management practices, namely the height and timing of sward cuts, cattle grazing and inorganic fertilizer inputs, were investigated by considering changes in the beetle species diversity and composition along a time series. This was intended to provide information to underpin future developments of agri-environmental policy for improved grasslands. The study presented here focused on beetle assemblages only. Beetles represent an important component of the grassland fauna in terms of overall abundance, species richness and the variety of functional groups they represent (Thiele 1977; Bohac 1999; Woodcock *et al.* 2005a). In addition, they are directly and indirectly dependent on plant assemblages and provide a link between plants and higher trophic levels, for example birds (Duffey *et al.* 1974; Vickery *et al.* 2001). By assessing beetle assemblage responses to management it is believed that recommendations of best practice will improve the biodiversity value of intensively managed lowland grasslands.

Materials and methods

STUDY SITE

A balanced replicated block design experiment was established on four UK farms, two each in Somerset (Bickenhall, N50°58'47":W2°59'29", South Hill, N50°57'40":W3°02'53") and Devon (Heywoods, N50°48'38":W3°55'40"; North Wyke, N50°46'14":W3°55'46"). Stocking densities on these farms ranged between 4.0 and 5.5 cattle livestock units ha⁻¹, and inorganic fertilizer inputs were typically 360 kg nitrogen ha⁻¹, 20 kg

Table 1. Summary of the management practices used to establish each of the seven experimental treatments in the margin plots. Treatment 1 is the experimental control

Management	Experimental treatments						
	1	2	3	4	5	6	7
NPK application	+		+	+			
Cut (5 cm) in May	+	+		+			
Cut (10 cm) in May			+		+		
Cut (5 cm) in July	+	+		+		+	
Cut (10 cm) in July			+				
Aftermath grazing	+	+	+				

phosphorus ha^{-1} and 80 kg potassium ha^{-1} . All sites were lowland improved grasslands and classified as species-poor MG7 *Lolium perenne* L. leys (Rodwell 1992). The grasses *Agrostis capillaris* L. and *Holcus lanatus* L. and forbs *Trifolium repens* L. (Leguminosae) and *Ranunculus repens* L. (Ranunculaceae) were associated with this grassland type. All farms were on clay loams and separated from one another by at least 8 km.

EXPERIMENTAL DESIGN

The experiment was established in 2003, and management practices were applied throughout 2003–05 to create seven experimental treatments. The seven treatments aimed to increase sward architectural complexity sequentially and were manipulations of existing swards already present within the grasslands (i.e. they were not resown). The sward was cut at one of two heights (5 or 10 cm) in May and July, depending on treatment (Table 1). Treatments 1, 3 and 4 received 225 kg ha^{-1} nitrogen (N), 22 kg ha^{-1} phosphorus (P) and 55 kg ha^{-1} potassium (K) of inorganic fertilizer. Treatments 1–3 were grazed by cattle in September until a target sward height of 5–7 cm was reached. Treatment 1, which was fertilized, cut in both May and July to a height of 5 cm and then aftermath grazed, was considered to be the control, representing what approximated normal intensive grassland management. Treatments 5–7 were the most extensively managed, receiving either a single vegetation cut in May (treatment 5) or July (treatment 6) or remaining unmanaged throughout the study period (treatment 7). All experimental plots were fenced off from the remainder of the field. For this reason, while treatment 7 was referred to as unmanaged, cattle exclusion management was actually in practice.

All experimental plots were 10 × 50 m with the long edge running parallel to the field boundary. The field boundary was represented by hedges rather than wire fencing. Three replicates of the seven experimental treatments were established at each farm, i.e. three replicate blocks per farm, with 12 replicates in total. For logistical reasons replicates were split between multiple fields, although the plots within a replicate block were of the same orientation. Experimental plots were not

positioned under overhanging trees. The allocation of the treatments within replicates was random.

Two additional experimental treatments were also established in the study systems. Treatment 8 was cultivated in early spring 2003 with spring barley undersown with a grass/legume ley. Treatment 9 was also cultivated in early spring 2003, and sown with a kale and quinoa seed mix. As both these treatments required the initial cultivation of the field margins, the analyses used in this paper considered only treatments 1–7, which represented manipulations of the existing grassland sward only.

VEGETATION SAMPLING

The average percentage cover of plant species and percentage cover of bare ground was determined in August of each year prior to the second sward cut. Five replicate 1 × 1-m (1-m²) quadrats were placed along the diagonal of each experimental plot and percentage cover within the quadrats was assessed by eye. Where more than one individual was involved in recording these measurements, at least five quadrats were completed together to ensure that percentage cover estimates were within a margin of error of no more than 5%. This approach was repeated in September of each year to assess the percentage cover of cattle dung.

