Effects of management practices on the ground beetle assemblages of grassland and related habitats (Coleoptera: Carabidae)

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Abstract

In their various rôles as herbivores, scavengers, predators and prey, the carabid beetles are an important component of the terrestrial invertebrate faunas of all kinds of habitat, responding to change in their environment by change in their numbers and in their species composition. The impact of habitat change and management pressure on the invertebrate fauna, and hence on the ecosystem as a whole, may be assessed by consideration of the carabid beetle assemblages.

In this study, the carabid assemblages of grassland, moorland and woodland habitats were assessed from a total of 110 sets of pitfall traps in central and southern Scotland and 113 sets in north-east England. Each grassland site was assigned to a management intensity band according to consideration of the sward type and age and intensity of cutting, grazing, inorganic fertilisation and organic inputs. Species composition was examined using multivariate analysis, and three aspects of the carabid faunas were investigated: diversity, rarity and body size.

Diversity was described by species richness, by Simpson's diversity index, and by the residual deviances of the regression of the log-transformed catch on the number of species. Of the three, the residual deviance performed best in terms of distinguishing between management intensity levels.

Rarity was described by the Individual Rarity Score, an index based on the recorded distributions of the species in Scotland and differing from previous rarity indices by taking into account the relative abundances of the species in the catch. By reducing the dependence of the index on the size of the catch, the *IRS* should allow more meaningful comparisons to be made between sites.

A novel method of describing body size was developed: the Weight Median Length (*WML*). This is the median point of the biomass distribution and takes account of the presence of larger species in the assemblage; although these

larger species may be present in relatively small numbers, they comprise a disproportionately large amount of the total biomass and are ecologically important both as predators and prey.

In a comparison of grassland, moorland and woodland habitats in north-east England, moorland sites were found to be the most diverse and species-rich and to support a carabid fauna of larger body size than grassland sites. Within the grassland sites, intensification of management resulted in a reduction both in species richness and in body size. The species composition of intensively managed sites differed from that of the less intensive, with management appearing to favour species associated with drier conditions.

Similarly, a study of data from 110 sets of pitfall traps in managed and unmanaged grassland in Scotland found a general reduction in diversity, rarity and body size as management intensified, with silage fields having especially low values of *WML*. Diversity and rarity fell sharply between the second and third levels of management. Multivariate analysis of the species composition also made a clear distinction between these levels, grouping sites in bands 1 and 2 separately from those in bands 3 to 5. A more detailed examination of the effects of the different components of management found that body size was dependent mostly on the type and age of the sward, while diversity and rarity responded to nutrient inputs.

In a subset of 36 of the 110 Scottish sites, the carabid assemblages of sown wildflower swards, sown grass and clover, and uncultivated grassland were compared. Body size, species richness and diversity were all highest in the unmanaged swards, and species richness and diversity were higher in wildflower swards than in sown grasses. The effects of organic nutrient input were investigated at sites receiving input of slurry, sewage sludge or faecal material from flocks of grazing geese, but no significant relationships could be elucidated due to the overwhelming effects of sward type and management intensity.

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1. Introduction: Carabid beetles in ecological and environmental studies

The ground beetles (Coleoptera: Carabidae) are of considerable value in ecological and environmental studies, satisfying the major criteria for suitability as indicators of environmental quality or change (Refseth, 1980; Foster, 1987; Pearson, 1994).

They are a well-characterised and much-studied group and relatively easy to identify, although determination of some species may require dissection of genitalia and occasionally female specimens present some difficulty (for example, specimens of *Agonum moestum* (Duft.) and *A. viduum* (Panz.)). Good keys to the adults are available (e.g. Lindroth, 1974). The taxonomy of the British Carabidae is well-established, although there are occasional revisions, e.g. the sibling species *Pterostichus nigrita* (Payk.) and *P. rhaeticus* Heer (Luff, 1990), the *Calathus melanocephalus / mollis / cinctus* complex (Aukema, 1990; Anderson & Luff, 1994) and the British species of *Asaphidion* (Speight *et al.*, 1986). The size of the group is manageable, with a United Kingdom list of 346 species (Eyre, 1993 unpubl.) of which approximately 185 have recent (post-1970) records from Scotland. The beetles themselves are comparatively easy to handle, ranging in size from the smallest species of *Tachys* at 1.5mm in length to the largest *Carabus* and *Calosoma*, over 30mm (Lindroth, 1974).

The Family Carabidae has a world-wide distribution excepting only the continent of Antarctica (Noonan *et al.*, 1992 p. v) and is represented in all habitats, including the major British habitat types of woodland, grassland, heath and moorland, wetlands and agricultural land. While some species may be described as eurytopic, many individual species or genera show marked preferences for particular habitat or environmental conditions (Thiele, 1977 p.45). These preferences result in differences in habitats being reflected in differences in the carabid assemblages.

1.1 Sampling of carabid beetles by pitfall trapping

The usefulness of carabid beetles in ecological studies depends not only upon a knowledge of their taxonomy, distribution and biology, but also on the existence of reliable and efficient sampling methods. The method of choice for sampling surface-active ground beetles is by pitfall trapping (Barber traps), i.e. a container partly filled with a preservative and killing agent, sunk into the soil so that its rim is level with the soil surface. There have been many criticisms made of the pitfall method (Greenslade, 1964a; Halsall & Wratten, 1988; Topping & Sunderland, 1992) and Adis (1979) provides an overview of 18 factors affecting its use, but provided the true nature of the data is borne in mind during analysis, the shortcomings are greatly outweighed by the advantages of being able to accumulate quantitative (albeit relative) data continuously over an entire season with a minimum of labour. Alternative sampling methods such as sweep-netting, vacuum sampling or quadrat counts suffer from drawbacks associated with the efficiency of the observer or of the technique under different conditions (Coulson & Butterfield, 1985). Soil sampling may give absolute densities of soil invertebrates, but like these other methods can provide only 'snap-shot' pictures of the fauna on particular occasions instead of the continuous record available from pitfall traps. In addition, diel activity patterns may be investigated by the use of time-sorting pitfall traps (Luff, 1978). Thiele (1977 p.13) considered pitfall trapping to be 'superior to all other methods' for quantitative sampling of carabid beetles.

The numbers and types of beetle taken in a pitfall trap are a function of two properties: the efficiency of the trap, and the susceptibility to being trapped - the 'trappability' - of the beetles.

Greenslade (1964a) found that the efficiency of pitfall traps depended on the nature of the surrounding litter or vegetation, traps catching more beetles when set in an area cleared of vegetation, while Mitchell (1963) found that trap efficiency varied directly with the dryness of the soil. Luff (1975) compared the performance of six types of trap both in the field and in the laboratory and found that effectiveness in trapping and retaining the catch could vary according to the size and material of the trap, although in all six cases efficiency of capture was quite high with between 60.5% and 84.3% of encounters, averaged across species, resulting in capture. These results contrast with those of Halsall and Wratten (1988), who recorded a maximum efficiency rate of 44% captures of *Nebria brevicollis* (F.) encountering polystyrene cups set in sand, and of Paling (1992), who found that *Pterostichus madidus* (F.) was taken in only 2.5% of trap encounters.

The trap-susceptibility of beetles will vary according to species as well as over time. Clearly, only those individuals which are moving on the surface of the ground are likely to encounter the trap; for this reason, pitfall catches are often referred to as a measure of the 'activity-density' of the fauna. While this is often represented as a limitation of the method, in ecological studies this measure of a species' activity levels could be seen as providing useful information, since only those species which are active at any time are likely to be contributing significantly to the ecosystem. A better term than 'activity-density' could be 'effective density' (Luff, 1987).

It should be remembered that pitfall trapping does not purport to sample the entire carabid fauna, any more than it seeks to sample the entire Coleoptera fauna; in effect it samples that subset of the fauna which is susceptible to being caught in pitfall traps. This seems obvious, but the method is occasionally criticised because of its failure to sample every species equally. Some species of carabid are more active in the vegetation than on the soil surface and so are less likely to be taken (Greenslade, 1964a). Some species encountering a trap will be better than others at perceiving and avoiding it, while some are better able to escape. Seven species observed by time-lapse video recording (Halsall & Wratten, 1988) differed significantly in their trappability, due largely to their behaviour on trap encounter rather than to differences in size, diurnalism or mean speed of movement. Level of locomotory activity will influence trappability. Greenslade (1964a) considered that larger beetles will encounter traps more often because they range farther than smaller beetles. While this seems probable, it could be that the type of locomotion is more important, whether rapid directed movement or a slower random walk. Paling (1992) observed that, for *P. madidus*, beetles engaged in directed movement did not pause to examine the trap and were taken in 76.2% of encounters, while those engaged in random walking activity were only trapped in 4.6% of encounters for males and 5.8% for females.

Random walk describes the locomotory behaviour of beetles foraging for food and consists of relatively slow walking with frequent changes of direction which tend to keep the beetle in the same general area. On entering an area of unsuitable habitat, or on failure to find food, the beetle switches to a period of directed movement, more rapid walking in a fixed direction (Baars, 1979a). Capture rates are higher for hungry beetles (Chiverton, 1984), possibly because they are more likely to exhibit this directed movement behaviour. A change to directed movement on encountering bare ground could partially account for Greenslade's (1964a) observation that traps surrounded by a cleared area were more efficient. In day-time observations of the nocturnal *Agonum dorsale* (Pont.), Luff (1975) recorded that up to 89% of encounters resulted in catches, but Halsall and Wratten (1988) recorded a night-time capture rate for this species of no more than 9%. One possible explanation for this discrepancy could be a greater degree of agitation, and therefore more directed walk activity, in nocturnal beetles obliged to be active by day. Similarly, during the reproductive period, males may be more likely to use directed walk as they search for females, while the females concentrate on foraging. This may lead to bias in the sex-ratios taken in traps (Ericson, 1979).

Because the pitfall catch is a function of two variables - trap efficiency and species trappability - problems arise in analysis of the absolute values of the catch data. It is not valid to compare the numbers of different species at the same site, because they will be taken in different proportions. Neither is it valid to compare the numbers of any one species at different sites or in different seasons, because the traps may be operating with different degrees of efficiency. No conclusions can be reached about any actual community structure, beyond a simple statement that certain species are known to be present. However, if it is assumed that the variation in trap efficiency at different sites affects different species equally, then it should be possible to use pitfall catch data to compare the relative composition of the carabid assemblages at different sites. If sampling continues over an entire season and the catches are pooled to give a year-sample, then it can be assumed that the catch for each species is approximately linearly related to its actual population density (Baars, 1979b). Thus, changes over time or differences between sites can be assessed using carabid pitfall catches, provided the sampling method is standardised, the sampling period is sufficiently long, and the data are expressed as presence/absence or as proportions of the total catch, rather than as actual abundances.

With these provisos always in mind, the study of carabid beetles by pitfall trapping has useful applications in the management of habitats, especially for conservation purposes.

1.2 Studies of carabid beetles in different habitat types

1.2.1 Woodland habitats

Thiele (1977 pp.18 - 26) considered that, in central Europe at least, carabid assemblages could be identified which were typical of particular forest plant communities or associations, although their distributions could be affected more by microclimatic and edaphic conditions than by the vegetation *per se*. The European forest carabid fauna was distinct from that of surrounding fields, but some 13 species were common to both types of habitat. These 13 species also occur in grassland, moorland or arable habitats in Britain. Of the remaining 32 species considered by Thiele to be typical of woodland, nine do not occur in Britain and no more than six of the rest were described by Eyre (1993 unpubl.) as woodland species in Britain, the majority being found also in moorland or grassland. This tends to support the contention of Eyre and Luff (1994) that there is no typical woodland assemblage of carabids in Britain, the woodland fauna being rather a subset of the species occurring in surrounding habitats. This difference between European and British woodland faunas is no doubt connected with the much smaller size, fragmented nature and younger age of British woodland patches.

The structure of the carabid and staphylinid community of an English deciduous woodland floor was described by Dennison and Hodkinson in a series of papers (1983a, 1983b, 1984a, 1984b), including discussion of feeding behaviour, diurnal and seasonal activity rhythms and species composition. Loreau (1984, 1987, 1990a, 1990b, 1992) investigated the population density, distribution, biomass and interspecific interactions of forest-floor carabids in Belgium, while the distribution, life cycle and phenology of the woodland species *Pterostichus oblongopunctatus* (F.) in the Netherlands was described by Brunsting (1981). Carabid assemblages of 41 woodlands in north-east England were analysed by Eyre and Luff (1994).

1.2.2 Grassland habitats

Ground beetle assemblages from 363 grassland sites throughout Britain were analysed by Eyre and Luff (1990), who concluded that ecologically meaningful habitat classifications were possible from carabid pitfall data alone. The habitat preferences of grassland species of *Pterostichus* were examined in relation to their responses to environmental variables by Rushton *et al.* (1991). The value to the beetle fauna of variation in the vegetation structure has been studied by Luff (1966), who examined the role of tussocks, by Parmenter & MacMahon (1984), examining the role of shrub architecture, and by Rushton *et al.* (1990), who looked at the effects of scrub management. The phenology and dynamics of a single grassland species, *Clivina fossor* (L.), were examined by Desender (1983). The effects of management practices on the ground beetle and other arthropod fauna of grasslands have been investigated by Walsingham (1978), Purvis and Curry (1978, 1981), Roberts and Morton (1985), and Rushton *et al.* (1989). The factors influencing grassland communities generally were reviewed by Usher (1978).

1.2.3 Moorland and heathland habitats

The life cycles of two species occurring in moorland habitats, *Carabus problematicus* Hbst and *C. glabratus* Payk., were described by Houston (1981) and by Butterfield (1986). Bauer (1989) examined the distribution of carabid and staphylinid beetles in a mosaic habitat of limestone outcrops and peat moorland, categorising species according to their habitat preferences. The effects of fragmentation of habitat on heathland spiders and beetles, including carabids, were assessed by Hopkins and Webb (1984). Holmes *et al.* (1993) attempted to determine which factors were affecting the distribution of ground beetles in Welsh peatlands under different management regimes, and the effects of grazing intensity on the carabid assemblages of Irish upland heath have been investigated by McFerran *et al.* (1994). The relationship between ground beetle communities and heathland flora was examined by Gardner (1991), while the relationships of moorland invertebrate communities, including carabid beetles, with soil, vegetation and spatial factors were investigated by Sanderson *et al.* (1995).

1.2.4 Wetland habitats

Wetland carabids have been studied by Murdoch (1966, 1967), who considered that most species could be classified as preferring either wet or dry conditions, and by Dawson (1965) who compared the habitat preferences, life cycles and feeding habits of eight species. Šustek (1994) examined the effects of hydrological management on the carabid fauna of an afforested floodplain in Central Europe.

1.2.5 Agricultural habitats

Carabids are an important component of agricultural ecosystems and their rôle as predators of pest species has received much attention (Mitchell, 1963; Sunderland, 1975; Speight & Lawton, 1976; Chiverton, 1988; Kennedy, 1994). The timing and intensity of agricultural operations, as well as microclimatic conditions prevailing in different crops, are bound to have a profound effect on the carabid assemblages. In particular, winter cereals, with autumn cultivation, are likely to sustain a higher proportion of spring breeding species with adult overwintering stages, while spring cultivation will favour autumn breeders which overwinter as larvae (Thiele, 1977 p. 28ff; Hance, 1990). A higher proportion of spring breeders in winter cereals as compared with spring-sown root crops may be partly attributable to a general preference among spring breeders for the drier, warmer conditions found in cereal crops. Where crop rotation is practised, the patterns of dominance in the carabid fauna are likely to change from year to year, but the species composition overall will more probably reflect management intensity in general rather than crop types in particular. Recent research into the biology of ground beetles in agricultural land has been reviewed by Luff (1987). Environmental and management factors affecting the distribution of ground beetles in agricultural land, including pasture, have been investigated by Baker and Dunning (1975), Dritschilo and Erwin (1982), Hokkanen and Holopainen (1986), Eyre *et al.* (1989, 1990) and Fan *et al.* (1993). Speight and Lawton (1976) found that the activity of predatory ground beetles (Carabidae and Staphylinidae) in cereal fields was related to the amount of weed cover, although Purvis and Curry (1984) concluded that activity of carabids in a sugar beet crop was influenced by the use of farmyard manure, but not by weed cover. Conversely, Tucker (1992) related Coleoptera density in grassland to the age of the sward, but not to farmyard manure applications. The effects of applications of manure, sewage sludge and other organic waste material on arthropod populations generally were reviewed by Pimentel and Warneke (1989). The importance of fallow or uncultivated strips, field edges and hedgerows as hibernation sites or refuges for ground beetles has been investigated by Jones (1976), Desender *et al.* (1981), Desender (1982), Wallin (1985), Duelli (1990), Alderweireldt *et al.* (1992) and Lys and Nentwig (1992). Van Dijk (1986) followed the changes in the carabid fauna of a previously arable field as the oligotrophic conditions of the surrounding heathland were restored.

