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Effects of management practices on the carabid faunas of newly established wildflower meadows in southern Scotland

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The replacement of perennial ryegrass with broad-leaved wildflower swards has been suggested as a means of achieving an increase in diversity, but in order to assess the value of these swards as wildlife habitats, it is necessary to determine how the invertebrate fauna is affected by their establishment and by subsequent management practices. The carabid faunas of nine sites of varying sward type and management practices were analysed in 1989 and 1993. Management had a detrimental effect especially on the larger species, and tended to favour those species preferring drier conditions. The wildflower swards did support a more diverse carabid fauna, but with no sign of any re-establishment of the natural fauna found in unmanaged habitats in the same area. Recolonisation by this fauna, if possible at all, is likely to take considerably longer than five years.

1. Introduction

In recent years, United Kingdom and European Union agricultural policy has encouraged a trend towards the extensification of grassland management practices, with a view to enhancing wildlife conservation and increasing species diversity. The replacement of perennial ryegrass swards by commercial mixtures of broad-leaved wildflowers has been suggested as one means of achieving this increase in diversity (Wells *et al*. 1989, Ash *et al*. 1992). While it is a relatively simple matter to monitor changes in botanical composition resulting from management, it should not be assumed that diversity of the fauna will necessarily follow the same patterns. The value of the habitat for birds, reptiles and small mammals will be dependent, to a large extent, on the nature of the invertebrate fauna it supports. Species diversity of insects and other arthropods does not depend on botanical species diversity in a simple manner. Insects may be affected more by the architecture of the sward than by its actual species composition (Southwood *et al*. 1979). In order to assess the value of sown wildflower swards as wildlife habitats, it is necessary to determine how the invertebrate fauna is affected by their establishment and by subsequent management practices.

When new wildflower swards were established at the Scottish Agricultural College's experimental farm, the opportunity arose to monitor the effects of sward type and management practices on the carabid fauna, as revealed by changes in species composition, diversity, rarity value and body size.

2. Methods

In 1987 the Scottish Agricultural College (SAC) began field-scale experiments on commercial wildflower mixtures at the Crichton Royal Farm, Dumfries, southern Scotland, on soil classed as medium loam overlying clay. Two fields (known as Bungalow Meadow and Lochbank) were ploughed and re-seeded in August 1987, with successful establishment of twelve flower species, two clovers and five grasses (Fisher *et al.* 1993). Basic management thereafter consisted of no fertilisation, one cut per year in July, aftermath grazing by cattle and winter grazing by sheep. Each field was subdivided into two paddocks and at Bungalow Meadow one paddock received winter application of cattle slurry equivalent to 100 kg N/ha/year, while at Lochbank one paddock underwent an extra cut in May of each year.

Additional fields with differing sward types and/or management were selected (Table 1). Wet Lochbank was a small area at the foot of the sloping Lochbank field, adjacent to a conservation area with a pond, scrub and tall herbs. Its management was the same as Lochbank One-cut, but the soil was peatier and less free-draining and the botanical composition differed from the rest of the field, being dominated by *Holcus lanatus* and *Ranunculus repens*. Acrehead Clover was a perennial ryegrass/white clover sward established in 1987 by direct drilling with clover after treatment of a ryegrass pasture sward with paraquat. Management included one or two cuts per year. Acrehead Ryegrass was perennial ryegrass pasture established in 1979 and grazed by cattle and sheep. Netherwood was perennial ryegrass established in 1988 and cut three times per year. These three sites all received cattle slurry and inorganic fertiliser, but Acrehead Clover received no inorganic nitrogen. The surrounding land use at Crichton was predominantly pasture, with small areas of woodland and hedgerow. As a control and in order to determine the nature of the fauna in unmanaged grassland sites in the same area, a semi-natural, unmanaged grassland site was identified at Caerlaverock National Nature Reserve. This was one of few undisturbed grassland sites in the area on non-peaty soil, and consisted of dense, tussocky vegetation with surrounding deciduous and coniferous woodland.