Vertical drop pins were used to assess the sward architectural complexity of four vegetation classes, the grasses, forbs (excluding Leguminosae), Leguminosae and dead vegetation. These categories were chosen based on known responses of beetles to sward architecture. For example, epigeal predatory species have been associated with complex grass swards (Dennis, Young & Gordon 1998) while many phytophagous beetles feed on forbs, with a large number specializing on legumes (Hoffman 1950,58). The method uses 10 3-mm diameter pins (separated by 10 cm) lowered vertically through the sward of each plot. The number of contacts of each vegetation category at 5-cm intervals up each pin was recorded. This provided detailed stratified information on the vertical distribution of plant structures, referred to here as sward architecture. A modified version of the Shannon–Wiener diversity index was used to summarize information from the drop-pin frames into a single parameter:

$$H'_{\text{arch}} = \sum p_i \times \log_e p_i$$

where H'_{arch} is the index of sward architectural complexity and p_i the proportion of the total number of contacts with the drop pin in a particular plot at each height interval i . Sward architecture was measured four times each year, these periods corresponding with the beetle sampling dates in April, June, July and September. High H'_{arch} scores meant the sward had a high level of architectural complexity in terms of height and density of plant structures. Plant nomenclature followed Clapham, Tutin & Warburg (1993).

BEETLE SAMPLING

Adult beetles in the experimental margins were sampled using a Vortis suction sampler (Burkard Co. Ltd, Rickmansworth, UK) during 2003, 2004 and 2005. In each year, the beetles were sampled on dry days during April, June, July and September between 10:00 and 16:00 h. Both the June and September sampling rounds occurred as close as possible to 2 weeks after the sward cutting management had been applied. In each plot, 75 × 10-second suction (0.26% of a plot's area) were taken for each sampling date. Suction sampling is a standard technique for the quantitative collection of grassland beetles (Gibson, Hambler & Brown 1992; Brown & Hyman 1995; Woodcock *et al.* 2005a). The Vortis suction sampler is designed to prevent dislodged vegetation impeding airflow (Southwood & Henderson 2000).

Beetles of Carabidae, Staphylinidae (excluding Aleocharinae but including Pselaphinae), Chrysomelidae, Coccinellidae, Elateridae, Apionidae and Curculionidae were identified to species. Aleocharinae beetles were not identified to species for reasons of taxonomic intractability and were excluded from all subsequent analyses (except as a component of the overall beetle abundance). The choice of which beetle families were identified was made on an a priori basis and reflected the dominance of these families within grasslands (Woodcock *et al.* 2005a). Beetles were assigned to functional groups on the basis of larval feeding strategy as either predominantly predatory or phytophagous, and then for the phytophagous species as seed/flower-, root/stem- or foliage-feeding strategies (Thiele 1977; Mills 1981; Douget 1994; Bohac 1999; Hoffman 1950–58). Nomenclature follows Strejcek (1993), Luff & Duff (2001), Morris (2003) and Lott & Duff (2003).

DATA ANALYSIS

All analyses were based on the summed abundances of each beetle species for a particular year. The response of beetle abundance ($\log_e n + 1$), species richness ($\log_e n + 1$), Shannon–Wiener diversity and Shannon–Wiener evenness to margin management treatments were assessed using a repeated-measures analysis with mixed models in SAS 8.02. The analysis was divided into three parts. Model I had fixed effects of margin treatment, year and the interaction between these two factors. Year was set as a repeated-measure within the analysis, and an autoregressive covariance structure was used to account for covariance between subsequent sample years. Site, field nested within site and replicate block nested within field were used as the random effects to account for uncontrolled random variation, both within and between sites (Schabenberger & Pierce 2002). Field represented the physical area of land delimited by hedges within which multiple experimental plots were situated; an individual field could therefore contain only part of a replicate block of seven treatments. The significance of between-treatment differences in the

response variables was assessed using *post-hoc* pairwise comparisons of the least-square means values derived from the mixed models described above (Schabenberger & Pierce 2002). It was possible that any response in beetle species richness to the treatments represented an artefact resulting from positive correlations between beetle abundance and species richness. To correct for such a potential bias, the analysis of beetle species richness was repeated with beetle abundance ($\log_e n + 1$) as a covariate.