1.3 Studies of the biology of carabid beetles

The scientific literature contains an ever-increasing body of information on all aspects of carabid biology, including several volumes dealing solely with the Carabidae (e.g. Thiele, 1977; den Boer *et al.* (eds.), 1986; Stork (ed.), 1990; Desender *et al.* (eds.), 1994).

In terms of the biology and life history of individual species, the European Carabidae are better known than most other families of Coleoptera, although physiological research in particular has tended to concentrate on a few species, and much remains to be learned, especially about the rarer and more specialised species.

A knowledge of feeding behaviour, foraging and diet is central to an understanding of life history. Hengeveld (1980a) reviewed the literature on the diet of carabids and concluded that the present state of knowledge was insufficient to allow 'much ecological speculation', largely due to the small scale or laboratory-based methods of many studies. From his own study of the gut contents of adults of 24 carabid species trapped in the field (Hengeveld, 1980b), he concluded that all were polyphagous to some degree, with no clear separation of carnivorous and phytophagous species. Similarly, five species from the genera *Amara, Harpalus, Pterostichus* and *Stenolophus* were found to accept both weed seeds and maggots, with varying degrees of preference (Hagley *et al.*, 1982). Nevertheless, it remains the case that some genera, notably *Harpalus* and *Amara,* are often referred to in the literature as herbivorous (e.g. Lindroth, 1974). Hengeveld found it was possible to distinguish broadly between the Carabinae and Harpalinae, the former consuming more arthropods and the latter more plant material. This distinction seemed to be related to the degree of specialisation, or selectivity of prey, the generalists feeding opportunistically on both plant and animal material and the specialists seeking out particular prey items, often springtails (Collembola). These specialists included *Loricera pilicornis* (F.) and species of the genera *Leistus* and *Notiophilus*. Although these species share a common prey preference, their habits are nevertheless very different, *Notiophilus* being a diurnal visual hunter which seizes its prey with its mandibles (Bauer & Kredler, 1993), and *Leistus* and *Loricera* both nocturnal, detecting their prey by chemical cues and then trapping it in a setal cage (Bauer, 1985).

The relationship of food supply with development, body size and fecundity of *Notiophilus* spp. has been investigated by Ernsting *et al.* (Ernsting & Huyer, 1984; Ernsting *et al.*, 1992), who found that adult body size and fecundity were strongly influenced by temperature, which increased food consumption and growth rate but decreased larval development time. Adult body size was also found to be dependent on larval food supply for *Calathus melanocephalus* (L.) and *Pterostichus versicolor* (Sturm) (van Dijk, 1994) and for *N. brevicollis* (Nelemans, 1988), larvae in the field being highly active predators which rarely attained the maximum size possible in laboratory-reared specimens.

Population dynamics and life cycles have been investigated for a number of species and communities. Manga (1972) estimated total metabolism, production, respiration and energy flux for a population of *N. brevicollis*.

Dynamics of natural populations of at least 64 species at 92 sites in the Netherlands have been followed for more than 25 years (den Boer, 1970, 1981, 1985, 1990; Baars & van Dijk, 1984a, 1984b), yielding important results on the density fluctuations and survival of isolated populations in relation to dispersal power. Studies on phenology, dynamics and habitat preferences of individual species or groups of species are very numerous, and include: the distribution of, and movements between, populations of *N. brevicollis* (Greenslade, 1964b); laboratory tests on soil pH preferences of seven species (Paje & Mossakowski, 1984); the relationships of species distribution, wing development, colour polymorphism and diurnalism with habitat and altitude (Greenslade, 1968); reproduction and longevity in two species (van Dijk, 1979); the role of density-dependent regulation in experimental populations of *P. oblongopunctatus* (Brunsting & Heessen, 1984); the role of predation by rodents in population control (Parmenter & MacMahon, 1988).

1.4 Carabid beetles in habitat assessment

When a site is assessed for its conservation value, the criteria most commonly considered include diversity, rarity, naturalness, typicalness and area (Usher, 1980; Margules & Usher, 1981). Since the decisions on selection and funding of conservation schemes are often taken ultimately by policy-makers who are not biologists, it is desirable that these criteria should be quantified, so that an objective measure of the relative values of different sites may be obtained.

1.4.1 Diversity

The concept of biological diversity is of obvious interest and importance; its quantification, however, is by no means simple. So many different indices of diversity have been proposed and applied in different circumstances that Hurlbert (1971) was led to describe species diversity as a 'nonconcept'. Critiques and comparisons of various indices include those of Menhinick (1964), Whittaker (1972), DeJong (1975), Peet (1975) and Giavelli *et al.* (1986). In its simplest form, the species diversity of a single habitat or area (α-diversity) is represented by S, the species richness or number of species present in the area. The species richness of a sample, however, is related to the sample size or sampling effort, rarer species being added as the sample size increases. Diversity indices encompass a further component, the degree of dominance (concentration) or of equitability (evenness) in the sample. Simpson's index (Simpson, 1949) allows computation of both concentration and equitability, which are partially inversely related (Whittaker, 1972). Concentration, C, is the sum of the importance values or proportions of the species in the sample, while equitability is a function of the variance of the species importance values. The Shannon-Wiener index is essentially a measure of equitability. Both it and Simpson's C are relatively independent of sample size, provided samples are not too small (Whittaker, 1972). In practice, any index of diversity is likely to be related to species richness, and Hill (1973) concluded that S was not 'any less reputable' a statistic than other, derived, indices such as those of Simpson or Shannon, and recommended that both species richness and a derived index should be included in any assessment of diversity.

A third diversity index still widely used is Williams' alpha (Fisher *et al.*, 1943), which is based on the logarithmic series distribution of species abundances. Preston (1948, 1962a, 1962b) showed that species abundances are better described by the lognormal distribution. The number of individuals per species is expressed on a logarithmic scale, each class being termed an octave when logarithms to the base 2 are used; the number of species per octave is then seen to follow an approximately normal distribution, with the majority of species having an intermediate number of individuals and fewer species having a very large or very small number. An important feature of this distribution is that it is truncated by a 'veil line' cutting off the left arm of the curve at some point before it approaches the abscissa. It is assumed that the curve would reach an asymptote with the abscissa at both ends were every species recorded, but the difficulty - or impossibility - of sampling the rarest species means that there are always unoccupied octaves at the low end of the scale. Increasing sampling effort so as to record more rare species does not alter the shape of the curve; it merely moves it farther to the right as more of these octaves are revealed. The lognormal distribution has been found to be appropriate for a variety of natural communities (Preston, 1948, 1962a, 1962b), although not for all (Preston, 1980), either due to shortcomings of the sampling regime or to real ecological conditions. May (1975) referred to the 'ubiquity' of the lognormal distribution in species-rich communities and gave theoretical reasons why it is the most likely distribution both for communities at equilibrium and for those dominated by opportunistic species.

Refseth (1980) assessed the value of carabid beetles for habitat classification for conservation purposes, and thought consideration of both diversity indices and similarity indices to be necessary, although the concept of similarity between habitats is closely related to the concept of β-diversity. Ricklefs (1987) argued for the role of historical and regional processes to be taken more into account in explaining observed community diversity.

Diversity of insects is not necessarily related to species diversity of the vegetation in a simple manner. In a study of secondary succession from fallow field to birch woodland (Southwood *et al.*, 1979), the diversity of Heteroptera and adult Coleoptera rose with the plant diversity, but remained relatively high when the diversity of the plants fell with increasing dominance of woodland species. The diversity of plant structure and architecture may be of greater importance to carabid beetles, and other insect groups, than the actual plant species diversity.

Diversity is often considered to be highest when a habitat suffers a moderate or intermediate level of disturbance (Connell, 1978; Abugov, 1982). The intensity of disturbance has been defined as the product of the size of the area affected and the frequency of the disturbance (Petraitis *et al.*, 1989). In an agricultural situation, management activities take place in fields with fixed boundaries, so that the intensity of disturbance resulting from management operations would become a function solely of their frequency. This simplistic definition of disturbance intensity apparently equates the ploughing of a field with less destructive operations such as rolling or mowing. A better measure of disturbance would take account of the amount of resource destroyed or renewed or the magnitude of the disturbance itself, along with its frequency and the size of the area affected (Miller, 1982). Sousa (1984) listed five descriptors commonly used to describe disturbance: area; magnitude; frequency; predictability; turnover rate.

Disturbance increases habitat heterogeneity on a spatial and/or temporal scale. In an agricultural context, the spatial component tends to be on a field scale and the temporal component may be the more important. Abugov (1982) considered the importance of the temporal phasing of disturbance across a group of habitat patches. Taking each field on a farm to be a discrete habitat patch, the effects of disturbance might be related to whether the patches (fields) were disturbed by management operations in or out of phase with each other.

Habitats can be ordinated on two axes according to their degree of heterogeneity in space and time, and the ecological strategies of species related to their position on the habitat templet. Three positions on the templet correspond to three well-defined strategies: the *r*-strategy in short-lived, disturbed but favourable habits; the *K*-strategy in stable, favourable habitats; and the adversity selection strategy in stable but unfavourable habitats (Southwood, 1977, 1988; Greenslade, 1983). A similar approach was taken by Grime (1974, 1977), who devised a triangular ordination for the classification of herbaceous plants according to their ecological strategies. The three vertices of the triangle represent maximum importance of competition, stress and disturbance respectively. In this scheme, the ruderal strategy is equivalent to the *r*-strategy of the Southwood / Greenslade model, the competitive strategy to the *K*- strategy and the stress-tolerating strategy to the adversity-selection strategy. Stress is defined as resource limitation or toxic effects of the environment, while disturbance involves physical disruption from biotic or abiotic causes. Both of these models assume a trade-off between competitive ability and ability to tolerate stress and disturbance. Competitively dominant species (*K*-strategists) are generally thought to be poor tolerators of disturbance (Connell, 1978), so that the elimination of competitive species as disturbance increased would allow the establishment of those species which were poor competitors but good tolerators (*r*-strategists), so increasing diversity. This may be particularly true when the limiting resource being competed for is space: for instance, Hemphill and Cooper (1983) found that disturbance promoted diversity of filter-feeding insects in a stream by preventing the slow-growing superior competitor from occupying so much of the substratum that the opportunistic colonisers would be excluded. However, a diversity bottleneck could occur at intermediate levels of disturbance if some species were both good competitors and also tolerant of moderate disturbance (Petraitis *et al.*, 1989). As disturbance increased, the poor tolerators would disappear but the presence of the competitive tolerator would prevent colonisation by the uncompetitive *r*-strategists, until a point was reached at which the dominant species also disappeared, leaving a largely unoccupied habitat available for colonisation by a different suite of species. The triangular model of Grime precludes the existence of species adapted to habitats which are both unstable and unproductive, and also fails to take account of the persistence of poor competitors in a community by the avoidance of competition, rather than by superior stress- or disturbance-tolerating abilities (Loehle, 1988).

Huston's (1979) general hypothesis of species diversity treats community structure as a dynamic equilibrium between rate of population increase and frequency of population reduction resulting from disturbance. In this model, anything which tended to increase rate of growth, such as increased energy flow, would reduce diversity because the superior competitors would also increase more rapidly, allowing a faster approach to competitive exclusion. Occasional population reduction increases diversity by preventing the achievement of competitive equilibrium. The position of maximum diversity along the disturbance gradient will be at some intermediate level, but the actual position depends on the dynamic equilibrium between these two forces.

1.4.2 Rarity

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 10km squares would be appropriate; Eyre (1993 unpubl.) has assigned rarity scores to Scottish carabid beetles on this basis. On a more local scale, such as county, 2km x 2km squares, or tetrads, would be more suitable (Dony & Denholm, 1985; Eyre & Rushton, 1989). This has the obvious virtue of simplicity, plus the advantage that scores can readily be updated as records improve. Examination of the species inventory of a site then allows calculation of an accumulated site score which should convey information on the relative 'quality' of the fauna at different sites. The major disadvantages of this method are concerned with the reliability of the records. Some species will have higher rarity scores than they merit because of under-recording of their preferred habitat - whether remote, difficult terrain, or 'degraded' agricultural land not frequented by entomologists. The solution to this problem clearly lies in improved sampling and recording, of commoner species as well as rare ones. Scoring on a geometric scale (e.g. a score of 1 for species recorded from 128 or more 10km squares, rising to a score of 128 for those recorded from only one square) buffers the scores to some extent against changes in the records.

One cause of under-recording is the relatively greater difficulty of catching and identifying certain species. Foster (1987) found that a modification of the calculated species scores for water beetles according to his own special knowledge of the species produced site scores which appeared to have real ecological meaning. Similarly, it is possible to manipulate scores so that greater weight is given to co-occurring relict species which may be in urgent need of conservation effort, as opposed to pioneer species which are rare by virtue of being associated with highly disturbed, transitory habitats (Foster *et al.*, 1992). This approach has value in conservation assessment, but requires special knowledge of the phenology and habits of the species, and perhaps overly complicates a system attractive for its simplicity. The presence of near-ubiquitous species in a sample conveys little useful information and it may be appropriate to limit consideration to those species recorded from fewer squares. The proportion of rarer species in the sample can then be calculated (Dony & Denholm, 1985), or a 'rarity association value' obtained by summing the scores for the rarer species in the list (Eyre & Rushton, 1989).

Site scores will be dependent 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 (Foster, 1987; Eyre & Rushton, 1989; Foster *et al.*, 1990, 1992) or to an 'individual rarity score' by dividing by the number of individuals in the catch. This circumvents the problem of the length of the species list, whereby a sample of many common species may have a similar total rarity score to a sample of a few rare species. Such aggregations of rare species often indicate sites of important conservation value.

1.4.3 Naturalness

Naturalness is a concept which is difficult to quantify, to the extent that its usefulness in objective assessments must be limited. Few, if any, habitats exist in Britain which have not been altered at some time in their history by the activities of humans. Indeed, many of the habitats considered by the general public to be most valuable and unspoiled exist as a direct result of past management practices. Calcareous grasslands and coppiced woodlands are examples. It may be most useful to think of naturalness as a function of stability: natural habitats are those which have remained largely unchanged in recent times. This should be quantifiable, but would require the availability of the appropriate records.

A potentially useful approach to site assessment and the monitoring of change is to examine the invertebrates (or vegetation, or indeed any other suitable assemblage) according to their functional group rather than taxonomic identity. Information is then needed on species traits such as life histories, habitat preferences and feeding requirements. The functional groups associated with particular habitats have a more obvious ecological meaning than mere lists of species, and changes in functional groups can be related more easily to changes in actual environmental conditions. A further advantage is that functional groups are independent of geographical range; similar habitats in different parts of the world should support similar functional groups even though the actual species composition may be very different. Such differences may be found within a relatively small geographical area, creating difficulties for comparisons based on species lists. The functional group or species traits approach has been taken especially in studies of riverine or wetland systems, for instance by Castella *et al.* (1994), Hills *et al.* (1994), Murphy *et al.* (1994) and Richoux (1994).