The carabid faunas of these nine sites were sampled by pitfall trapping from April to September in 1989 and again in 1993. At each site, two replicate lines of traps were set approximately 20 m apart. Each line consisted of nine plastic cups, 8.5 cm diameter and 10 cm deep, partly filled with ethylene glycol and set flush with the ground surface at two metre intervals. Monthly catches were pooled to give two replicate totals (A & B) for each site in each year. Species totals were converted to percentages and the sites classified by Two-Way Indicator Species Analysis, TWINSPAN (Hill 1979a), and ordinated by Detrended Correspondence Analysis, DECORANA (Hill 1979b). Species nomenclature follows Pope (1977) and the habitat preferences of the species were established from the literature (e.g. Lindroth 1974).

The 'quality' of a fauna has components of both richness, or diversity, and of rarity, in terms of the proportion of rare species it contains. The simplest, most appropriate estimator of diversity is species richness, S, the number of spe-

Table 1. Sward type and management practices on nine sites at Crichton Royal Farm and Caerlaverock National Nature Reserve, Dumfriesshire, southern Scotland. Intensity of management assessed on a four-point scale: zero (–), low (+), moderate (++) and high (+++).

Site	Sward type	Cutting	Grazing	Inorganic inputs	Organic inputs
Bungalow slurry	Wildflower	+	++	–	+++
Bungalow no slurry	Wildflower	+	++	–	–
Lochbank one-cut	Wildflower	+	++	–	–
Lochbank two-cut	Wildflower	++	++	–	–
Lochbank wet	Wildflower	+	++	–	–
Acrehead clover	Ryegrass/ white clover	+	++	++	+++
Acrehead ryegrass	Perennial ryegrass	–	+++	+++	++
Netherwood ryegrass	Perennial ryegrass	+++	++	+++	+++
Caerlaverock NNR	Semi-natural grassland	–	–	–	–

cies taken. Comparisons of *S* across sites would be sensitive to variation in sample size (Whittaker 1972) which, in this case, relates to the efficiency of pitfall traps in different types of vegetation (Greenslade 1964) as well as to the size of the area being sampled (Williams 1943). It is necessary to estimate diversity by a derived index which is less sensitive to sample size. Species diversity in this study was estimated both by species richness, *S*, and by (*D*), the complement of Simpson's Index (Simpson 1949, Whittaker 1972).

In order to quantify rarity values of habitats, species may be assigned Rarity Scores according to the number of grid squares from which they have been recorded. On a national scale, records from 10 km squares would be appropriate; Eyre (unpublished report) has assigned rarity scores to Scottish carabid beetles on this basis. Scoring on a geometric scale buffers the scores to some extent against changes in the records. Site scores will be dependent to some extent on the level of sampling effort; as sampling increases, so will the number of rarer species taken. Standardisation of sampling effort, as by pitfall trapping, should reduce the variation due to this cause, but the varying efficiency of traps in different habitats means that total scores still cannot be directly compared. Total scores may be converted to a 'species quality score' by dividing them by the number of species taken (Eyre & Rushton 1989, Foster 1987, Foster *et al*. 1990, 1992) or to an 'Individual Rarity Score' by dividing by the number of individuals in the catch. This helps to circumvent the problem of the length of the species list, whereby a sample of many common species may have a similar total rarity score as a sample of a few rare species. Such aggregations of rare species often indicate sites of important conservation value.

Individual Rarity Score (*IRS*) was calculated for each assemblage according to the formula:

$$IRS = [\sum(n_i R_i)]/N,$$

where n_i is the number taken of species i, R_i is the Species Rarity Score for species i and *N* is the total number of individuals in the catch. Species Rarity Scores were calculated on the basis of a score of 1 for species recorded from 128 or more 10 km squares, 2 for 64–127 squares, 4 for 32–63 squares, 8 for 16–31 squares, 16 for 8–15 squares, 32 for 4–7 squares, 64 for 2–3 squares, and a score of 128 for those previously recorded from only one square. This index differs from previous rarity indices (e.g. those of Foster (1987) and of Eyre and Rushton (1989)) by taking species' relative abundances into account. The quantitative nature of pitfall trap data permits this. The absolute value of the *IRS* for each site may have little meaning, but valid comparisons are possible between sites where data have been collected in a comparable manner.