As continuous environmental measures for each margin plot would be influenced by the margin treatments, testing their effects on beetles was not possible using the analysis of model I. Therefore a second analysis (model II) using the same repeated-measures mixed model design with fixed effects of the continuous environmental variables, year and the interactions between year and the continuous environmental variables was used. Continuous environmental variables were: (i) sward architecture of the grasses (GA), forbs (FA), legumes (LA) and dead vegetation (DA); (ii) percentage cover of bare ground (BG); (iii) percentage cover of dung (dung); (iv) plant species richness (PSR); (v) percentage cover of the dominant forbs *Leguminosae* spp. (%Le), *Rumex* spp. (Polygonaceae) (%Ru), *Ranunculus* spp. (Ranunculaceae) (%Ra), *Plantago* spp. (Plantaginaceae) (%Pl), *Cirsium* spp. (Compositae) (%Ci) and *Taraxacum* spp. (Compositae) (%Ta); and (vi) percentage cover of the dominant grasses tussock grasses (%Tu), *Lolium perenne* L. (%LP) and *Agrostis stolonifera* L. (%AS). A final analysis (model III) was used to determine whether the significant continuous environmental parameters of model II explained additional variance to that of the treatment effects of model I. In all cases, model simplification was by deletion of non-significant factors, except where a factor was part of a significant interaction. Calculation of the model degrees of freedom used the iterative Satterthwaite's method (Schabenberger & Pierce 2002). Differences between treatments in plant species richness and sward architecture were also tested using the methods described for model I.

To assess changes in the functional structure of the beetle assemblages in response to margin management treatments, the analysis described above for model I was repeated. Response variables were logit transformations of the proportion of the total abundance of beetles that were predatory. This analysis was repeated for the root/stem-, seed/flower- and foliage-feeding functional groups, although they were considered only as proportions of the total abundance of the phytophagous beetles.

Changes in the structure of the beetle assemblages were assessed using the linear ordination method of partial redundancy analysis (pRDA). This was chosen on the basis of the short gradient lengths determined from a preliminary detrended correspondence analysis (DCA) (gradient length 2.16). The inclusion of species in this analysis was restricted so that beetles represented by only one individual were excluded. In all

Table 2. Model I (MI): results of repeated-measures analysis with mixed models used to test responses of beetle abundance, species richness ($\log_e n + 1$), Shannon–Wiener diversity and evenness to margin management treatments (treat) and their interaction with year (year). Model II (MII): considers only continuous environmental measures of variation. Model III (MIII): determines whether the addition of the significant treatment effects of model I to those of model II results in a significant increase in the explained variance. Only significant effects have been shown for model II. See the Methods for environmental variable abbreviations. NA, analysis not applicable; NS, $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Positive or negative correlations are indicated by + or – in parentheses, where three consecutive symbols represents the direction of correlations for successive years (2003–05)

Abundance ($\log_e n + 1$)	Species richness ($\log_e n + 1$)	Species diversity	Species evenness
MI			
Treat: $F_{6,81.1} = 3.60^{**}$	Treat: $F_{6,79.1} = 12.5^{***}$	Treat: NS	Treat: NS
Treat × year: $F_{12,156} = 5.61^{**}$	Treat × year: $F_{12,156} = 4.16^{**}$	Treat × year: NS	Treat × year: $F_{12,158} = 2.51^{**}$
Year: $F_{2,156} = 95.5^{***}$	Year: $F_{2,156} = 15.9^{***}$	Year: $F_{2,170} = 19.2^{**}$	Year: $F_{2,158} = 9.45^{***}$
MII			
Year: $F_{2,211} = 30.6^{***}$	Year: NS	Year: $F_{2,208} = 15.4^{***}$	Year: $F_{2,189} = 16.1^{***}$
Sward architecture	Sward architecture	Sward architecture	Sward architecture
GA × year: $F_{2,209} = 18.1^{***}$ (+ + +)	GA × year: $F_{2,206} = 6.03^*$ (+ + +)	FA × year: $F_{2,207} = 3.28^*$ (+ + +)	FA × year: $F_{2,190} = 3.45^*$ (+ + –)
LA: $F_{1,186} = 34.1^{***}$ (+)	FA: $F_{1,208} = 3.96^*$ (+)	LA: $F_{1,185} = 5.37^*$ (–)	LA × year: $F_{2,181} = 5.35^{**}$ (– – –)
	LA: $F_{1,199} = 11.6^{***}$ (+)		DA × year: $F_{2,178} = 8.25^{**}$ (– – –)
	DA: $F_{1,228} = 9.02^{**}$ (+)		
Plant percentage cover	Plant percentage cover	Plant percentage cover	Plant percentage cover
%Ru × year: $F_{2,205} = 4.17^*$ (– – –)	%Ru: $F_{1,172} = 7.54^{**}$ (–)	%Ru × year: $F_{2,185} = 3.76^*$ (– – –)	%Ra × year: $F_{2,183} = 8.60^{**}$ (– – –)
%Ra: $F_{1,177} = 5.96^*$ (–)	%Tu × year: $F_{2,205} = 8.48^{**}$ (+ + –)	%Ra × year: $F_{2,198} = 4.78^{**}$ (– – –)	%Tu × year: $F_{2,180} = 4.10^*$ (+ + –)
%Tu × year: $F_{2,216} = 4.77^{**}$ (+ + –)	%LP × year: $F_{2,207} = 9.12^{**}$ (+ + –)	%Tu × year: $F_{2,195} = 10.1^{**}$ (+ + –)	%Ci × year: $F_{2,188} = 3.93^*$ (+ + +)
%Ci: $F_{1,158} = 5.34^*$ (–)		%Ci × year: $F_{2,192} = 5.43^{**}$ (+ + –)	%Ta × year: $F_{2,194} = 3.00^*$ (+ + –)
		%LP × year: $F_{2,207} = 9.76^{**}$ (+ + –)	%Pl: $F_{1,195} = 3.87^*$ (–)
		%AS × year: $F_{2,208} = 6.80^{**}$ (+ + –)	%LP × year: $F_{2,192} = 7.54^{**}$ (– – –)
		Other	%AS × year: $F_{2,198} = 5.03^{**}$ (– – –)
		PSR: $F_{1,151} = 12.2^{***}$ (–)	Other
			PSR: $F_{1,191} = 9.36^{**}$ (–)
MIII			
$\chi^2_{12} = 0.80$, NS	$\chi^2_{17} = 3.87$, NS	NA	$\chi^2_{20} = 7.32$, NS