1.4.4 Typicalness

The quantification of the concept of typicalness depends on the existence of methods to classify and ordinate sites according to the species present. The methods of multivariate analysis reduce these data, in which each site occupies a unique position in multidimensional species space (as many dimensions as there are species in the list), to a more manageable condition where similar sites are grouped together in ecological space of a few dimensions. This reduction is possible because of a certain redundancy in the data; groups of species respond in similar fashion to change along an environmental gradient (Gauch & Whittaker, 1981). Detrended Correspondence Analysis, DECORANA (Hill, 1979a), produces an ordination of both samples (sites) and species simultaneously by a process of reciprocal averaging. Species ordination scores are averages of the site ordination scores, and *vice versa*. The refinement of detrending removes the 'arch effect', which arises from the dependence of the second and subsequent axes on the previous ones and is often seen as a shortcoming of earlier reciprocal averaging techniques (but see Wartenberg *et al.*, 1987, who considered the arch to be a real and important feature of the data structure). Distances along each axis are measured in units of the standard deviations of the species turnover, and the eigenvalue for each axis is a measure of the amount of variance accounted for by that axis. The essential purpose of multivariate analysis is to recover as much as possible of the total variance in the data in as few dimensions as possible; however, in field data, such as pitfall catches, a significant amount of the variance is 'noise'. Eigenvector ordinations such as DECORANA preferentially extract structural variance in the first few axes with relatively high eigenvalues, relegating noise to higher axes of low eigenvalue (Gauch, 1982a). Since ordination scores are derived from a series of averaging procedures, they are very robust to sampling errors in the input data, rounding of all digits after the first having little impact (Gauch, 1982a). This makes the method particularly suitable for the kind of data obtained from pitfall trapping. Causal relationships between environmental variables and species composition may be inferred from correlations of axis score with measured variables. Canonical Correspondence Analysis, or CANOCO (ter Braak, 1986), uses an eigenvector technique to relate multivariate data to known environmental gradients. When data are to be compared from large numbers of sites, possibly surveyed at different times and by different people, DECORANA is to be preferred to CANOCO, because of the difficulties in collecting the appropriate environmental data.

Two-Way Indicator Species Analysis, TWINSPAN (Hill, 1979b), is a divisive polythetic hierarchical method of classification. The starting point is the first axis of a reciprocal averaging ordination of the sites, which is divided into two groups at its centre of gravity. Species are assigned indicator values according to their affinity with either side of the division and indicator scores are calculated for the sites, which are then re-divided on the basis of these scores. Divisions are repeated for the desired number of levels, resulting in end-groups which can be thought of as being arranged along an ecological gradient. Indicator species are identified for each division, and new sites may be assigned to the appropriate end-group according to the presence or absence of these species.

A perceived flaw in the methodology of TWINSPAN and similar classification methods is that the samples are constrained to belong solely to one side of each division, resulting in end-groups with hard boundaries. An alternative approach applies fuzzy-set theory, which permits samples to have degrees of membership of different sets. This may be closer to ecological reality, and fuzzy clustering can produce end-groups more closely related to environmental conditions than TWINSPAN does (Equihua, 1990). The techniques of fuzzy clustering, DECORANA and Procrustes rotation have been combined by McCracken (1994) in an analysis of moorland ground beetle and vegetation communities.

Once a group of sites has been classified into 'types' and ordinated according to species composition, a new site can be assessed for its degree of typicalness by finding the position it would occupy in the ordination and measuring its distance from the central point, or centroid, of the type (Eyre *et al.*, 1986; Eyre & Rushton, 1989; Luff *et al.*, 1989). Habitats are increasingly being assessed by these methods of multivariate analysis of ground beetle assemblages (Hopkins & Webb, 1984; Bauer, 1989; Luff *et al.*, 1989; Eyre *et al.*, 1989, 1990; Rushton *et al.*, 1989, 1990; Eyre & Luff, 1990, 1994; Gardner, 1991; Holmes *et al.*, 1993; McFerran *et al.*, 1994).

1.4.5 Area

The value of a site for conservation purposes is related to its size and its position in relation to other similar sites (Diamond, 1975). Larger areas can sustain more species according to a form of the Arrhenius equation, $N = KA^z$ where N is the number of species, A is the area and K and z are constants (Williams, 1943; Preston, 1962a). This assumes equilibrium conditions, and it must be remembered that because of edge effects and the presence of vagrant individuals, small habitat patches may appear to be more species-rich than the centres of larger patches (Webb & Hopkins, 1984). Small populations suffer less risk of local extinction if recolonisation is possible from neighbouring populations (Preston, 1962b; den Boer, 1990). Hanski (1982) found a positive correlation between species' local abundance and distribution; species which have a low abundance and are therefore more susceptible to local extinction, also occur at fewer sites and have a lower probability of re-founding by immigration. These rare species he termed 'satellite' species, while those which are locally abundant and regionally common are 'core' species. Gaston and Lawton (1989), however, failed to find support for the core-satellite hypothesis in communities of herbivorous insects on bracken, and suggested (Gaston & Lawton, 1988a) that both local abundance and regional distribution were dependent on body size, so that their apparent correlation was not due to a causal relationship, but rather two effects of a single determinant, namely body size. In isolated populations, selection may operate against dispersal power (since individuals dispersing from the population are lost and not replaced), thus further decreasing the chance of re-founding after local extinction (den Boer, 1990). The effects of habitat fragmentation on one flightless, stenotopic species of carabid, *Agonum ericeti* (Panz.), were found to be such that populations confined to patches of less than five hectares had a mean potential survival time of only 19 years (de Vries & den Boer, 1990).

Dony and Denholm (1985) found that both the species richness and the proportion of locally rare species of plant present in a woodland flora were dependent on area.

Having determined values for the diversity, rarity and typicalness of a site, it is possible to examine the relationships between these parameters. It would clearly be desirable to be able to incorporate measures of all these criteria in a single quantity which could be used in the assessment and comparison of different sites. Dony and Denholm (1985) suggested a combination of regressions of species richness and rarity on area to produce a single index of conservation value. Eyre and Rushton (1989) found no general correlation between rarity and typicalness for water beetle and ground beetle data in north-east England.

1.5 Body size

For each species of carabid beetle, body length may be expected to vary in a normally-distributed fashion between established minimum and maximum values reported in the taxonomic literature. A particular assemblage of species should thus give rise to a characteristic distribution of mean body lengths, and if particular assemblages of species are typical of particular habitats, it follows that similar patterns should exist in the body size distributions between sites. Larochelle (1980) listed 203 species of bird in Europe and Asia known to prey on carabid beetles. In particular, they form a significant part of the diet of both adults and foraging chicks of certain wading birds. To meet their energy requirements in a foraging time limited by weather conditions these birds require a good supply of large prey (Byrkjedal, 1989; Galbraith, 1989; Beintema *et al.*, 1990) and their best strategy is to seek a relatively small number of large beetles rather than a large number of smaller ones. Since biomass increases approximately as the cube of length, longer insects are of greater value as food items than a similar total length of small insects. Moreover, Kaspari and Joern (1993) found a highly significant negative correlation between body mass and the proportion of indigestible chitin in adult Coleoptera, so that a large beetle has more nutritive value than the same total biomass of smaller ones. Foraging and handling times are reduced when a predator takes a few large prey items instead of numerous small ones.

The commonest species in an assemblage are likely to be of small to intermediate size (though not the smallest) while larger body size is associated with lower numbers both of individuals and of species. These relationships, between body size, species number and abundances, have been the subject of numerous studies (Hutchinson & MacArthur, 1959; Schoener & Janzen, 1968; Peters & Wassenberg, 1983; Brown, 1984; Brown & Maurer, 1986; Gaston & Lawton, 1988b; Morse *et al.*, 1988; Blackburn *et al.*, 1990, 1993; Griffiths, 1992; Gaston *et al.*, 1993; Currie, 1993; Gregory & Blackburn, 1995). Total arthropod biomass in tropical forest has been found to increase with mean body size across all habitat types and trophic groups while abundance appeared to fall (Stork & Blackburn, 1993), even allowing for possible under-sampling of the smallest species. These results support the conclusion of Maurer and Brown (1988) that larger species represent a relatively large proportion of community biomass. Similarly, the flow of energy through an ecosystem may be concentrated disproportionately in larger individuals (van Valen, 1973), although Griffiths (1992) concluded that small species were energetically as important as large ones in communities. Borgmann (1987) considered that different models of biomass flow in a pelagic system could be reconciled when underlying assumptions about the complexity of food webs, somatic growth and reproduction were taken into account.

Body size may be of considerable importance in interspecific interactions. The theory of character displacement (Brown & Wilson, 1956) states that when the ranges of two similar species overlap, coexistence will only be possible if they diverge in one or more morphological, ecological, physiological or behavioural characters. Hutchinson (1959) stated that two species from the same trophic group could only coexist if their feeding structures, and hence body size, differed in size by a minimum critical ratio, which he deduced to be 1.3:1. The general applicability (or otherwise) of Hutchinson's ratio has been much discussed (Roth, 1981; Simberloff & Boecklen, 1981; Lewin, 1983; Tonkyn & Cole, 1986; Eadie *et al.*, 1987; Greene, 1987).

The degree of habitat overlap between species of grassland *Pterostichus* was found to be related to body size (Rushton *et al.*, 1991), larger species being more likely to co-occur. Larger species may be less likely to compete with each other for prey than smaller species, since they are able to utilise a wider range of prey sizes (Wilson, 1975), although it is disputed whether such competition can be demonstrated in carabid beetles, and indeed Wilson suggested that it should only occur among top predators and not among small arthropods. One exception would be when the arthropods were the top predators in a system, such as in carabid cave beetles (van Zant *et al.*, 1978). The competitive exclusion principle states that if two species compete for the same resource, or niche space, then one will inevitably exclude the other. Hutchinson's (1959) size ratios are related to the theories of character displacement (Brown & Wilson, 1956), competitive niche shift (den Boer, 1986) and limiting similarity (MacArthur, 1965), which allow co-occurring species to continue to coexist by occupying slightly different niches. In carabid beetles, congeneric species are often closely related ecologically, occupying similar niches and therefore likely to occur in the same habitats. Den Boer (1980, 1986) found that congeners coexisted more frequently than expected from a random distribution, and concluded that competitive exclusion should be considered an unusual, rather than expected, outcome of species interactions. Two hypotheses are proposed to explain this coexistence of similar species: either, the pressures of environmental and biotic conditions, including predation, are normally so severe that numbers never approach carrying capacity and competition does not take effect; or, under favourable conditions, the slight differences between species are sufficient to allow the occupation of slightly different niches, so avoiding competition. These two hypotheses are not mutually exclusive. In a review of the literature on interspecific competition in ground beetles, Niemalä (1993) found no examples of competitive exclusion, and while half of the 32 papers reviewed reported the present or past operation of competition, Niemalä considered the evidence to be generally weak or inconclusive. Studies which support the operation of competition in ground beetle communities include those of: Lenski (1982, 1984) on the effects of food limitation on woodland species of *Carabus*; Brandl and Topp (1985) who found size ratios of *Pterostichus* species to be consistent with the operation of interspecific competition in moorland communities, but not in woodland or grassland; van Zant *et al.* (1978) on cave beetles; Loreau (1990a, 1990b) on forest floor communities. Loreau considered there was 'weak' evidence for intraspecific competitive regulation of the dominant species, *Abax ater (A. parallelepipedus)*, but not for the less abundant species in the community, which never attained sufficient numbers for density-dependent effects to be important. Thiele (1977 p.61) concluded from a series of laboratory and field observations that interspecific competition was possible but unlikely under natural conditions, and that when it occurred it would not result in ecological separation of species.

Adult body size in insects generally may be related to the length of development time available (Schoener & Janzen, 1968) and to food intake. Thiele (1977 pp.42 - 43) thought that the observed increase in average body size of inland carabid faunas as compared with coastal ones was due to an increased availability of food. Also important are various environmental conditions, especially moisture. Smaller insects are more susceptible to desiccation and the average body size of an assemblage has been found to be greater in drier conditions (Janzen & Schoener, 1968; Schoener & Janzen, 1968; Šustek, 1994). The number of small adult insects in sweep-net samples of tropical forest understorey vegetation was found to decrease with increases in temperature, insolation, wind velocity and saturation deficit, which were all related to a decrease in foliage density and vegetation height, lower soil moisture and more fluctuating conditions of atmospheric humidity and temperature (Janzen & Schoener, 1968). The use of ground beetle body size distributions as indicators of habitat quality was suggested by Šustek (1987), who found that body size was reduced in degraded or unfavourable habitats.

Quite apart from consideration of parameters such as body size, diversity or rarity, the structure of the carabid species assemblage itself may be of considerable use in habitat assessment. Coulson and Butterfield (1985) identified seven distinct invertebrate communities of peat and upland grassland in northern England, utilising certain ground beetles among other taxa as indicator species. McCracken (1994) identified five distinct habitat types in an analysis of moorland ground beetles, while similar analysis of vegetation data from the same sites suggested the existence of only three habitat types.

The impact of different management practices on the ecosystem of a habitat may be assessed by comparative studies of the carabid beetle faunas; such studies should ideally include information on species composition, species richness and diversity, rarity scores and body size.

2. Methodology

2.1 Sampling methods

Data on the carabid assemblages of 55 locations in central and southern Scotland (Appendix 1) were collected by pitfall trapping. At each location, traps consisted of two replicate sets of nine plastic cups, 8.5cm diameter and 10cm deep, partly filled with ethylene glycol (commercial antifreeze) and set flush with the ground surface about two metres apart. The traps were emptied and re-set at approximately monthly intervals throughout the season, usually from late March to early October. The catch was pooled for each set of nine traps and stored in 70% alcohol before being sorted and the carabids identified to species level. Nomenclature followed Pope (1977) except for *Pterostichus rhaeticus* Heer (Luff, 1990) and *Calathus cinctus* Motschulsky (Aukema, 1990; Anderson & Luff, 1994); Appendix 2 is a checklist of the species taken at the Scottish sites. Monthly catches were pooled to give two replicate annual totals for each site.

2.2 The sites

Pitfall trapping was carried out by the author in 1993 at six grassland and moorland locations: Caerlaverock, Hule Moss, Islay, Kelton, Middleton and Vane Farm (a total of 17 sites with two replicate sets of traps at each). In 1994 the author trapped at two improved grassland locations in Ayrshire: Mauchline and Muirkirk (four sites of two replicates) and at a new RSPB Reserve on the Solway coast, formerly improved grassland and arable land as well as sand dunes: Mersehead (four sites of two replicates).

In 1989 and again in 1993, the Scottish Agricultural College (SAC) conducted pitfall trapping at Caerlaverock Castle (one site with two replicates) and in four improved grassland fields at the Crichton Royal Farm, Dumfries: Acrehead, Bungalow, Lochbank and Netherwood (eight sites with two replicates in each of two years). The carabid beetles from these traps were identified by the author, with the exception of the catch of May 1989.

In 1990, SAC carried out pitfall trapping at five unimproved grassland locations in Ayrshire: Auchalton, Cairn Hill, Feoch, Macawston Farm and Shewalton (12 sites with two replicates). The data on the carabid catches were made available for analysis.

In addition, data from trapping programmes in grassland, moorland and woodland sites in north-east England were provided to the author for analysis.

2.3 Management intensity

For each of the Scottish sites, data were collected on sward type, sward age, cutting, grazing, inorganic fertilisation and organic inputs. Each of these aspects of the management regime was scored on a four-point scale, from 0 to 3 in ascending order of intensity (Table 2.1).

Natural or semi-natural vegetation scored 0, sown broad-leaved mixtures 1, sown grass and clover mixtures 2 and sown grasses 3. Uncultivated swards scored 0, permanent pastures more than 10 years old 1, pastures between 5 and 10 years old 2, and young grass or arable land 3. Defoliation and fertilisation regimes were scored: none 0, low 1, moderate 2 and high 3. These scores were summed to arrive at a total Management Score lying between 0 and 18 for each site. Sites were then assigned to one of five bands of Management Intensity as follows: Score 0 -2, Intensity Band 1; Score 3 - 6, Intensity Band 2; Score 7 - 10, Intensity Band 3; Score 11 - 14, Intensity Band 4; Score 15 - 18, Intensity Band 5 (Appendix 3).