A further parameter which was calculated for the carabid fauna of each site was the Weight Median Length,

Table 2. Percentage abundances of the commonest species taken in three sward types in 1989 and 1993, omitting those species which nowhere attained more than 1% of the total catch.

	Unmanaged		Wildflowers		Grasses	
	1989	1993	1989	1993	1989	1993
Abax parallelepipedus (Pill. & Mitt.)	9	17				
Agonum dorsale (Pont.)			3	1	1	1
Agonum muelleri (Hbst.)			1		5	5
Amara communis (Panz.)				4		
Amara ovata (F.)			1			2
Amara plebeja (Gyll.)		1		1	2	2
Bembidion aeneum Ger.	3					
Bembidion guttula (F.)	5			5	1	
Bembidion lampros (Hbst.)			5	17	4	40
Bembidion unicolor Chaud.	2	9	2			
Calathus melanocephalus (L.)			2	1		1
Carabus granulatus L.	2	9				
Carabus nemoralis Müll.	1	1	1	2		
Clivina fossor (L.)	8	1	1	1	2	2
Loricera pilicornis (F.)	10		9	2	14	3
Nebria brevicollis (F.)		1	17	16	11	4
Pterostichus diligens (Strm.)		3				
Pterostichus madidus (F.)			1	5	2	1
Pterostichus melanarius (Ill.)	3		42	37	49	30
Pterostichus niger (Schall.)	22	22	7	3	1	1
Pterostichus nigrita (Payk.)	6	12	2	2		
Pterostichus rhaeticus Heer	1	8				
Pterostichus strenuus (Panz.)	24	12	4	5	1	2
Trichocellus placidus (Gyll.)	2					

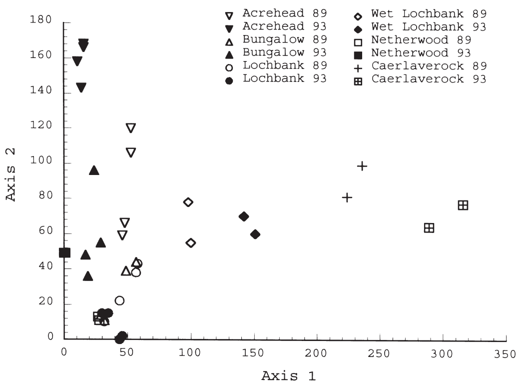

Fig. 1. DECORANA ordination of nine sites at Crichton Royal Farm and Caerlaverock National Nature Reserve, Dumfriesshire, southern Scotland, in 1989 and 1993. See text and Table 1 for details of sites.

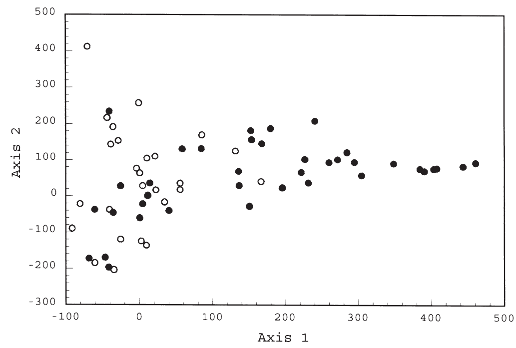

Fig. 2. DECORANA ordination of the carabid species of nine sites at Crichton Royal Farm and Caerlaverock National Nature Reserve, Dumfriesshire, southern Scotland, in 1989 and 1993. Species are classified according to habitat preferences reported in the literature: open symbols – species associated with dry or open habitats; filled symbols – species associated with wet or damp habitats.