cases, abundances of individual species were summed within a particular year and \log_{10} transformed. Following ter Braak & Šmilauer (2003), the temporal change in beetle assemblage structure was tested based on interactions of environmental variables with year (e.g. Env.Var. × 2003, Env.Var. × 2004 and Env.Var. × 2005). Sample year (2003, 2004 and 2005), field, replicate block and site were also included as covariables, with the latter three of these used as blocking factors. Individual sample year was treated as a temporal split-plot within the analysis, and samples were permuted freely between whole plots only. In all cases, significance was tested for each interaction individually using Monte Carlo permutation tests of both canonical axes under a reduced model (1000 permutations). The main environmental variables were the seven treatments (coded individually by nominal environmental variables), which were tested both individually and overall. Additionally, the continuous environmental variables described above were tested. The analysis was carried out in CANOCO 4.5.

Results

A total of 33 102 beetles was identified to one of 225 species (see Appendix S1 in the supplementary material), of which 42 species were represented by singletons. Staphylinidae (excluding Aleocharinae) were the most abundant ($n = 13 894$) and species rich (73 species), followed by Carabidae (46 species, $n = 7284$). Other

families identified were the Apionidae (16 species, $n = 4535$), Curculionidae (42 species, $n = 3460$), Chrysomelidae (37 species, $n = 2419$), Coccinellidae (7 species, $n = 1293$) and Elateridae (4 species, $n = 270$). Plant species richness, while increasing generally between 2003 and 2005 ($F_{2,165} = 18.4$, $P < 0.001$), neither differed between treatments ($F_{6,86.3} = 1.50$, $P > 0.05$) nor showed an interaction with year ($F_{12,153} = 0.59$, $P > 0.05$). Grass sward architecture, which represented the dominant component of sward architecture, showed a treatment ($F_{6,89.5} = 79.9$, $P < 0.001$) and overall year effect ($F_{2,170} = 110.9$, $P < 0.01$) only. The architecture of grasses, forbs, legumes and dead vegetation increased from treatment 1 to 7.

Model I tested the response of beetle abundance, species richness, diversity and evenness to the management treatments and their interaction with year (Table 2). Significant effects of sample year were found in all cases, although only beetle diversity did not show a significant year × treatment interaction. Only beetle abundance and species richness were characterized by an overall treatment effect (for pairwise comparisons see Appendixes S2 and S3 in the supplementary material). In general, by 2005 the extensively managed treatments (5–7) supported the highest abundances and species richness of beetles relative to the other treatments (Fig. 1a,b). This pattern was reversed in the case of beetle evenness (Fig. 1d). To test that the response of beetle species richness was not an artefact of increasing beetle abundance, this latter parameter was included as a