Level	**Sward type**	**Sward age**	**Cutting intensity**	**Grazing intensity**	**Inorganic inputs**	**Organic inputs**
0	Natural or semi-natural	Uncultivated	None	None	None	None
1	Sown broad-leaved mixtures	Pasture >10 years old	Low	Low	Low	Low
2	Grass and clover mixtures	Pasture 5 - 10 years old	Moderate	Moderate	Moderate	Moderate
3	Grasses	Pasture <5 years old	High	High	High	High

Table 2.1. Management intensity scores for four levels of six management parameters.

This scheme was based on qualitative rather than quantitative data and placed sites into fairly broad categories rather than into a strict order relative one to the other. This was felt to be desirable, given the often incomplete information available from farmers and other land managers. The categories were similar to those used by Luff *et al.* (1990) to describe the management of 55 grassland sites in north-east England, but were based on somewhat less-detailed information. The resulting five management intensity bands were therefore broadly comparable to the five management categories of Luff *et al.*, but not exactly equivalent to them. The setting of the score levels for each category and of the cut-off points between the five management bands was necessarily subjective to some extent; however, once the categories had been decided, assigning each site to its appropriate management band was entirely an objective process.

The sites were classified by TWINSPAN (Hill, 1979b) and ordinated by DECORANA (Hill, 1979a) according to their carabid species compositions. Three aspects of the carabid assemblages were examined: species richness and diversity, rarity and body size. The relationships between management intensity of the habitats, the classification and ordination of the sites, and the diversity, rarity and body size of their carabid assemblages, were analysed.

2.4 Species diversity

The simplest expression of species diversity is S, species richness. Since S is sensitive to sample size, which varied in this study from an annual catch of just 49 (FEOC90J1) to 1606 (MERS94A1), an index based on proportional abundances was to be preferred. The complement of Simpson's Index was selected:

$$D = 1 - \Sigma p_i^2$$

where p_i is the catch of species i expressed as a proportion of the total catch.

Simpson's index is relatively insensitive to sample size and reflects the degree of concentration of the fauna in the dominant species. This version was preferred to the more commonly used

$$D = 1 - \Sigma[n_i(n_i-1)/N(N-1)]$$

since it avoided the loss from the calculation of those species taken as single specimens. Whittaker (1972) considered the first form more appropriate for the expression of dominance in the assemblage. It is in fact the limit of the second form for large samples, and in the present study the indices calculated from the two formulae were found to differ only in the third decimal place, if at all. Hill (1973) recommended the use of the reciprocal of the index rather than the complement, for theoretical reasons. This would have had the advantage of yielding values greater than one, but for purposes of comparing different sites, the choice of complement or reciprocal seemed immaterial.

2.5 Rarity

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 10km squares would be appropriate; Eyre (1993 unpubl.) 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 degree 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 (Foster, 1987; Eyre & Rushton, 1989; Foster *et al.*, 1990, 1992) or to an 'Individual Rarity Score' (*IRS*) by dividing by the number of individuals in the catch. The quantitative nature of pitfall catch data allows the calculation of an *IRS* for each site, making the rarity value to some extent independent of the size of the catch. This index differs from previous rarity indices (for instance, those of Foster (1987) and of Eyre and Rushton (1989)) by taking species' relative abundances into account. 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.

The Individual Rarity Score, *IRS*, was calculated for each assemblage using the information on post-1970 records of the Scottish carabid fauna in Eyre (1993 unpubl.), according to the formula

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

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 recorded from only one square.

2.6 *Body size*

A mean body length figure was obtained from the taxonomic literature for each species (Lindroth, 1974) and a value was calculated for the median body length of the carabid beetles in each annual pitfall catch by analysis of the frequency distribution of the metric variable body length (expressed to 0.1mm). This was the conventional and familiar number median length (*NML*). By definition, 50% of the beetles caught were of body length greater than the *NML*. This statistic gives equal importance to those variates above and below the median, and does not reflect the disproportionately greater contribution to the total biomass made by the larger individuals (van Valen, 1973; Maurer and Brown, 1988; Stork & Blackburn, 1993). To reflect the greater ecological importance of larger species, a statistic was sought which would give greater weighting to these. An analogy was seen with the calculation of Number Median Diameter and Volume Median Diameter used to measure droplet size in the application of pesticide sprays (Matthews, 1975), and this gave rise to the calculation of the Weight Median Length (*WML*) as follows.

The original data collected from the trapping programmes listed the number of ground beetles caught of each species, of known mean length. Length was converted to weight using the formula:

$\text{WEIGHT} = 0.03069 \, x \, \text{LENGTH}^{2.63885}$

(Jarošík, 1989). This formula describes the length to weight relationship specific to adult carabid beetles and differs only slightly from the general relationship for insects derived by Rogers *et al.* (1976), which was:

$\text{WEIGHT} = 0.0305 \, x \, \text{LENGTH}^{2.62}$.

Each weight value was multiplied by the corresponding number of beetles caught, the products summed to give an estimate of the total carabid biomass in milligrams, and the biomass of each species expressed as a proportion of the total. From this, a cumulative percentage graph was plotted on probability paper and the weight median length or *WML* estimated (see worked example in Table 2.2).

Later, a formula was developed which allowed calculation of *WML* without the need for graphical methods.

2.7 Statistical analyses

Species composition was analysed by multivariate techniques, i.e. detrended correspondence analysis, DECORANA (Hill, 1979a), and two-way indicator species analysis, TWINSPAN (Hill, 1979b). Relationships between species composition, diversity, rarity, body size, habitat type and management practices were explored using non-parametric statistics (e.g. Spearman's rank-order correlation coefficient, Mann-Whitney U-test) and generalised linear interactive modelling, GLIM (Baker & Nelder, 1978).

Species	**Length mm**	**Weight (W) mg**	**Number in catch (N)**	**NxW**	**NxW / Biomass**	**Cumulative % of Biomass**
Dyschirius globosus	2.6	0.382	6	2.292	0.0002	0.02
Bembidion unicolor	3.1	0.608	1	0.608	0.0000	0.02
B. guttula	3.2	0.661	2	1.321	0.0001	0.03
B. properans	3.8	1.040	2	2.080	0.0002	0.05
Dyschirius politus	4.4	1.531	1	1.531	0.0001	0.06
Amara tibialis	5.2	2.379	42	99.924	0.0075	0.81
Dromius linearis	5.2	2.379	3	7.138	0.0005	0.86
Notiophilus aquaticus	5.2	2.379	14	33.308	0.0025	1.12
Bembidion tetracolum	5.5	2.759	7	19.311	0.0014	1.26
Badister bipustulatus	5.6	2.893	1	2.893	0.0002	1.28
Amara familiaris	6.4	4.115	2	8.230	0.0006	1.34
A. communis	7.0	5.213	5	26.065	0.0020	1.54
A. plebeja	7.0	5.213	4	20.852	0.0016	1.70
Leistus rufescens	7.0	5.213	12	62.555	0.0047	2.17
Elaphrus riparius	7.2	5.615	1	5.615	0.0004	2.21
Loricera pilicornis	7.2	5.615	7	39.307	0.0030	2.51
Calathus melanocephalus	7.4	6.036	29	175.052	0.0132	3.82
Amara aenea	7.5	6.254	67	419.013	0.0315	6.98
Calathus cinctus	7.9	7.173	38	272.574	0.0205	9.03
C. mollis	7.9	7.173	72	516.455	0.0389	12.91
C. erratus	10.2	14.078	161	2266.561	0.1706	29.97
Pterostichus nigrita	10.8	16.370	1	16.370	0.0012	30.09
Nebria brevicollis	12.0	21.617	3	64.851	0.0049	30.58
Calathus fuscipes	12.2	22.581	331	7474.214	0.5624	86.82
Amara aulica	12.6	24.587	4	98.349	0.0074	87.56
Laemostenus terricola	15.2	40.337	1	40.337	0.0030	87.86
Cychrus caraboides	16.5	50.090	2	100.181	0.0075	88.62
Pterostichus niger	17.8	61.188	12	734.258	0.0552	94.14
Broscus cephalotes	19.5	77.840	10	778.403	0.0586	100.00
		Total Biomass		13289.647		

Table 2.2. Calculation of Weight Median Length (*WML*) of carabids at site MERS94D2. From examination of the cumulative biomass distribution, *WML* = 12.06mm.

3. Effects of management intensity on the carabid assemblages of grassland in central and southern Scotland

Fifty-five locations in southern Scotland were assigned to five bands of management intensity, as described in Section 2.3 and Appendix 3. The carabid assemblages from two replicates at every site were determined, giving 110 sets of data. A total of 50,609 individuals of 114 species were identified (Appendix 2).

3.1 Multivariate analysis of carabid assemblages

For each of the 110 sites, the catch of each species was expressed as a percentage of the total year-catch for the site. The sites were then classified by Two-Way Indicator Species Analysis, TWINSPAN (Hill, 1979b), and ordinated by Detrended Correspondence Analysis, DECORANA (Hill, 1979a).

The TWINSPAN classification resulted in 11 end-groups after four levels of division (Fig. 3.1).

The first division separated 25 sites of management intensity bands 1 and 2 from all the rest. Twenty-two of these 25 were upland sites at altitudes over 140m, and all except SHEW90N2 (a reclaimed coup at Shewalton sand-pits) had a natural or semi-natural sward which had never been cultivated. All were grazed (SHEW90N2 by rabbits), but none was cut or received any inorganic nitrogen. Indicator species for this half of the division were *Carabus violaceus*, *Pterostichus rhaeticus*, *C. problematicus*, *P. diligens* and *Patrobus assimilis*. The presence of a single specimen of *P. diligens* was sufficient to classify SHEW90N2 with this group as a borderline positive.

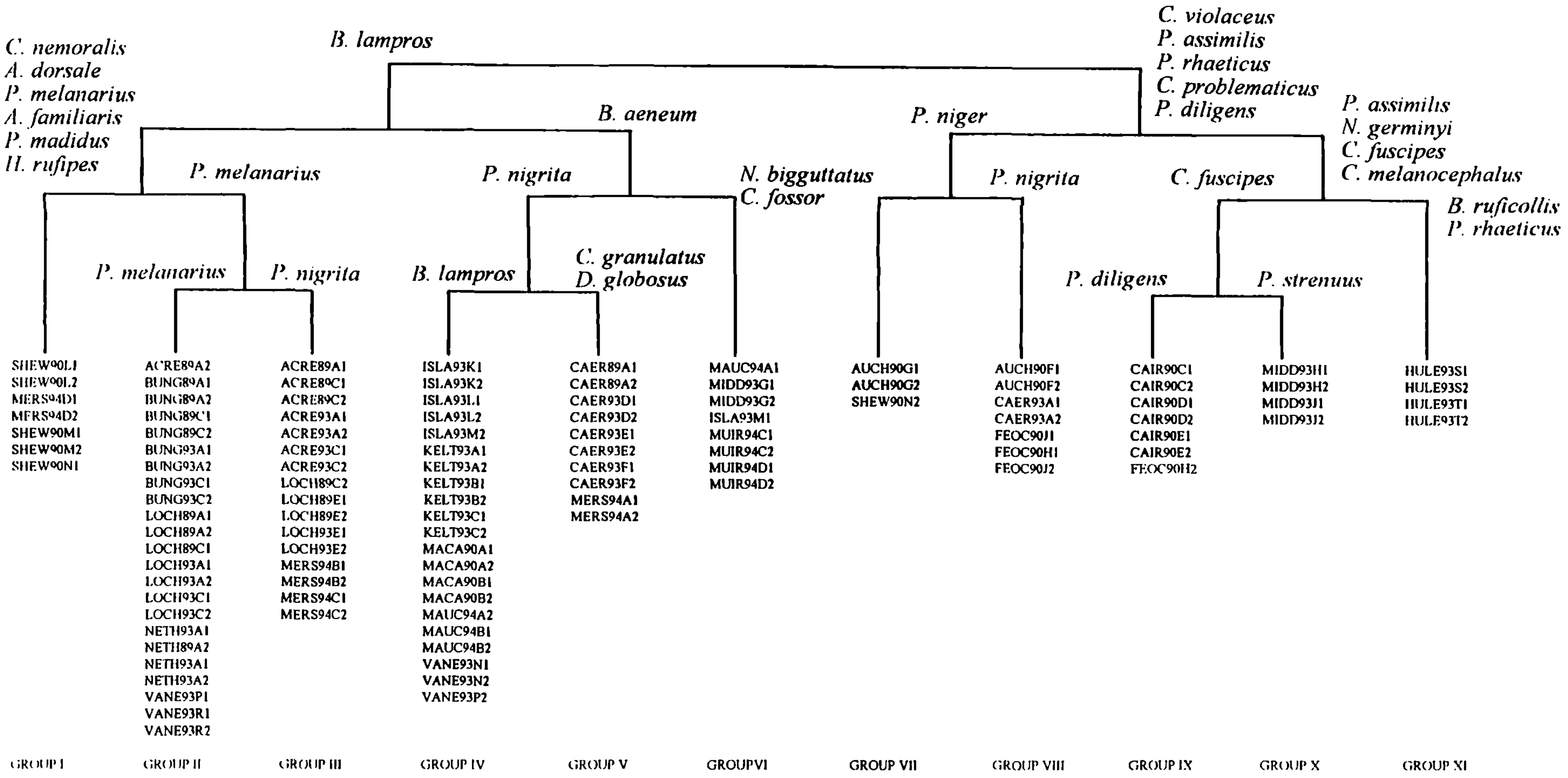

Figure 3.1 End-groups resulting from TWINSPAN classification of the carabid assemblages of 110 sites in central and southern Scotland.

The major half of the first division included all the more intensively managed sites as well as most of the lowland ones. The only indicator for these sites was *Bembidion lampros.*

The 11 TWINSPAN end-groups were:

Group I. Seven sites on a dry sandy substratum, including the Mersehead sand-dunes and five of the six Shewalton sand-pits sites. Indicated by the absence of *Pterostichus melanarius.*

Groups II and III. These two groups, indicated by the presence of *P. melanarius*, between them contained all of the Crichton Royal Farm sites as well as three Vane Farm and four Mersehead sites. MERS94B1&2 were on a banking between wet pasture and arable land, while MERS94C1&2 were in cereal stubble, uncultivated during the sampling period. Apart from VANE93P1 (wet, uncultivated rank grass on the shore of Loch Leven), all of these sites underwent a moderate to high intensity of management. The two groups were separated by *P. nigrita* in Group II and by relatively higher numbers of *P. melanarius* in Group III.

Group IV. Indicated by *B. lampros*. Twenty-one sites of moderate to high management intensity, apart from VANE93P2 and the four Macawston Farm sites. These four were old pasture, receiving no inputs but heavily grazed by horses.

Group V. Ten sites on the Solway coast, including saltmarsh and grassland at Caerlaverock National Nature Reserve, semi-natural rank grass at Caerlaverock Castle in 1989, and old wet pasture at Mersehead. None of these sites was cut, all but Caerlaverock Castle were grazed, and only Mersehead received any artificial inputs. Indicated by *Carabus granulatus* and *Dyschirius globosus.*

Group VI. Eight sites of relatively high management intensity, all except ISLA93M1 (Islay) over 100m altitude, and all except MIDD93G (Middleton Moor rough grazing) cut for silage. Separated from Groups IV and V by *Notiophilus biguttatus* and *Clivina fossor.*

Groups VII and VIII. Nine herb-rich meadow sites plus the probably misclassified SHEW90N2. Indicated by relatively large numbers of *Pterostichus niger.*

Groups IX, X and XI. Fourteen of these 15 sites were all above 230m, with a sward of heather or rough grass and a low intensity of management. They were characterised by *P. assimilis*, *Notiophilus germinyi*, *Calathus fuscipes* and *C. melanocephalus.* FEOC90H2 (Feoch meadows) was probably misclassified because of a relatively low catch of *P. niger* compared with the other meadow sites. The Group XI *Calluna* moorland sites, Hule Moss, were separated from Groups IX and X by *Bradycellus ruficollis* and *P. rhaeticus.*

In the DECORANA ordination, both of the first two axes (Appendix 4) showed a high degree of similarity between replicates (z-test for matched pairs: z-score -0.022 and -0.002 respectively). The first two axes were plotted, showing management intensity (Fig. 3.2).