WML, which is the median point of the biomass distribution of the fauna (Blake *et al.* 1994).

The relationships between sward types, DECORANA scores, *S*, *D*, *IRS* and *WML* were examined using non-parametric statistics (Spearman's rank-order correlation coefficient, Mann-Whitney *U*-test).

3. Results

A total of 11 200 carabid beetles of 57 species were identified in 1989 and 10 518 of 60 species in 1993, giving a total list of 67 species. Of these, 43 occurred in very low numbers, with 24 more abundant in at least some of the sites (Table 2).

The number of species taken in each set of traps, *S*, was lowest at the unmanaged Caerlaverock and highest in the wildflower swards (Table 3). The differences across all three sward types were highly significant (Table 4). Diversity, as measured by *D*, was also significantly lower in the grass swards, but this time was highest at Caerlaverock. The catch at Caerlaverock, which was a relatively small habitat patch, was low in both years (175 and 454 respectively), resulting in a short species list. The use of *D* to estimate diversity to some extent compensates for differences in the length of the species list. Rarity (*IRS*) was not found to vary significantly with sward type, but the four highest values were recorded at the four Acrehead sites in 1993. Body size (*WML*) was significantly different only at Caerlaverock, where the average beetle was over 20% larger than the average in grass swards. The large value of *WML* at Caerlaverock was associated with relatively high abundances of *Abax parallelepipedus*, *Carabus granulatus* and *Pterostichus niger*, all of which were absent or scarce elsewhere.

Classification of the carabid data by TWINSPAN resulted in six end-groups at the fourth level of division, characterised by: Caerlaverock; Wet Lochbank; Acrehead; Netherwood 1989 and Lochbank 1989; Bungalow Meadow; Netherwood 1993 and Lochbank 1993. Caerlaverock was separated from the rest at the first division, for which the indicator species was *Bembidion lampros* in the managed sites.

Ordination of the first two DECORANA axes (Fig. 1) separated Caerlaverock from the managed sites on the major axis, with Wet Lochbank in an intermediate position and the remainder compressed into the first 20% of the axis. Axis 1 was correlated significantly with diversity (Table 5) and with rarity and axis 2 was correlated with rarity. No correlations were found between any of the parameters.

In an ordination of the species scores (Fig. 2) those species reported in the literature to be associated with 'dry' or 'open' habitats were confined to the left half of the ordination while species of 'wet' or 'damp' habitats were more or less evenly spread across the first axis.

The compression of the major axis (Fig. 1) justified the removal of the extreme outlier Caerlaverock and a fresh analysis of the managed sites only (Gauch 1982 p. 159). This achieved a greater separation on both axes (Fig. 3) and clarified any changes occurring between 1989 and 1993, but with a loss of explanatory value, the eigenvalues for the first two axes dropping from 0.524 and 0.181 to 0.269 and 0.118 respectively.

The major DECORANA axis could be broadly related to sward structure and to moisture conditions, Caerlaverock and Wet Lochbank having the rankest vegetation and the wettest substrate. Between 1989 and 1993, all of the managed sites except Lochbank

Table 3. Weight Median Length (*WML*) in mm, species richness (*S*), diversity (*D*) and rarity (*IRS*) of the carabid faunas of 18 sites (two replicates per site) at Crichton Royal Farm and Caerlaverock National Nature Reserve, Dumfriesshire, southern Scotland in 1989 and 1993, along with the median values for each sward type.