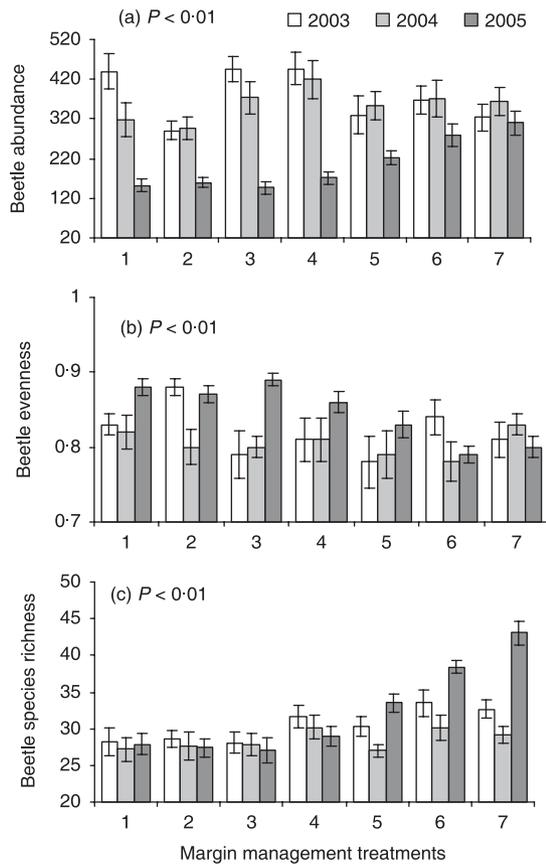


Fig. 1. Response of beetle abundance (\pm SE) (a), species richness (\pm SE) (b), and Shannon–Wiener evenness (\pm SE) (c) to the seven field margin management treatments and sample year. Significance values (P) indicate the significance of the interaction between treatment and year.

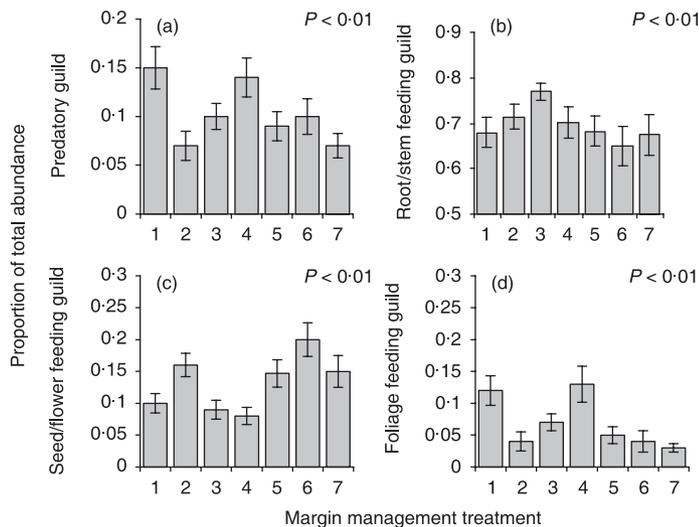


Fig. 2. Response to field margin management treatment of the proportional representation of beetles in four functional groups, the predatory (a), root/stem (b), seed/flower (c) and foliage (d)-feeding species (\pm SE). The response variable represents the proportion each functional group makes up of the total beetle abundance (n). The exception is for the root/stem-, seed/flower- and foliage-feeding groups which were represented as proportions of the phytophagous beetles abundance only.

covariate. While beetle species richness was positively correlated with abundance ($F_{1,228} = 89.5$, $P < 0.001$), significant responses to the effects of treatment ($F_{6,78} = 9.14$, $P < 0.001$), year ($F_{2,159} = 60.6$, $P < 0.001$) and treatment \times year ($F_{12,155} = 2.72$, $P < 0.01$) remained. Patterns of species richness between the treatments remained similar to those of the original model uncorrected for beetle abundance (Fig. 1b). Therefore the response of beetle species richness to treatment was not an artefact of treatment differences in abundance.

Model II tested the interaction between the continuous environmental measures and year on beetle abundance and species richness, diversity and evenness. Significant responses to sward architecture, the percentage cover of floral groups and their interaction with year were found for beetle abundance and species richness, diversity and evenness (for the full list of effects see Table 2). Both beetle diversity and evenness also showed significant negative correlations with plant species richness. The significant continuous environmental parameters of model II did not, however, explain any additional variance when added to the significant treatment and year effects of model I.

Responses to margin management treatments were found for the functional structure of the beetle assemblages (Table 3). The proportional abundance represented by the predatory, root, foliage and seed/flower feeding functional groups all showed significant responses to treatment (Fig. 2a–d) and, with the exception of the foliage feeders, significant treatment \times year interaction. Both the predatory functional group and the foliage feeders also showed a significant year effect.