The major axis accounted for 55% of the total variance and was clearly related to management, with almost all sites at intensity bands 1 and 2 scoring over 100. Possible misclassifications appeared to be BUNG93A, LOCH93A and MACA90A & B, all assigned to band 2, and VANE93P, band 1, which appeared among the more intensively managed sites. BUNG93A and LOCH93A were both wildflower meadows sown in 1987 and were assigned to a low management band because of low intensity of cutting and fertilisation. MACA90 was old pasture,

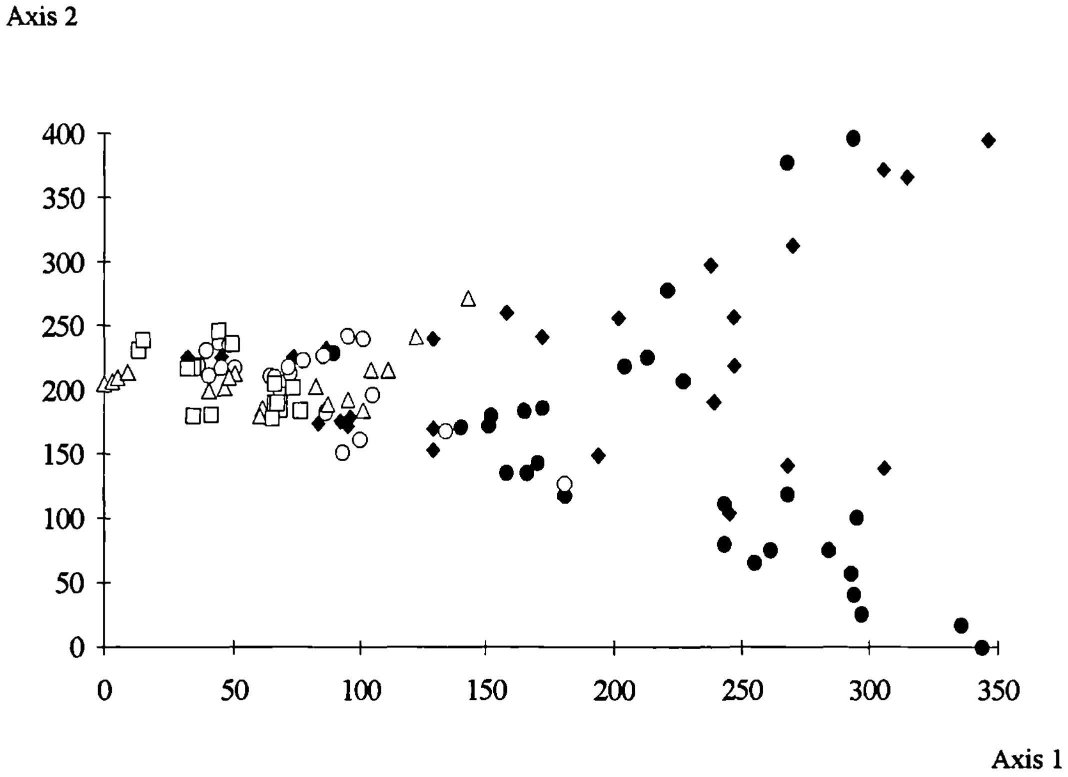

Figure 3.2. The first two axes of the DECORANA ordination of the carabid assemblages of 110 sites in central and southern Scotland.

● Management band 1

◆ Management band 2

○ Management band 3

△ Management band 4

□ Management band 5

intensively grazed but, according to the farmer, with no cutting or fertilisation. Both in 1990 and in 1992 when this site was revisited the sward was open and sparse, with much bare ground. VANE93P was semi-natural wet grassland on the edge of Loch Leven, lightly grazed but with no cutting or artificial inputs, although recent problems with eutrophication of the loch suggest a possible input of nitrogen by run-off from surrounding pasture. The highest scoring higher-intensity site on Axis 1 was ISLA93L, assigned to band 3. This was old pasture, rather wet and weedy, grazed but not cut and with moderate fertilisation.

Axis 2, explaining 48% of the total variance, was not related to management but appeared to reflect moisture levels. Moisture often emerges as an important determining factor of the carabid assemblage when habitats of similar general type are compared (Luff *et al.*, 1989; Rushton *et al.*, 1991). In this case, the effects of management practices appeared to be of rather greater importance, with moisture effects superimposed on them. The upper arm of the forked pattern in Fig. 3.2, towards the top right, contained the driest sites, Mersehead sand-dunes and Shewalton sand-pits, while the lower arm contained wetter sites such as Hule Moss and Feoch Meadows. The intensively managed, productive sites, which could be expected to have intermediate moisture levels, were all clustered in a fairly narrow band on the second axis.

Ordination of the species scores (Appendix 5, Fig. 3.3) confirmed this pattern, with the species arranged into three broad groups: those associated with the managed sites positioned low on the first axis and intermediate on the second; the moorland species in the lower arm of the fork; and species preferring dry habitats (e.g. members of the genera *Amara, Calathus* and *Harpalus*) in the upper

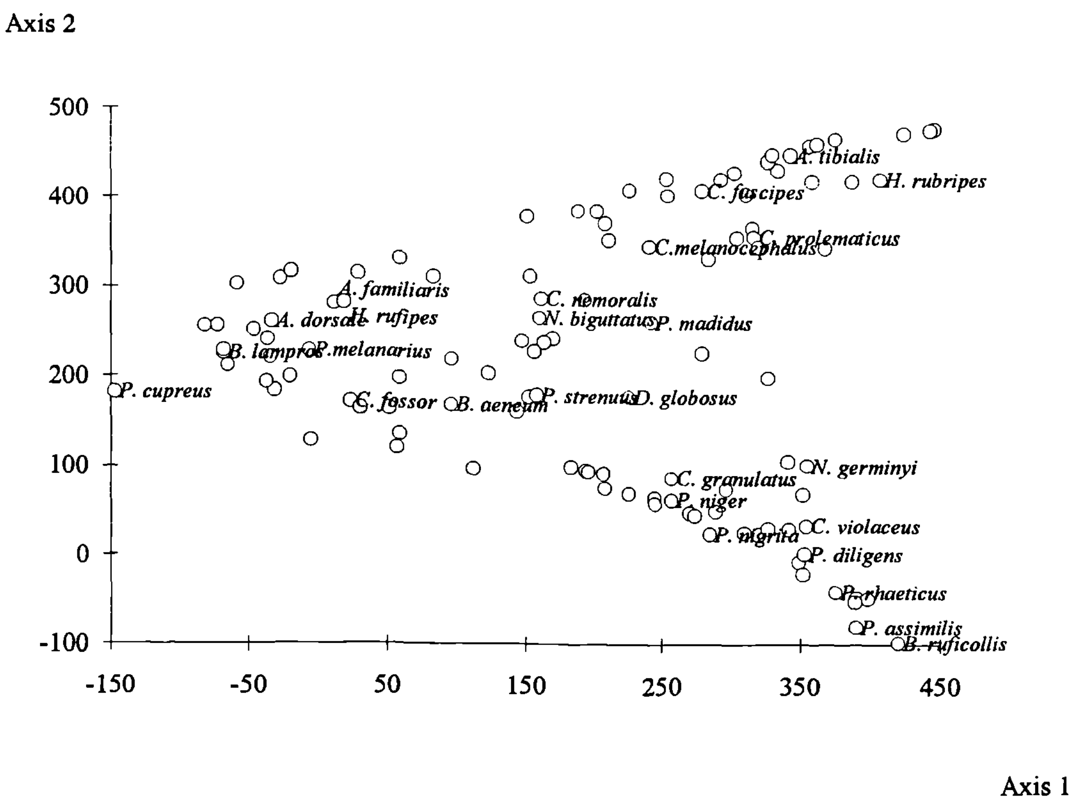

Figure 3.3. DECORANA ordination of the carabid species scores of 110 sites in central and southern Scotland, showing the positions of TWINSPAN indicator species.

arm. Comparing the species ordination with the TWINSPAN classification (Fig. 3.1), the lower arm of the fork in the ordination corresponded to Group XI, Hule Moss, and the upper fork to Group I, Shewalton and Mersehead dunes. The two extremes of the TWINSPAN ordering of the sites thus appeared at opposite extremes of the second DECORANA axis, but otherwise the TWINSPAN groups were arranged in order on the first axis. The carabid assemblages overall were affected by two trends of almost equal importance, as suggested by the similar eigenvalues for the two axes: management and moisture. There was a high degree of similarity among the assemblages of the more intensively managed sites, but the communities of more natural sites varied widely according to whether the habitat could be classed as wet or dry.

3.2 Species richness and diversity

The simplest measure of species diversity is *S*, the number of species found. The value of *S* in this study ranged from 9 to 33 (Appendix 6) with an overall mean of 20.0. Species richness differed highly significantly between management bands (Table 3.1), with the most speciose sites tending to be less intensively managed (Fig. 3.4). The highest mean values of *S* were at management intensity bands 2 and 3 and the lowest values at bands 4 and 5 (Fig. 3.5). Very low values sometimes indicated problems with the sampling regime; for instance, the lowest values of *S* in band 1 were at FEOC90J1&2 (9 species each), which suffered from flooding and took a total of only 49 and 77 specimens respectively. ISLA93M1&2 (band 4) had to be removed earlier than usual due to farm management requirements and took 9 and 10 species, 98 and 171 specimens. A short sampling season, however, was not inevitably linked to a low catch. The two exceptionally species-rich sites in band 5 (Fig. 3.4) were MERS94C1&2, two replicates in a field of cereal stubble which was sampled only until ploughing in August, yet yielded 527 and 642 specimens of 28 and 29 species respectively.

The open conditions in this field, with much bare ground and an abundance of weed seeds, would be attractive to dispersive colonisers, including both diurnal predators and the more phytophagous species.

Management band	Log(catch)	*S*	Residual	*D*	*IRS*	*WML* mm
1 (n = 28)	5.475	20.0	-0.412	0.787	4.99	15.3
2 (n = 26)	5.745	22.0	-0.273	0.821	4.24	13.3
3 (n = 22)	6.255	21.4	0.287	0.717	2.14	12.8
4 (n = 18)	5.840	16.8	0.255	0.730	2.35	11.8
5 (n = 16)	6.109	17.3	0.484	0.718	2.32	11.2
K-statistic	13.77	15.16	29.74	19.98	18.22	23.51
p-value	<0.01	<0.01	<0.001	<0.001	<0.01	<0.001

Table 3.1. Mean values of log(catch), *S*, residual, *D*, *IRS* and *WML* for five management intensity bands, with results of Kruskal-Wallis tests for differences between the bands. Log(catch): logarithm of the number of carabid beetles. *S*: number of species. Residual: residual deviance of the linear regression of log(catch) on *S*. *D*: Simpson's diversity index. *IRS*: individual rarity score. *WML*: weight median length. See Section 2 for calculation of management band, *D*, *IRS* and *WML*.

It may be expected that the number of species found would be dependent upon the size of the catch, and that a regression of catch size on species number would suggest a linear relationship. Catches ranged from 49 to 1606 (Appendix 6) and differed highly significantly according to management band (Table 3.1).The highest catches were at sites of intermediate management intensity, and the lowest at band 1, although this was somewhat distorted by the low catch at FEOC90J (Figs. 3.6 and 3.7). Examination of the catch data for the 110 sites showed the variance to be much greater than the mean; the data were therefore transformed to natural logarithms to stabilise the variance and help to normalise the

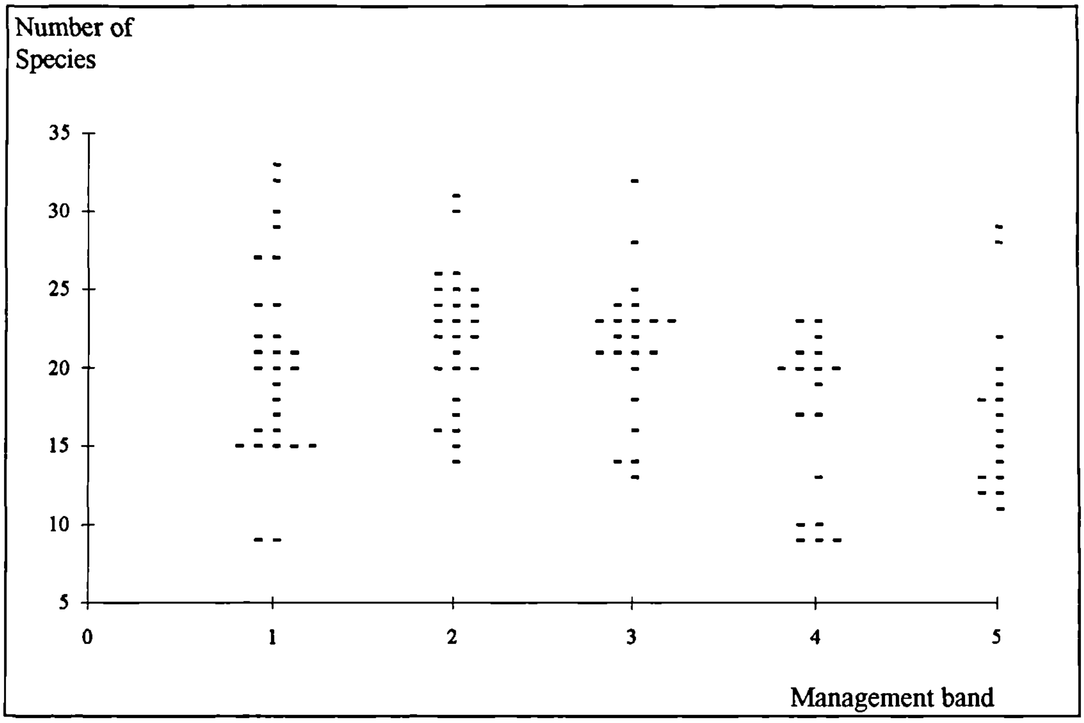

Figure 3.4. *S*, the number of species taken at 110 sites in five management intensity bands.

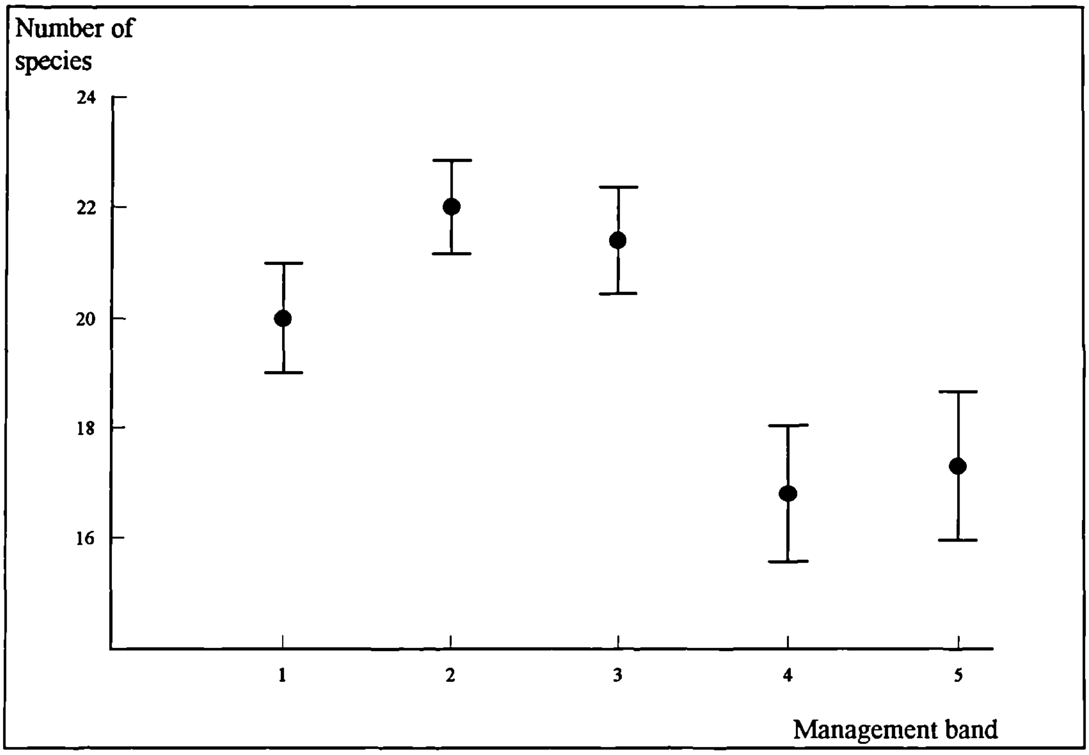

Figure 3.5. Means and standard errors of the numbers of species taken at 110 sites in five management intensity bands.