Site and Year	*WML*	*S*	*D*	*IRS*
Wildflower swards				
Bungalow Slurry A 1989	14.40	23	0.842	2.12
Bungalow Slurry B 1989	14.40	23	0.856	2.09
Bungalow Slurry A 1993	14.10	23	0.729	2.60
Bungalow Slurry B 1993	14.10	21	0.776	2.70
Bungalow No Slurry A 1989	14.00	21	0.687	1.84
Bungalow No Slurry B 1989	14.00	21	0.693	1.88
Bungalow No Slurry A 1993	14.40	26	0.754	2.41
Bungalow No Slurry B 1993	14.40	24	0.751	2.90
Lochbank One-cut A 1989	14.30	23	0.802	1.79
Lochbank One-cut B 1989	13.70	24	0.819	2.03
Lochbank One-cut A 1993	13.90	21	0.713	2.18
Lochbank One-cut B 1993	13.90	22	0.790	2.01
Lochbank Two-cut A 1989	13.80	22	0.500	1.91
Lochbank Two-cut B 1989	13.90	18	0.640	1.88
Lochbank Two-cut A 1993	14.10	22	0.803	2.06
Lochbank Two-cut B 1993	14.20	21	0.707	2.17
Wet Lochbank A 1989	13.30	25	0.877	3.10
Wet Lochbank B 1989	14.30	24	0.826	2.60
Wet Lochbank A 1993	11.90	18	0.824	2.01
Wet Lochbank B 1993	11.80	25	0.880	2.81
Median	14.05	22.5	0.783	2.10
Grasses				
Acrehead Clover A 1989	12.70	20	0.842	2.31
Acrehead Clover B 1989	13.80	17	0.818	2.22
Acrehead Clover A 1993	13.60	20	0.685	3.15
Acrehead Clover B 1993	13.40	19	0.676	3.11
Acrehead Ryegrass A 1989	14.10	21	0.740	2.23
Acrehead Ryegrass B 1989	14.50	23	0.768	1.95
Acrehead Ryegrass A 1993	13.70	20	0.688	3.38
Acrehead Ryegrass B 1993	13.80	23	0.620	3.28
Netherwood Ryegrass A 1989	12.90	17	0.540	1.75
Netherwood Ryegrass B 1989	13.90	20	0.495	1.80
Netherwood Ryegrass A 1993	13.90	19	0.677	2.76
Netherwood Ryegrass B 1993	13.90	22	0.678	2.86
Median	13.80	20.0	0.682	2.53
Unmanaged				
Caerlaverock NNR A 1989	17.40	15	0.860	2.00
Caerlaverock NNR B 1989	17.40	15	0.824	1.82
Caerlaverock NNR A 1993	18.60	16	0.879	3.12
Caerlaverock NNR B 1993	17.80	15	0.827	1.57
Median	17.60	15.0	0.844	1.91

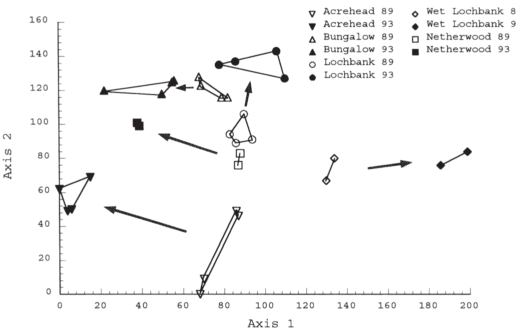

Fig. 3. DECORANA ordination of eight sites at Crichton Royal Farm, Dumfriesshire, southern Scotland, in 1989 and 1993, showing changes in position between the two years. See text and Table 1 for details of sites.

became more distinct from the semi-natural unmanaged sites on the major DECORANA axis. Since there was no change in management at Caerlaverock between 1989 and 1993 it is likely that its change in position in the ordination was due to some general difference between the years, for instance in weather. If the major axis is interpreted as relating to moisture levels, then both of the wet sites became wetter between 1989 and 1993 while the rest became, if anything, drier or more open, presumably as an effect of management. The correlations of axis 1 DECORANA score with *D* and *IRS* might suggest that the changes in the ordination between the two years was associated with a general decrease in diversity and increase in rarity. No significant difference was found in *D* between 1989 and 1993 (Mann-Whitney test, $p = 0.562$), but from Table 3, diversity at Bungalow Meadows fell where slurry was applied, and rose where it was not. Diversity fell at Lochbank One-cut but rose from a very low 1989 level at Lochbank Two-cut. Rarity values did increase significantly between 1989 and 1993 (Mann-Whitney test, $p < 0.01$).