Beetle assemblage structure was analysed using pRDA to assess the significance of both margin management treatment and secondary environmental factor interaction with year. The interaction between margin treatment and year had a significant effect on the beetle assemblage, accounting for 16.7% of the unexplained model variance. When the individual treatment and year interactions were tested, significant effects on beetle assemblage structure were found for treatment 1 ($F = 1.54$, $P < 0.05$), treatment 2 ($F = 2.44$, $P < 0.01$), treatment 3 ($F = 1.84$, $P < 0.05$), treatment 4 ($F = 1.79$, $P < 0.01$), treatment 5 ($F = 1.42$, $P < 0.05$), treatment 6 ($F = 2.88$, $P < 0.01$) and treatment 7 ($F = 3.34$, $P < 0.005$). There were also clear differences in the successional trajectories of the treatments between 2003 and 2005 (Fig. 3). In particular, the successional trajectories of the more extensively managed treatments (6 and 7) were moving in the opposite direction to those of the control plots. Conversely, treatments 3 and 4, which received NPK fertilizer, were characterized by successional trajectories similar to those of the control (treatment 1). In addition to the treatment effects, significant environmental parameter interactions with year were also found for sward architectural components (grass, legumes and dead vegetation) as well as dung density, bare ground cover and plant species richness. The interaction between year and the percentage cover of the legumes,

Table 3. Response to margin management treatments of the proportion of the total abundance made up of predatory species. This analysis was repeated to assess the proportion of the overall abundance of phytophagous beetles composed of root/stem-, foliage- and seed/flower-feeding functional groups. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, $P > 0.05$

	Treatment	Year	Year × treatment
Predatory	$F_{6,76.4} = 5.17^{***}$	$F_{2,148} = 4.73^{**}$	$F_{12,154} = 2.65^{***}$
Phytophagous			
Root feeders	$F_{6,90.7} = 4.60^{***}$	$F_{2,156} = 0.61$, NS	$F_{12,161} = 4.35^{***}$
Foliage feeders	$F_{6,95.3} = 11.6^{***}$	$F_{2,162} = 12.3^{***}$	NS
Seed/flower feeder	$F_{6,67.6} = 13.6^{***}$	$F_{2,153} = 0.77$, NS	$F_{12,161} = 2.03^*$

Table 4. Results for partial redundancy analysis of beetle assemblage responses to both management treatment and the floristic composition and architectural structure of the field margins. All significances were tested using Monte Carlo permutation tests (1000 permutations) of both canonical axes. See the Methods for environmental variable abbreviations. * $P < 0.05$; ** $P < 0.01$; NS, $P > 0.05$

Environmental variable	F	Explained variance (%)	Environmental variable	F	Explained variance (%)
Treatment × year	2.19**	16.7	Plant percentage cover		
Sward architecture			%Le × year	1.63*	2.4
GA × year	2.33**	3.1	%Tu × year	1.44**	2.0
FA × year	NS	–	%LP × year	NS	–
TA × year	4.30**	5.6	%AS × year	1.31*	1.8
DA × year	2.21**	2.9	%Ru × year	NS	–
Others			%Ra × year	1.36**	1.8
Dung × year	1.00*	1.5	%Pl × year	NS	–
BG × year	1.41**	2.0	%Ci × year	1.66*	2.2
PSR × year	1.69**	2.4	%Ta × year	NS	–