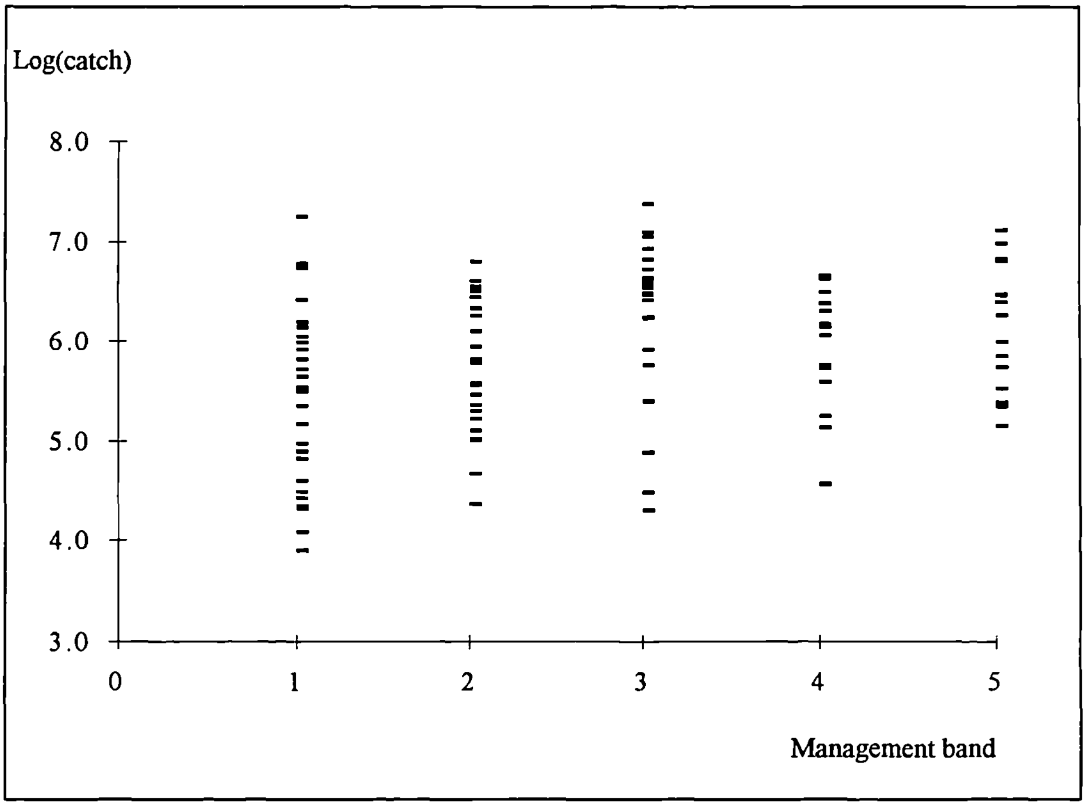

Figure 3.6. The logarithm of the number of individuals taken at 110 sites in five management intensity bands.

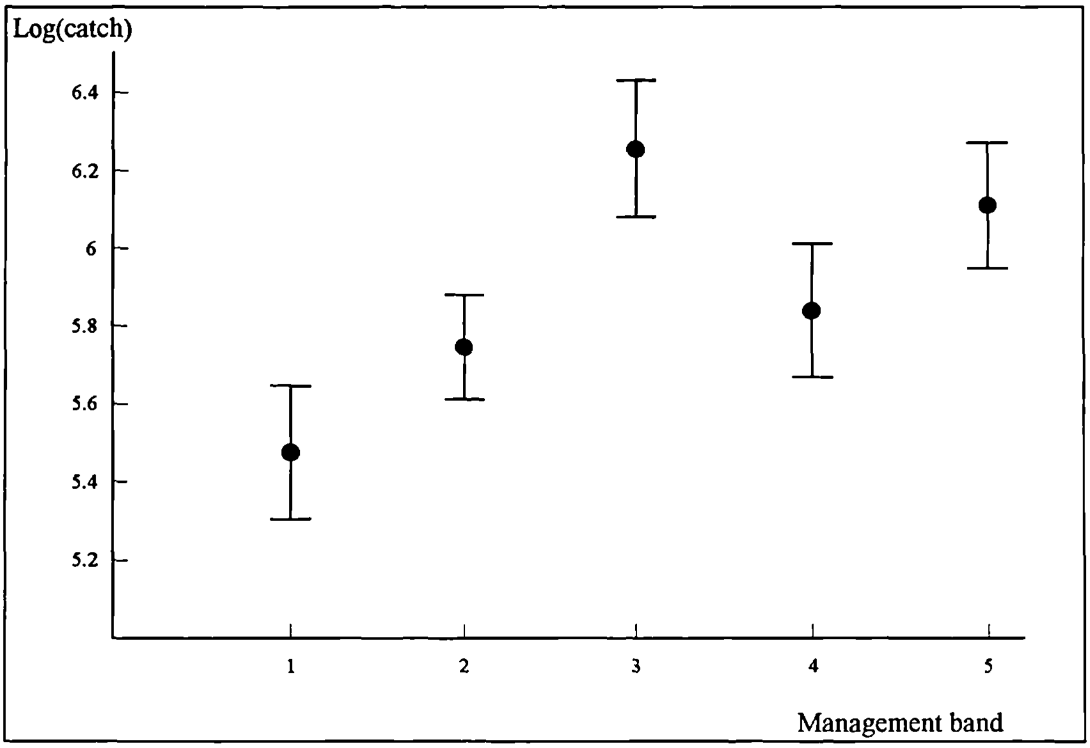

Figure 3.7. Means and standard errors of the logarithms of the numbers of individuals taken at 110 sites in five management intensity bands.

distribution. After transformation, approximately 70% of the data were within one standard deviation of the mean and a normal distribution was therefore assumed. Menhinick (1964) considered that a better estimate of diversity of sweep-net catches was obtained from the relationship of S with the square-root transformed catch than with the log-transformed catch. However, consideration of the distribution of the present data clearly showed the natural logarithm to be the more appropriate transformation, in terms of normalisation of the distribution and stabilisation of the variance. From theoretical considerations also, the geometric nature of population growth suggests that the logarithm is the natural descriptor of population densities (May, 1975).

The regression of log(catch) on S resulted in a highly significant linear relationship (log(catch)= 4.174+ 0.0838S, t = 7.112 at 108 d.f.) and produced a division of the data which broadly reflected management intensity (Fig. 3.8). Points above the regression line were mostly moderate to high management intensity, and those below the line were mainly bands 1 and 2.

Luff (in prep.) has suggested that an examination of the residuals of such a regression could be used to quantify species diversity. A high positive residual suggests a site with a large catch but relatively few species, while a high negative residual suggests a species-rich assemblage with lower abundances - a more even fauna. In this study of 110 sites, the residual deviances of the regression resulted in a better discrimination between management bands than any other measure of diversity, with bands 1 and 5 at opposite extremes (Table 3.1). Management bands 1 and 2 were found to have mainly negative residuals, bands 3, 4 and 5 positive residuals (Appendix 6, Figs. 3.9 and 3.10).

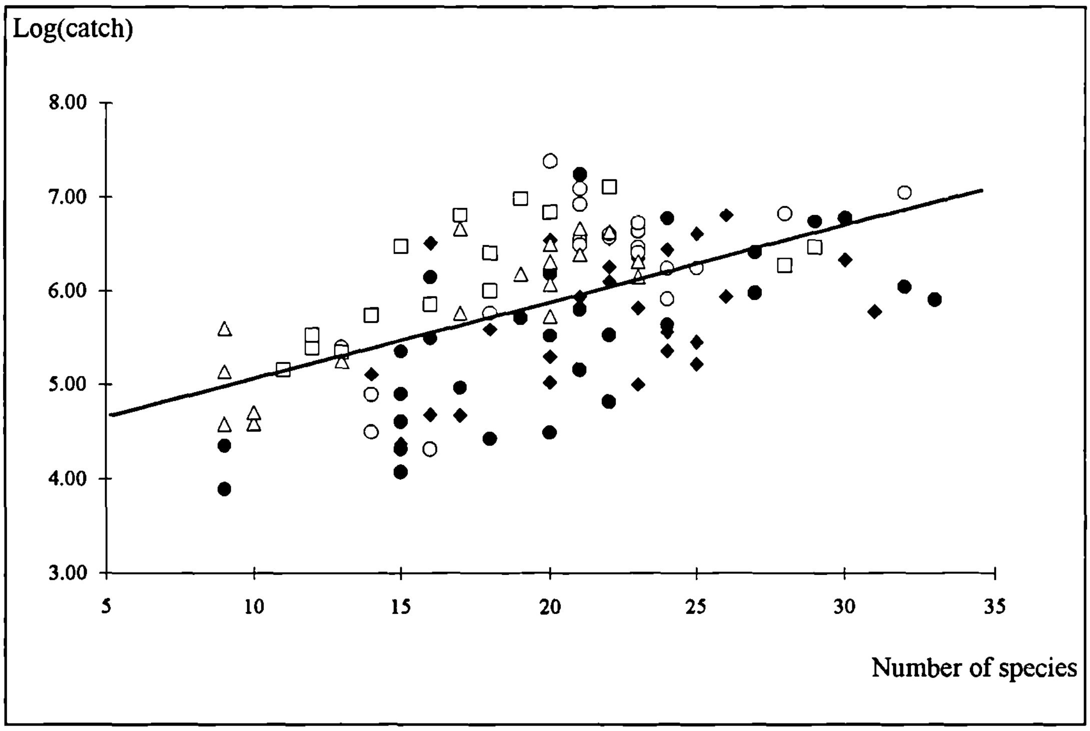

Figure 3.8. Linear regression of the natural logarithm of the number of individuals on the number of species (*S*) taken at 110 sites in five management intensity bands. The regression equation is:

Log(catch) = 4.174 + 0.0838*S*.

● Management band 1

◆ Management band 2

○ Management band 3

Δ Management band 4

□ Management band 5

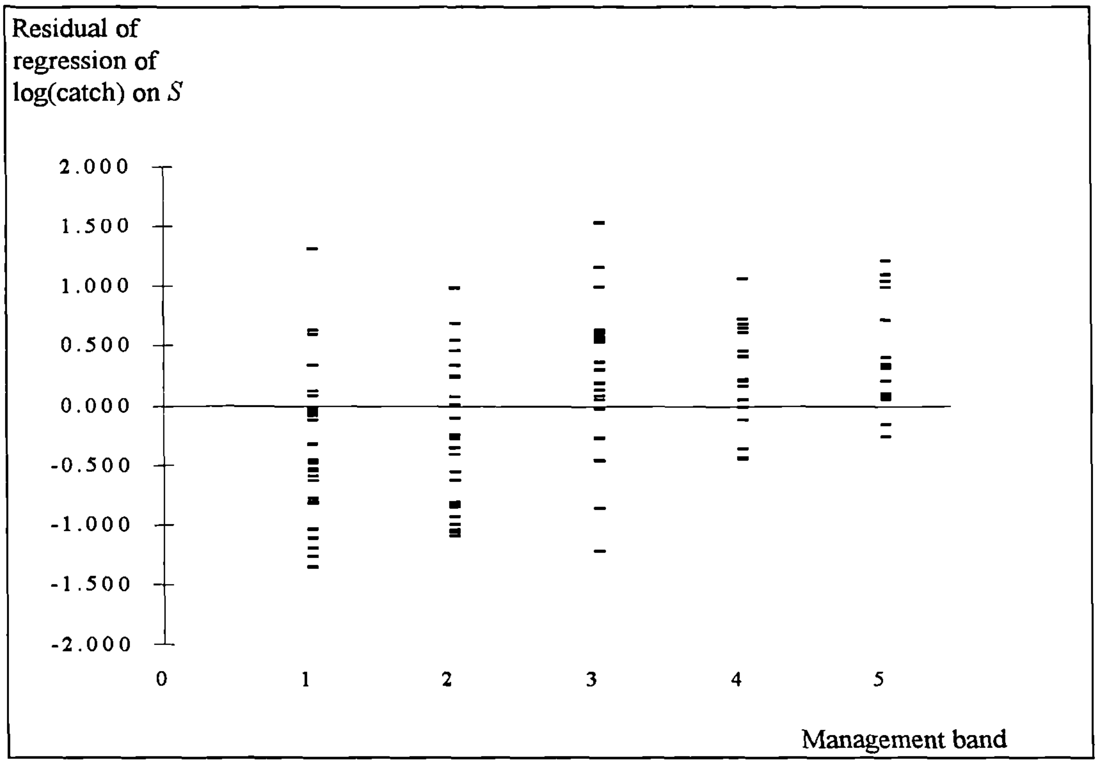

Figure 3.9. The residuals of the linear regression of log (catch) on number of species, according to management intensity band.

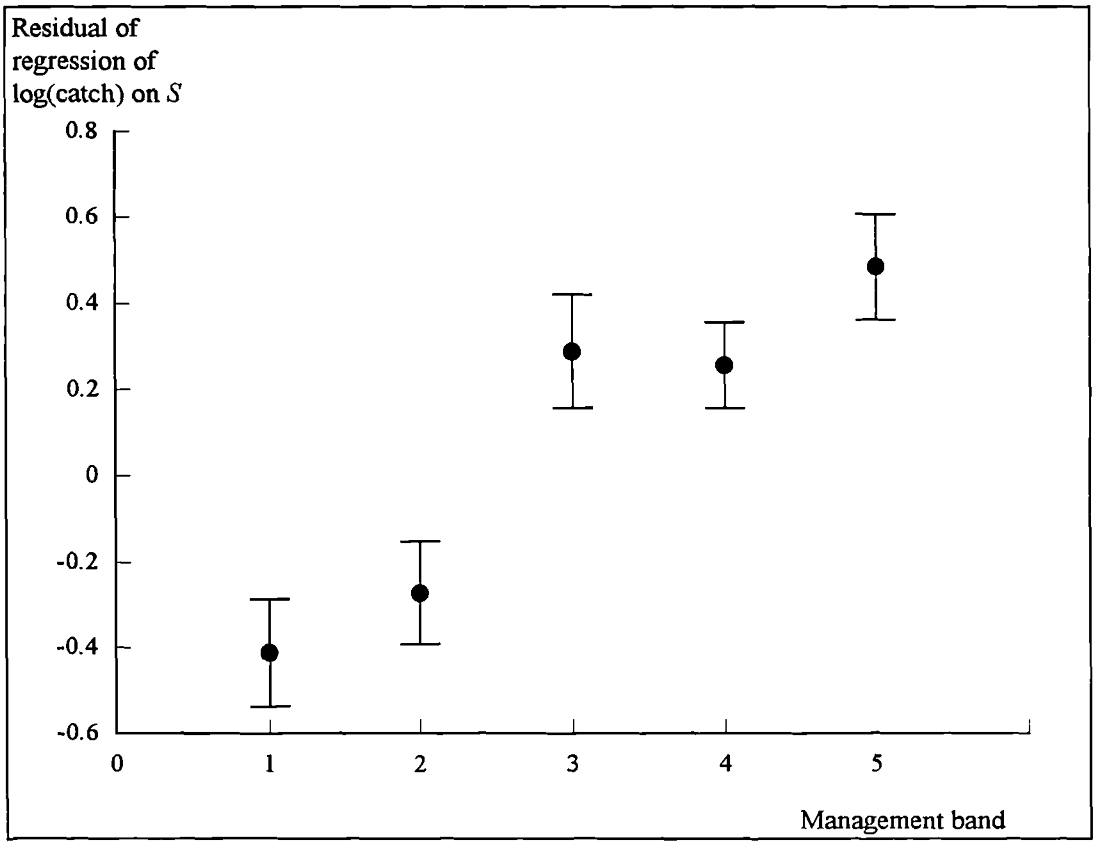

Figure 3.10. Means and standard errors of the residuals of the linear regression of log (catch) on number of species, according to management intensity band.