Changes in the species composition between the two years included an increase in abundance of *Bembidion lampros*, a species associated with dry, open conditions, at all the managed sites except Wet Lochbank. *Loricera pilicornis* was present at every site but declined everywhere in abundance between 1989 and 1993. *Carabus nemoralis*, the largest beetle in the catch, was absent from Netherwood Ryegrass and almost so from Acrehead, but increased somewhat in abundance at all the wildflower sites.

Members of the genus *Amara*, which is generally associated with dry, open habitats, increased at all the managed sites except Acrehead Clover. At Netherwood Ryegrass, *Amara* spp. increased from less than 1% of the catch in 1989 (3 species), to 10% of the catch (7 species) in 1993. The decrease at Acrehead Clover was due to relatively large numbers of *Amara plebeja* in 1989, some 5% of the catch at that site, dropping to 1% in 1993. This is a highly dispersive species often associated with disturbed land and its high abundance in 1989 could suggest that Acrehead Clover took longer than the other sites to begin recovery from the cultivation operations which took place in 1987.

The sown wildflower sites were at the opposite end of the second axis from Acrehead Clover and Ryegrass. In 1989, Acrehead Clover occupied an extreme position on this axis but by 1993 had converged with Acrehead Ryegrass. This, along with the TWINSPAN end-group consisting of all the Acrehead samples together, suggests that following the perturbation of paraquat treatment and drilling with clover in 1987, the carabid fauna of Acrehead Clover gradually returned to a composition similar to that of the neighbouring Acrehead Ryegrass. Brust (1990) found that paraquat application had a detrimental effect on larger carabid species, possibly due to habitat destruction rather than direct toxicity, but concluded that there were no long-term effects, recolonisation occurring after about 28 days. However, it may be that the additional disturbance of drilling operations, followed by an intensification of management in the form of cutting rather than

Table 4. Summary of results of Mann-Whitney tests for significant differences in median values of species richness (*S*), diversity (*D*), rarity (*IRS*) and body size (*WML*) across three sward types.

	WML	*S*	*D*	*IRS*
Unmanaged: wildflowers	$p < 0.01$	$p < 0.01$	$p < 0.05$	*n.s.*
Unmanaged: grasses	$p < 0.01$	$p < 0.01$	$p < 0.01$	*n.s.*
Wildflowers: grasses	*n.s.*	$p < 0.01$	$p < 0.05$	*n.s.*

grazing, combined to delay the re-establishment of the original fauna at Acrehead Clover.

4. Discussion

The multivariate analysis showed that the carabid faunas of the managed sites were quite distinct in species composition from that of the unmanaged Caerlaverock Nature Reserve. They were to some extent related to moisture levels, which is one of the most important factors affecting ground beetle assemblages (Eyre *et al.* 1990). Carabid species composition appeared to be dependent more upon sward type and past history of the site than upon any effects of the specific management practices such as grazing, cutting and fertilisation.

Diversity is often considered to be highest when a habitat suffers a moderate level of disturbance (e.g. Grime 1973, Connell 1978). Disturbance may be any physical event which removes some or all of the occupants of a habitat, leaving unoccupied niche space and increasing habitat heterogeneity, either spatial or temporal (Sousa 1984). Wet habitats may be subject to disturbance as a result of flooding or waterlogging, and are also likely to be nutrient-poor, keeping diversity high (Huston 1979). It might be expected that cultivation operations would be followed at some stage by a rise in diversity as new habitat was colonised by pioneer species, and later by a reduction in diversity as an equilibrium situation was approached. However, the number of species able to colonise and later to become established would depend upon the initial severity and the frequency of repetition of the disturbance, and it is unlikely that equilibrium conditions would be reached in agricultural habitats subjected to any form of management. Botanical diversity at the wildflower sites over the same period was not affected by cutting regime, but was reduced by the application of slurry (Fisher *et al.* 1993). Slurry application may also have been associated with reduced diversity at Bungalow Meadows, but it was not possible to show any significance of this effect.