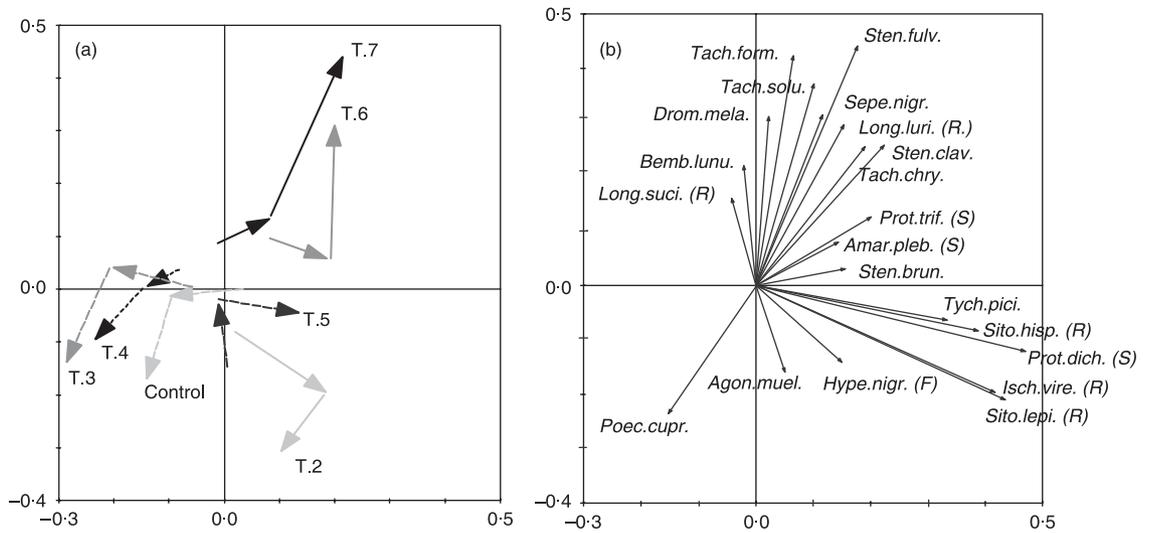


Fig. 3. Ordination diagrams of the pRDA for years 2003–05 based on the beetle assemblages. (a) The temporal interaction between sample year and the control and management treatments (T.2–T.7). The change with time of the beetle assemblages is emphasized by the connection of the centroids of the year × treatment interaction with arrows, from the 2003 × treatment (start of first arrow) to the 2004 × treatment (end of first arrow) to the 2005 × treatment (end of second arrow). (b) The companion beetle species scatter plot to (a). Only the 22 species with the best fit to the first two axes of the ordination have been shown, with the first four letters of the generic and specific names (see Appendix S1 for abbreviations). Species functional group was predatory unless otherwise indicated by: S, seed/flower feeding; F, foliage feeding; R, root/stem feeding.

tussock grasses, *Cirsium* spp., *Ranunculus* spp. and *Agrostis stolonifera* also had a significant effect on beetle assemblage structure (Table 4). When all the significant interactions were included in a single model (treatment ×

year and environmental variable × year), the beetle assemblage was significantly correlated with the environment and explained 39.7% of the variation in the species data not accounted for by the covariables.

Discussion

By managing field margins, the availability of extensively managed habitats within conventionally managed improved grasslands can be increased. As margin management will influence both flora and fauna, assessing the relative benefits of alternative practices is important if they are to be implemented as part of agri-environment schemes (McCracken & Bignal 1998). One of the clear implications of extensification of field margin management (i.e. the absence of NPK fertilizer, grazing and multiple silage cuts) was a change in the successional trajectory of the beetle assemblages away from what was characterized by the control (Fig. 3). This change was most clearly seen for those treatments that were either unmanaged (treatment 7) or received a single sward cut in May (treatment 5) or July (treatment 6). By 2005, the assemblages of these treatments were characterized by greater proportions of seed/flower-feeding beetles. Interestingly, of those treatments receiving multiple silage cuts each year (treatments 1–4), treatment 2, which was unique in receiving no NPK fertilizer, differed in its successional trajectory from that of the control. The occurrence of what appeared to be a successional change in the structure of the beetle assemblages of treatment 1 (control) was, however, unexpected. This successional change is thought to have been driven by the drier conditions that characterized the 2004 and 2005 sample years. This could have caused an overall reduction in beetle abundance, particularly in 2005, as well as successional shifts in beetle species composition in the control, most probably in response to changes in the plant assemblages as the plots became drier.

The continuous measures of both sward architecture and plant percentage cover were often characterized by strong year interactions. For example, the effect of grass sward architecture showed consistent positive correlations with beetle abundance and species richness for 2003, 2004 and 2005. This reflects the importance of structurally complex tussock grasses in providing an increased diversity of niches for epigeal beetles (Dennis, Young & Gordon 1998; Morris 2000). Legume architectural complexity also had positive effects on both beetle abundance and species richness, an effect attributed to the increased availability of reproductive structures important for a number of phytophagous beetles, in particular the Apionidae (Woodcock *et al.* 2005a; Hoffman 1950–58). Conversely, legume sward architecture was negatively correlated with beetle evenness, an effect also seen for all years. This reduction in evenness is attributed again to members of the Apionidae, principally the seed-feeding weevil *Protapion dichroum* (Bedel), which became dominant species in architecturally complex legume swards.

The responses of beetle abundance and species richness, diversity and evenness to plant percentage cover and sward architecture were not always consistent in their direction between years. This was most apparent for grass percentage cover, in particular that of the

tussock grasses, and was attributed to successional shifts in beetle assemblages in response to margin management. As species composition changed throughout the succession, so did the characteristics of how the overall assemblage responded to plant percentage cover and sward architecture. In each case these changes would reflect the individual species' traits of the assemblages within each treatment and year.

Beetle abundance and species richness and evenness also responded to treatment and year interactions. Between 2003 and 2005 this was characterized by increases in beetle abundance and species richness in the extensively managed treatments (5–7) relative to that observed in the more intensively managed treatments (1–4). Increased sward architectural complexity and the establishment of key floral species in the extensively managed treatments would have increased the relative importance of these treatments in terms of beetle abundance and species richness by 2005 (Duffey *et al.* 1974; Morris 2000; Woodcock *et al.* 2005a). Conversely the levels of beetle evenness in the intensively managed treatments were proportionally higher relative to treatments 5–7, a difference that became more pronounced from 2003 to 2005. This was potentially a result of the drier conditions in 2004 and 2005 impacting negatively on dominant beetle species associated with the improved grassland treatments (Frampton, van den Brink & Gould 2000).