Possible misclassifications suggested by the regression were, once more, MACA90A1&2 (band 2, residuals 0.689 and 0.985), VANE93P1 (band 1, residual 0.625), and AUCH90G1&2 (band 1, residuals 0.594 and 1.305). Auchalton Meadows was an unmanaged, semi-natural site but a high abundance of *Pterostichus madidus* F. (51% and 66% of the catch) reduced the overall diversity even though *S* was relatively high. As in the DECORANA ordination, ISLA93L1&2 (band 3, residuals -1.215 and -0.858) also appeared to have been misassigned.

Simpson's Diversity Index, *D*, is related to the degree to which the fauna is concentrated in the most abundant species. This measure of diversity also differed very highly significantly across the management bands (Table 3.1), with the highest values of *D* - the least concentrated assemblages - in management bands 1 and 2 and the lowest in bands 3, 4 and 5 (Appendix 6, Figs. 3.11 and 3.12). Two exceptionally low values of *D* in band 1 (Fig. 3.11) were AUCH90G2 (66% *P. madidus*) and MERS94D1, a sand-dune site where 62% of the catch was *Calathus fuscipes*. A rise in *D* on the introduction of a moderate amount of management would be in line with the intermediate disturbance theory, and there did appear to be such an increase between bands 1 and 2. However, the main feature of the relationship of *D* with management was the sharp fall between bands 2 and 3, with no significant difference across the three higher intensity bands (Fig. 3.12). Mean residual deviances (Fig. 3.10) suggested a smoother trend from high to low diversity across the five bands, but with the same sharp drop between bands 2 and 3. According to Huston's (1979) model of community diversity as a dynamic equilibrium, the high diversity of the unmanaged sites

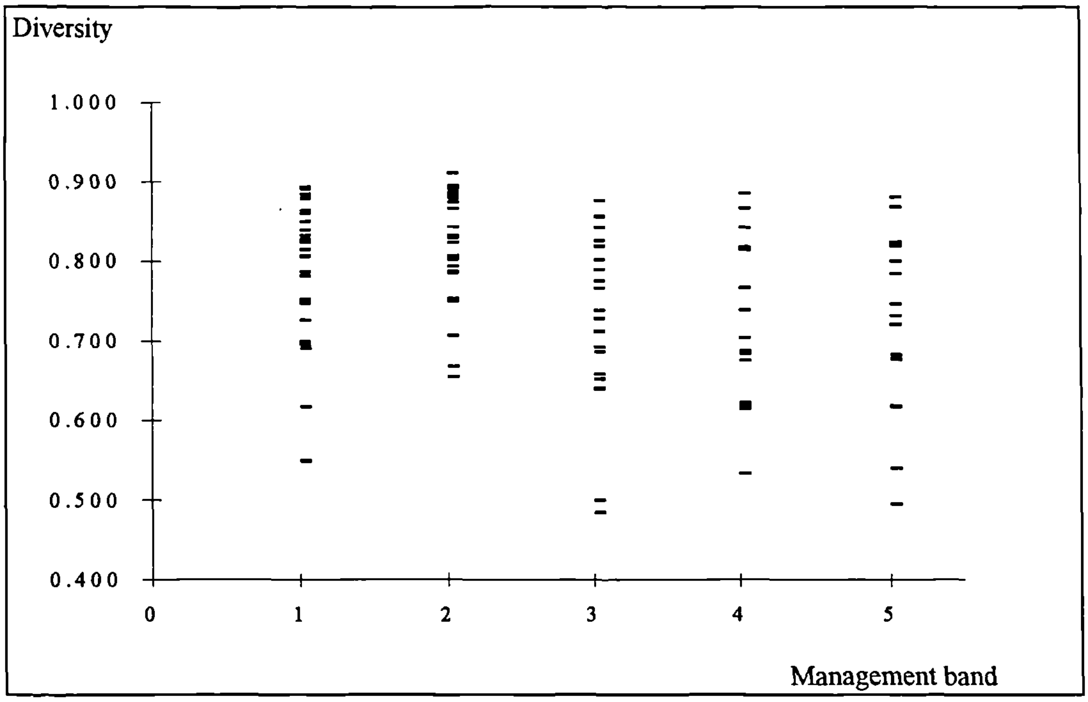

Figure 3.11. *D*, Simpson's diversity index, of the carabid faunas of 110 sites in five management intensity bands.

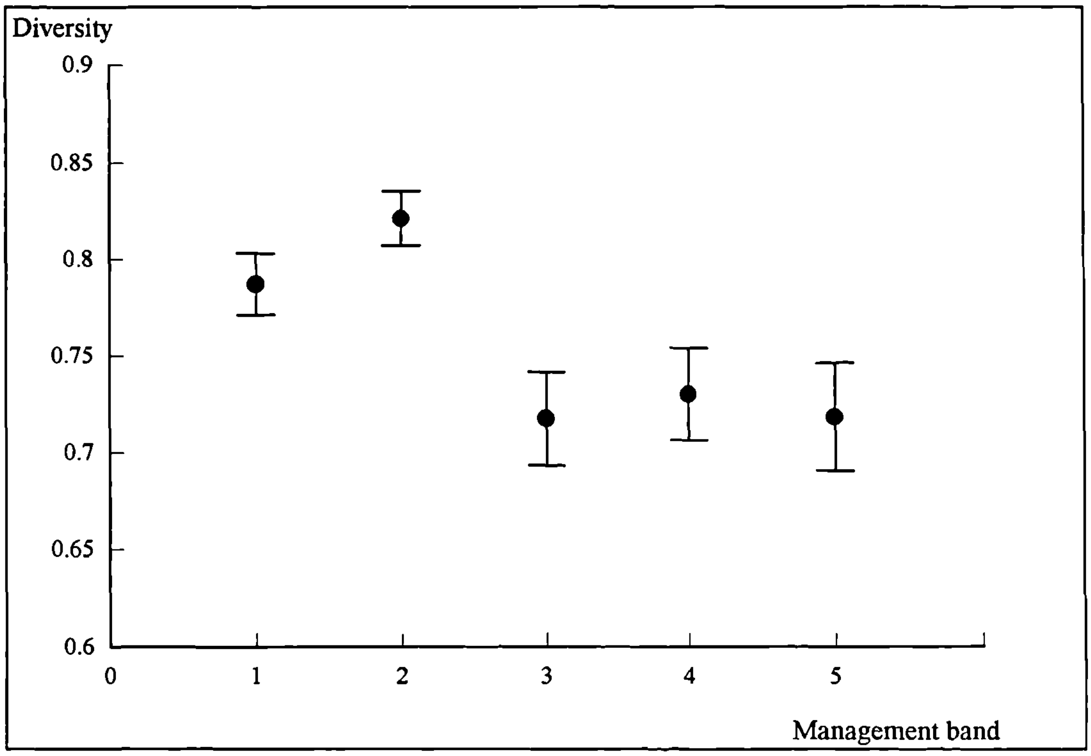

Figure 3.12. Means and standard errors of *D*, Simpson's diversity index, of the carabid faunas of 110 sites in five management intensity bands.

would be related to a low rate of population growth, i.e. low energy flow in the system, delaying the attainment of competitive exclusion. Such low-energy or impoverished habitats are likely to be sensitive to high frequencies of disturbance as the low intrinsic rate of population growth may not permit recovery. In systems where the energy flow is high, rapid population growth will accelerate the process of competitive exclusion, reducing diversity. Such high-energy systems may retain high diversity if the frequency of population reduction through disturbance is sufficiently high to prevent dominance by the superior competitors, yet not so high as to prevent recovery. The only location in this study which underwent regular destructive disturbance was the arable sites, MERS94C1&2, the only band 5 sites to have negative residuals, with 28 and 29 species and values of *D* of 0.869 and 0.881. This high diversity could be maintained by the interaction of high growth rates and frequent population reductions.

3.3 Rarity

The rarity value of each site was expressed as its Individual Rarity Score (*IRS*), as described in Section 2.5 (Appendix 6). As for the diversity index *D*, management bands 1 and 2 were significantly higher than bands 3, 4 and 5 (Table 3.1, Figs. 3.13 and 3.14). The use of the non-parametric rank-order Kruskall-Wallis test for differences among the bands (Table 3.1) overcomes the problem of outliers which was particularly evident in the *IRS* values of bands 1 and 2 (Fig. 3.13). Exceptionally high values were found at Shewalton sand-pits (SHEW90N1&2, band 2, *IRS* 18.20 and 11.85) and at Hule Moss (HULE93T1&2, band 1, *IRS* 21.27 and 14.48). These outlying points were due

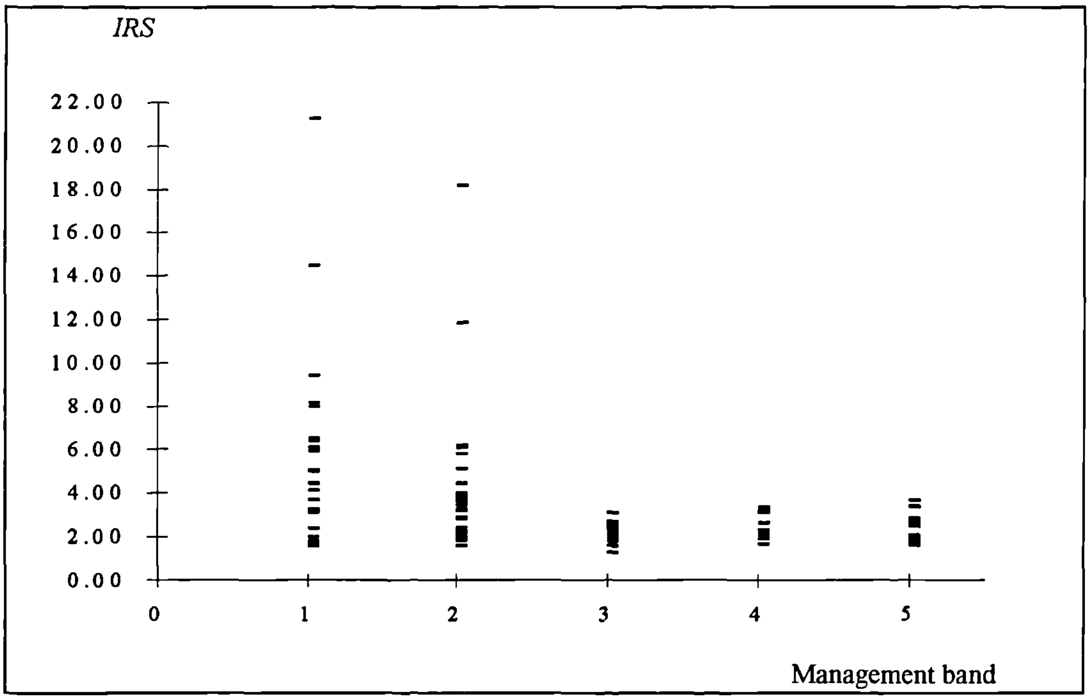

Figure 3.13. *IRS*, the Individual Rarity Scores of 110 sites in five management intensity bands.

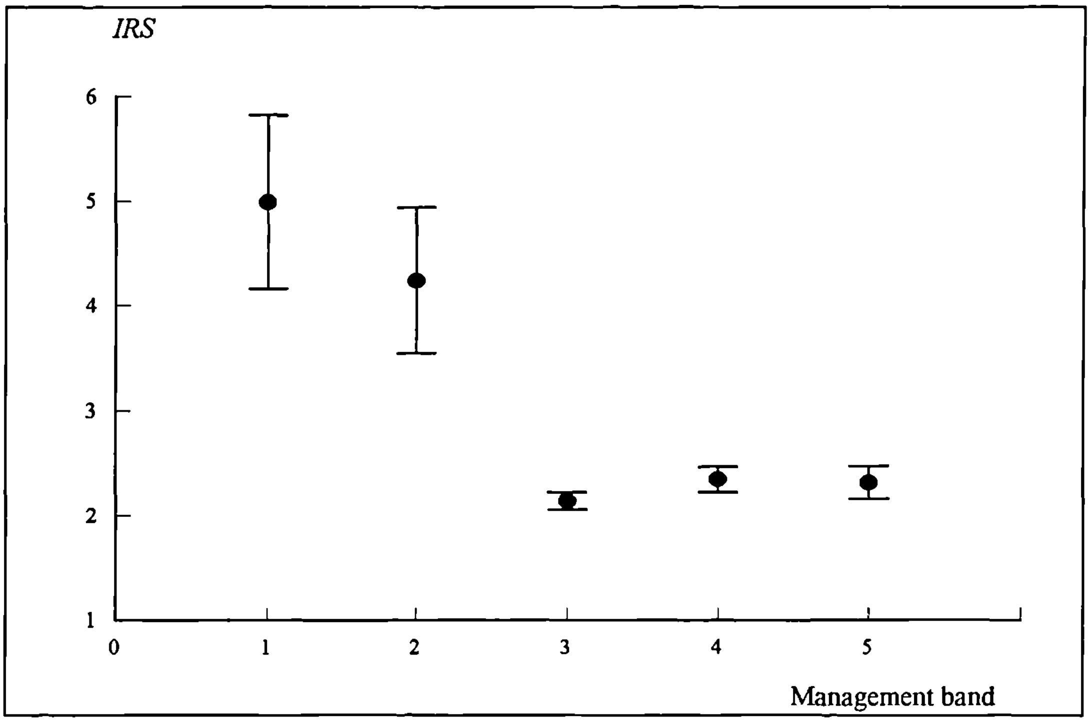

Figure 3.14. Means and standard errors of *IRS*, the Individual Rarity Scores of 110 sites in five management intensity bands.

to the presence, in large abundance, of species previously recorded from very few grid squares in Scotland - *Harpalus rubripes* at Shewalton and *Trechus secalis* at Hule Moss. It is likely that these species are simply dependent on specialised, uncommon habitat types and are locally abundant where that habitat occurs.

3.4 Body size

Body size was expressed as the Weight Median Length (*WML*), as described in Section 2.6 (Appendix 6). As with the other parameters, there was a significant difference among the management bands, in this case with a steady decline in mean *WML* as management intensity increased (Table 3.1, Figs. 3.15 and 3.16). The highest values of *WML* were found at SHEW90M1&2 (band 1, *WML* 22.6mm and 23.6mm), a wetter part of Shewalton sand-pits with rank vegetation and an abundance of the large species *Carabus nemoralis* and *C. problematicus*. Most of the lowest values were found in silage fields: ISLA93K1&2 (band 3, *WML* 7.9mm each), ISLA93M1 (band 4, *WML* 8.1mm), MUIR94C1 (band 5, *WML* 9.1mm), MUIR94D1&2 (band 4, *WML* 7.4mm and 7.1mm), KELT93C1&2 (band 5, *WML* 8.2mm and 8.4mm) and MAUC94A1 (band 5, *WML* 9.5mm).