Although there was no apparent relationship between rarity and sward type or management, rarity increased generally between 1989 and 1993, especially at the ryegrass and clover sites where it was very low in 1989. The wildlife conservation value of a habitat depends in part on the 'quality' of the fauna in terms of rarity, especially in the public's mind. The derived value, *IRS*, used here incorporates species abundances into the calculation, and is to some extent independent of the size of the sample. It will always be the case that increased sampling effort takes more rare species, but standardised pitfall trapping in similar-sized habitat patches effectively standardises sampling effort. The low catch and species richness at Caerlaverock could be accounted for by the small size of the habitat patch, surrounded by woodland. The fauna was nevertheless diverse, but with a low rarity value. This type of habitat is well-recorded by entomologists and there is always the possibility that scores based on recorded distributions will be biased, with species adapted to under-recorded but widespread habitats (such as agricultural land) having higher scores than their true distribution would merit. Some quantitative measure of rarity value is required and *IRS* has the value of simplicity and adaptability, being readily updated as records improve.

The average body size of the carabid fauna is of importance in wildlife conservation because of the large number of vertebrates, especially birds, known to prey on ground beetles (Larochelle 1980). *WML* has been found to decrease as intensity of management increases (Blake *et al.* 1994). These results suggest that the greatest impact on body size occurs on the first introduction of any management, since the unmanaged sites had a significantly higher value of *WML*. Subsequent intensification, within these limits at least, had little additional effect.

Populations of individual species of carabid beetles are known to fluctuate from year to year, with periodic local extinction and refounding likely to occur in the absence of any perturbation due to human activities (Den Boer 1981, 1985). Nonetheless,

Table 5. Spearman rank order correlation coefficient matrix for two DECORANA axis scores, species richness (*S*), diversity (*D*), rarity (*IRS*) and body size (*WML*). $n = 36$. * = $p < 0.05$, ** = $p < 0.01$.

	Axis 1	Axis 2	*S*	*D*	*IRS*
Axis 1					
Axis 2	0.088				
S	– 0.090	– 0.132			
D	0.821**	0.296		0.135	
IRS	– 0.365*	0.596**	0.263		0.039
WML	0.280	– 0.067	– 0.006	0.296	– 0.005

the usefulness of the Carabidae in habitat assessment and monitoring of change is now well-established (e.g. Eyre & Rushton 1989, Eyre *et al*. 1989).

This study has found that the carabid faunas of all types of managed grassland were less species-rich, less diverse and of smaller body size than the fauna of neighbouring unmanaged land. Management tended to favour those species which prefer drier conditions. The establishment of sown wildflower swards in place of less botanically diverse grass and clover did result in a more diverse carabid fauna, but with no sign of any re-establishment of the natural fauna found in unmanaged habitats in the same area. In a study of the restoration of natural oligotrophic conditions to arable land, van Dijk (1986) found little colonisation by the species of surrounding heathland after twelve years, although those species adapted to arable conditions decreased or disappeared almost immediately. Recolonisation by elements of the natural fauna, if possible at all, is likely to take considerably longer than five years.

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References

Ash, H. J., Bennet, R. & Scott, R. 1992: Flowers in the grass. Creating and managing grasslands with wildflowers. — English Nature, Peterborough.

Blake, S., Foster, G. N., Eyre, M. D. & Luff, M. L. 1994: Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. — Pedobiologia 38: 502–512.

Brust, G. E. 1990: Direct and indirect effects of four herbicides on the activity of carabid beetles (Coleoptera: Carabidae). — Pesticide Science 30: 309–320.

Connell, J. H. 1978: Diversity in tropical rain forest and coral reefs. — Science 199: 1302–1310.