For the seed/flower-feeding functional groups, and indeed for many phytophagous species, management extensification was seen to be beneficial. Increased abundance of plant reproductive structures as a result of the greater sward architectural complexity of the extensively managed treatments was beneficial in terms of many larval feeding resources (Morris 2000; Woodcock *et al.* 2005a). The proportional representation of the seed/flower-feeding beetles was lowest in those treatments receiving NPK fertilizer (treatments 1, 3 and 4). Increased availability of NPK fertilizer may have resulted in recruitment limitation, competitive exclusion or the loss or reduction in seed set of plants important for phytophagous beetles (Kirkham & Wilkins 1994; Tilman 1997). For example, the grass *L. perenne*, although found to decrease over the duration of the experiment, remained prevalent in these treatments and this may have excluded other plants important to phytophagous beetles (Mountford, Lakhani & Kirkham 1993). Treatment 2, while being grazed and receiving two silage cuts, supported higher proportional abundances of the seed/flower-feeding functional group. This is again attributed to the lack of NPK fertilizer in this treatment reducing the competitive displacement by dominant grasses of important floral species for the beetles.

Invertebrate responses to grazing are common in the literature (Thiele 1977; Gibson, Hambler & Brown 1992; Woodcock *et al.* 2005a). In this study, response to cattle grazing were subtle and only seen in an assemblage-level response to the percentage cover of dung. This relatively

small effect may be explained by the late application of grazing as a management practice (late August to September). The assemblage-level responses to dung density were, however, characterized by a relatively small proportion of the overall fauna, for example dung-associated species such as *Philonthus varians* (Paykull) (Staphylinidae).

Management in the intensive grasslands was extremely variable on a field by field basis, with stocking densities, timing of cutting and the application rate of NPK fertilizer differing considerably between fields within a single farm (Frame 2000). For this reason the control used in this study was not an unfenced area subject to the same management of individual fields, but rather an approximation of what was considered intensive grassland management. This management used for the control treatment could then be repeated for each replicate across all years. For this reason, both floral and beetle assemblages in the control treatments could have differed from what was found in the fields within which replicates were situated. While this difference was small, the choice of an artificial control could be interpreted as introducing some bias into the results; however, such an effect was believed to be minimal.

CONCLUSIONS

Without the implementation of alternative management practices to reverse downward trends in populations of grassland flora and fauna, it is likely that the conservation status of many currently infrequent or rare grassland species of a variety of taxa will become critical (Duffey *et al.* 1974; Blackstock *et al.* 1999; Asher *et al.* 2001; Vickery *et al.* 2001). Agri-environment schemes are now a mandatory component of European Community Rural Development Regulations and, while they may not always be effective (Kleijn & Sutherland 2003), they represent an important instrument for improving biodiversity in agricultural systems (Ovenden, Swash & Smallshire 1998). Conclusions from the 3 years of this study indicate that managing field margins can serve as a method for diversifying the structure of beetle assemblages while at the same time retaining the majority of the improved grassland under conventional management practices. Although many other invertebrates also respond to plant species richness and architecture, it is possible that the responses observed for beetles in this study may differ from those found for other orders (Meek *et al.* 2002). It is also true that the application of these management practices to field margins of different widths may also result in different responses in the beetle assemblages, particularly for narrow margins (< 2 m). There was some evidence for the benefits to beetle assemblages of stopping NPK fertilizer application, even when other conventional management practices were maintained. Such a simple modification of conventional improved grassland management may be useful as a cheap and simple practice to adopt in an agri-environment scheme, and has already been adopted by

the new Entry Level Stewardship Scheme in the UK (Option EK3 Permanent Grassland with very low inputs; Defra 2005). Its benefits, however, would be minimal relative to those associated with the more extensively managed treatments, which are either unmanaged or receive only a single sward cut each year. These extensively managed treatments, which were characterized by higher abundances and species richness of beetles, may have increased cost implications because they required livestock exclusion fences. Therefore, it may be more cost-effective to place whole fields under this form of extensive management, negating the need for additional fencing. If such a whole-field approach is to be undertaken, investigation into the benefits of creating additional spatial variation in sward structure, possibly by using patchworks of low-intensity cutting regimes, would be valuable. All these factors would need to be considered in terms of agri-environmental policy.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>.

Appendix S1. Mean abundances (\pm SE) in the experimental treatments (2003–05) for all species with a total abundance in excess of 200 individuals or species displayed in Fig. 3b.

Appendix S2. Pairwise comparisons for the beetle abundance response to field margin management treatments in 2003, 2004 and 2005.

Appendix S3. Pairwise comparisons for the beetle species richness response to field margin management treatment in 2003, 2004 and 2005.