Den Boer, P. J. 1981: On the survival of populations in a heterogeneous and variable environment. — Oecologia 50: 39–53.

— 1985: Fluctuations of density and survival of carabid populations. — Oecologia 67: 322–330.

Eyre, M. D. & Rushton, S. P. 1989: Quantification of conservation criteria using invertebrates. — Journal of Applied Ecology 26: 159–171.

Eyre, M. D., Luff, M. L. & Rushton, S. P. 1990: The ground beetle (Coleoptera, Carabidae) fauna of intensively managed agricultural grasslands in northern England and southern Scotland. — Pedobiologia 34: 11–18.

Eyre, M. D., Luff, M. L., Rushton, S. P. & Topping, C. J. 1989: Ground beetles and weevils (Carabidae and Curculionoidea) as indicators of grassland management practices. — Journal of Applied Entomology 107: 508–517.

Fisher, G. E. J., Baker, L. J. & Robertson, D. A. 1993: Effects of seed mixture, cutting/grazing and slurry on yield and composition of sown pastures. Grassland management and nature conservation. Occasional Symposium No. 28. — British Grassland Society, Reading: 195–199.

Foster, G. N. 1987: The use of Coleoptera records in assessing the conservation status of wetlands. — In: Luff, M. L. (ed.), Proceedings of a Meeting of the Agricultural Environment Research Group, University of Newcastle upon Tyne, 7 January 1987: 8–18.

Foster, G. N., Foster, A. P., Eyre, M. D. & Bilton, D. T. 1990: Classification of water beetle asemblages in arable fenland and ranking of sites in relation to conservation value. — Freshwater Biology 22: 343–354.

Foster, G. N., Nelson, B. H., Bilton, D. T., Lott, D. A., Merritt, R., Weyl, R. S. & Eyre, M. D. 1992: A classification and evaluation of Irish water beetle assemblages. — Aquatic Conservation: Marine and Freshwater Ecosystems 2: 185–208.

Gauch, H. G. 1982: Multivariate analysis in community ecology. — Cambridge University Press, Cambridge. 298 pp.

Greenslade, P. J. M. 1964: Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). — Journal of Animal Ecology 33: 301–310.

Grime, J. P. 1973: Control of species density in herbaceous vegetation. — Journal of Environmental Management 1: 151–167.

Hill, M. O. 1979a: TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. — Cornell University, New York.

— 1979b: DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging. — Cornell University, New York.

Huston, M. 1979. A general hypothesis of species diversity. — The American Naturalist 113: 81–101.

Larochelle, A. 1980: A list of birds of Europe and Asia as predators of carabid beetles including Cicindelini (Coleoptera: Carabidae). — Cordulia 6: 1–19.

Lindroth, C. H. 1974: Handbooks for the identification of British insects. Vol IV Part 2, Carabidae. — Royal Entomological Society, London. 148 pp.

Pope, R. D. 1977: A check list of British insects. Part 3: Coleoptera and Strepsiptera. — Royal Entomological Society, London.

Simpson, E. H. 1949: Measurement of diversity. — Nature 163: 688.

Sousa, W. P. 1984: The role of disturbance in natural communities. — Annual Review of Ecology and Systematics 15: 353–391.

Southwood, T. R. E., Brown, V. K. & Reader, P. M. 1979: The relationships of plant and insect diversities in succession. — Biological Journal of the Linnean Society 12: 327–348.

Van Dijk, T. S. 1986: Changes in the carabid fauna of a previously agricultural field during the first twelve years of impoverishing treatments. — Netherlands Journal of Zoology 36: 413–437.

Wells, T. C. E., Cox, R. & Frost, A. 1989: The establishment and management of wildflower meadows. Focus on Nature Conservation, No. 21. — Nature Conservancy Council, Shrewsbury.

Whittaker, R. H. 1972: Evolution and measurement of species diversity. — Taxon 21: 213–251.

Williams, C. B. 1943: Area and number of species. — Nature 152: 264–267.