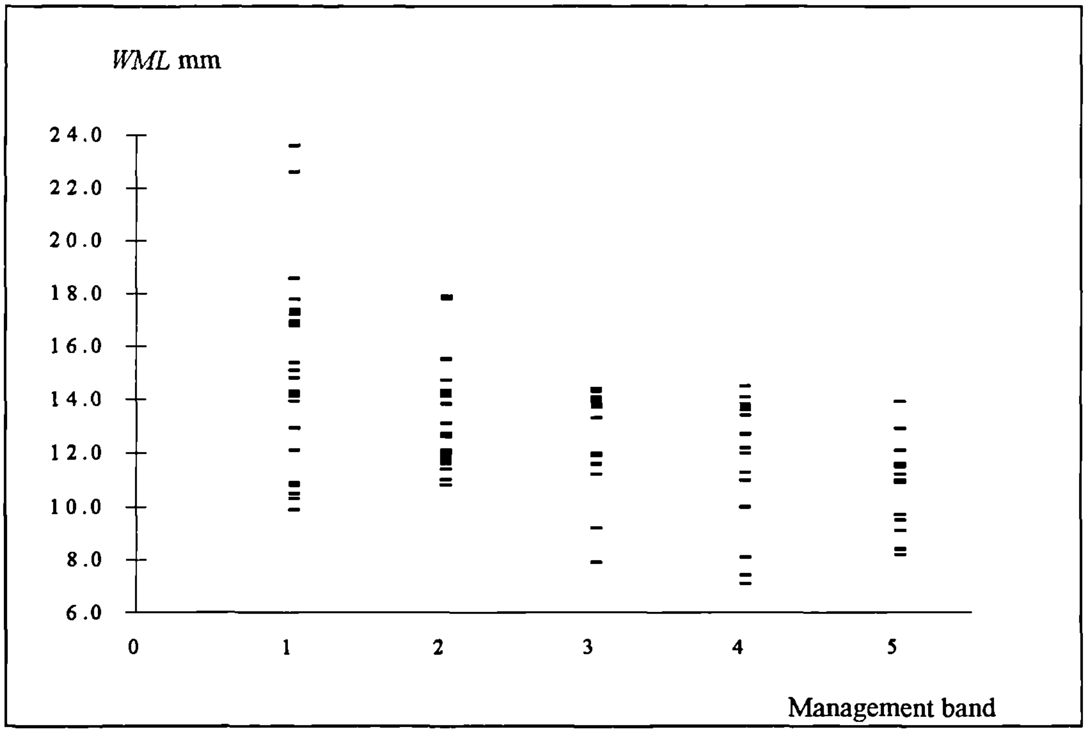

Figure 3.15. *WML*, the Weight Median Lengths of the carabid faunas of 110 sites in five management intensity bands.

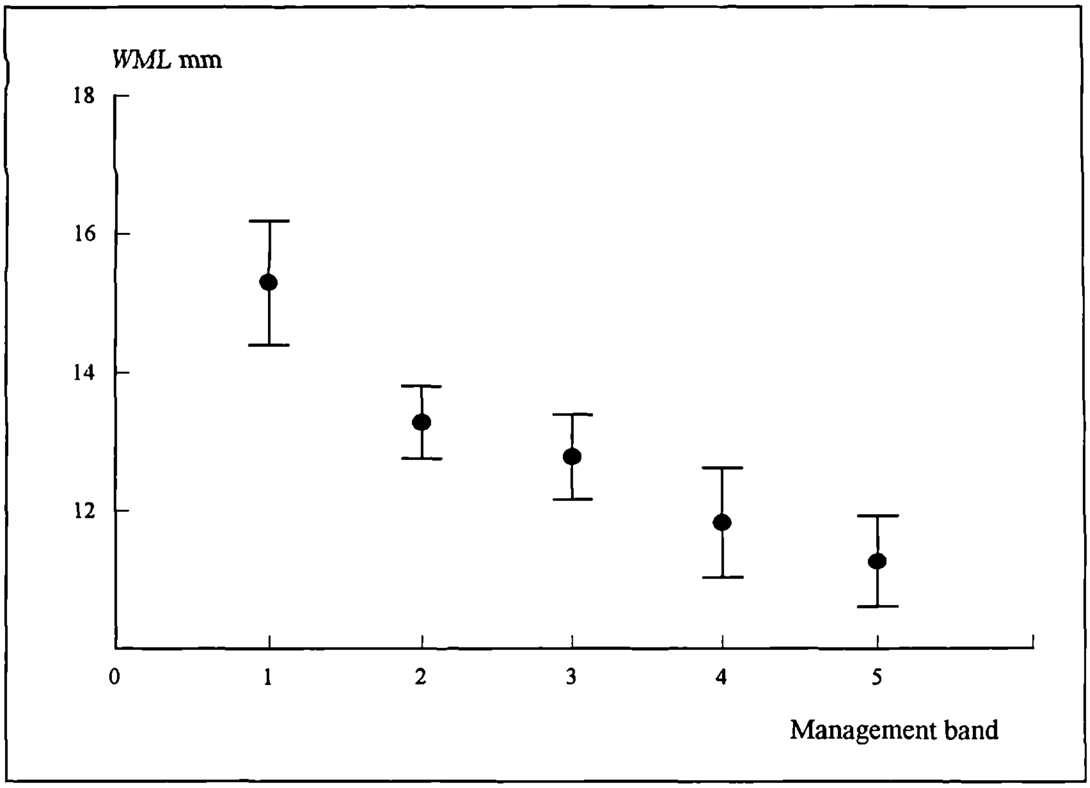

Figure 3.16. Means and standard errors of *WML*, the Weight Median Lengths of the carabid faunas of 110 sites in five management intensity bands.

3.5 Effects of the individual components of management

Six components of management were considered in assigning sites to management bands (Appendix 3): Sward type, Sward age, Cutting intensity, Grazing intensity, Inorganic inputs and Organic inputs. In order to examine which of these separate components had significant effects on species richness (*S*), diversity (*D*), Rarity (*IRS*) and Body size (*WML*) respectively, mathematical models were fitted to the data using Generalised Linear Interactive Modelling, GLIM (Baker & Nelder, 1978).

Fitting the full model (including all levels of all components) to the null model significantly reduced the deviance in every case. Each of the six components was removed from the full model in turn, the change in the deviance noted, and the significance of the change assessed by an F-test (Table 3.2). Mean values of *S, D, IRS* and *WML* were calculated for each level of each component (Table 3.3). The significance of the difference between each pair of means as the intensity of each component changed was tested by t = difference between the means / standard error of the difference (Appendix 7).

	Management component	Change in Deviance	F-statistic	p-value
S	Sward type	23.62	1.12	n.s.
	Sward age	122.50	5.82	<0.05
	Cutting	51.29	2.43	n.s.
	Grazing	248.6	11.81	<0.01
	Inorganic input	298.4	14.18	<0.01
	Organic input	334.6	15.90	<0.01
D	Sward type	0.0202	2.65	n.s.
	Sward age	0.0251	3.29	n.s.
	Cutting	0.0242	3.17	n.s.
	Grazing	0.0442	5.80	<0.05
	Inorganic input	0.0701	9.19	<0.01
	Organic input	0.1220	15.99	<0.01
IRS	Sward type	38.4	5.39	<0.05
	Sward age	54.6	7.56	<0.01
	Cutting	80.5	11.17	<0.01
	Grazing	59.8	8.29	<0.01
	Inorganic input	29.5	4.09	<0.05
	Organic input	5.5	0.77	n.s.
WML	Sward type	165.3	42.98	<0.001
	Sward age	127.0	33.02	<0.001
	Cutting	21.6	5.62	<0.05
	Grazing	28.2	7.34	<0.01
	Inorganic input	35.7	9.28	<0.01
	Organic input	29.3	7.62	<0.01

Table 3.2. The significance of the individual components of management for species richness (*S*), diversity (*D*), rarity (*IRS*) and body size (*WML*) of the carabid assemblages of 110 sites in central and southern Scotland.

	Management component	Level 0	Level 1	Level 2	Level 3	p-value
S	Sward type	21.6	22.1	18.0	17.4	n.s.
	Sward age	21.0	18.5	18.4	22.2	<0.05
	Cutting	20.8	20.9	16.6	17.0	n.s.
	Grazing	21.7	22.2	18.6	22.0	<0.01
	Inorganic input	21.4	20.0	17.8	16.8	<0.01
	Organic input	21.1	18.2	19.1	18.5	<0.01
D	Sward type	0.796	0.770	0.742	0.720	n.s.
	Sward age	0.802	0.810	0.724	0.750	n.s.
	Cutting	0.784	0.740	0.764	0.698	n.s.
	Grazing	0.814	0.771	0.751	0.755	<0.05
	Inorganic input	0.793	0.652	0.765	0.707	<0.01
	Organic input	0.780	0.646	0.804	0.738	<0.01
IRS	Sward type	4.90	3.15	2.85	2.29	<0.05
	Sward age	4.50	3.34	3.00	2.25	<0.01
	Cutting	4.21	2.40	2.14	2.31	<0.01
	Grazing	5.82	6.26	2.58	3.11	<0.01
	Inorganic input	4.13	2.04	2.25	2.37	<0.05
	Organic input	4.38	1.99	2.26	2.39	n.s.
***WML*mm**	Sward type	15.0	13.6	11.3	11.3	<0.001
	Sward age	14.3	14.0	12.0	13.5	<0.001
	Cutting	13.9	13.2	11.8	10.9	<0.05
	Grazing	15.7	13.5	12.7	12.7	<0.01
	Inorganic input	14.3	10.6	12.4	11.2	<0.01
	Organic input	14.1	10.7	12.6	12.1	<0.01

Table 3.3. Mean values of species richness (*S*), diversity (*D*), rarity (*IRS*) and body size (*WML*) according to the levels of intensity of six individual components of management, along with the significance of each component in the overall mathematical model (p-value). See Table 2.1 for explanation of Levels.

			Level 0	Level 1	Level 2
S	**Sward type**	Level 1	n.s.		
		Level 2	n.s.	$p<0.05$	
		Level 3	$p<0.05$	$p<0.01$	n.s.
	Sward age	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	n.s.	n.s.	$p<0.05$
	Cutting	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	$p<0.05$	$p<0.05$	n.s.
	Grazing	Level 1	n.s.		
		Level 2	n.s.	$p<0.05$	
		Level 3	n.s.	n.s.	$p<0.05$
	Inorganic input	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	$p<0.01$	n.s.	n.s.
	Organic input	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	n.s.	n.s.	n.s.

Table 3.4. The significance of the difference between pairs of means of species richness (*S*), for different levels of intensity of the six components of management. See Table 2.1 for explanations of Levels.

In the full model of the response to management (Table 3.2), species richness (*S*) was significantly affected by the age of the sward (F = 5.82), but even more by grazing (F = 11.81) and by nutrient inputs, both inorganic and organic (F = 14.18 and 15.90). No clear trends in mean species richness emerged with increasing levels of sward age, grazing or organic input, with means fluctuating somewhat (Tables 3.3 and 3.4), but mean species richness declined with increasing inorganic input, with a highly significant difference between level 0 (no input) and level 3. While sward type and cutting intensity were not as significant to the model as the other components, there was still a significant reduction in the means at levels 2 and 3 of sward type (grass-and-clover and grass swards) and at the highest level of cutting.

			Level 0	Level 1	Level 2
D	**Sward type**	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	n.s.	n.s.	n.s.
	Sward age	Level 1	n.s.		
		Level 2	p<0.05	p<0.05	
		Level 3	n.s.	n.s.	n.s.
	Cutting	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	p<0.05	n.s.	n.s.
	Grazing	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	n.s.	n.s.	n.s.
	Inorganic input	Level 1	p<0.01		
		Level 2	n.s.	p<0.05	
		Level 3	p<0.01	n.s.	n.s.
	Organic input	Level 1	p<0.01		
		Level 2	n.s.	p<0.01	
		Level 3	n.s.	p<0.05	p<0.05

Table 3.5. The significance of the difference between pairs of means of diversity (*D*), for different levels of intensity of the six components of management. See Table 2.1 for explanation of Levels.

Diversity as measured by *D* was affected in the full model by grazing (Table 3.2, F= 5.80) and by nutrient inputs (F = 9.19 and 15.99), with organic input again being the most important, suggesting that the effect of grazing was due to fertilisation rather than defoliation. There was no significant difference between the means at any level of sward type (Tables 3.3 and 3.5), suggesting that *D* could, potentially, be just as high in agricultural swards as in natural habitats, but there was a difference between levels 0 - 1 and level 2 of sward age. While diversity was highest in uncultivated and permanent pastures, it dropped in swards 5 to 10 years old but rose again in young swards less than 5 years old. As with species richness, there was a significant reduction in diversity between levels 0 and 3 of cutting intensity. No significant trend was apparent with levels of grazing, but diversity showed a significant drop between levels 0 and 1 of both inorganic and organic inputs, with a subsequent increase as inputs intensified. The difference between levels 0 and 1 was the difference between zero inputs and low levels of input, and in effect separated unmanaged habitats from managed ones. Generalising in terms of Huston's (1979) model, diversity appeared always to be higher in unmanaged habitats where nutrient levels and energy flow were low, resulting in a low rate of population growth, low abundances and little competitive displacement. Within managed habitats, diversity was relatively low but increased as moderate levels of nutrient input allowed recovery from disturbance, and fell again as greater input and faster growth rates allowed dominance by the superior competitors. The same process of increasing competitive displacement could also account for the lower diversity in pastures 5 to 10 years old, as compared to young swards.

In the full model of the response of rarity to management (Table 3.2), organic input was not significant but *IRS* was significantly affected by the other five components of management, especially cutting intensity (F=11.17). Rarity decreased steadily across the levels of sward type (Tables 3.3 and 3.6) but only the difference between levels 0 (semi-natural) and 3 (ryegrass) was significant.

			Level 0	Level 1	Level 2
IRS	**Sward type**	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	p<0.05	n.s.	n.s.
	Sward age	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	n.s.	n.s.	n.s.
	Cutting	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	n.s.	n.s.	n.s.
	Grazing	Level 1	n.s.		
		Level 2	p<0.05	p<0.01	
		Level 3	n.s.	p<0.01	n.s.
	Inorganic input	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	n.s.	n.s.	n.s.
	Organic input	Level 1	p<0.05		
		Level 2	p<0.05	n.s.	
		Level 3	p<0.05	n.s.	n.s.

Table 3.6. The significance of the difference between pairs of means of rarity (*IRS*), for different levels of intensity of the six components of management. See Table 2.1 for explanation of Levels.

No significant trends were found across the intensity levels for sward age, cutting intensity or inorganic input. Levels 0 and 1 together of grazing differed from levels 2 and 3, with zero or low grazing intensity sustaining a fauna of much higher rarity value than more intensive grazing. Grazing pressure affects botanical diversity, and from Table 3.3 the least botanically diverse sward (ryegrass) had the lowest rarity value. It is possible that, as with species richness and diversity, the nutrient input aspect of heavy grazing was important, rather than defoliation and botanical diversity. Sites with zero organic input (level 0) had a significantly higher rarity value than all other levels.

Body size was affected by all components of management in the full model, but overwhelmingly by sward type and age (Table 3.2, F = 42.98 and 33.02). Body size at levels 0 and 1 of sward type (semi-natural vegetation and sown wildflower swards) did not differ significantly from each other (Tables 3.3 and 3.7) and was larger than at levels 2 and 3 (grass-and-clover and ryegrass). As regards sward age, the lowest body size was found in swards 5 to 10 years old (level 2), rather than the youngest swards. This apparent anomaly may have arisen because the only swards less than 5 years old in the study were the two arable sites at Mersehead and the 16 sites at the Crichton Royal Farm in 1989; 10 of these 16 were wildflower meadows and fell into level 1 of sward type, which had a higher mean *WML* than levels 2 and 3. This degree of correlation means that caution must be used in inferring causal relationships, as two explanations could be possible: either the wildflower swards sustained larger carabids than other cultivated sward types in spite of recent cultivation; or, a proportion of the larger carabids survived for a time in the sward following cultivation, but were gone by the time the sward was more than five years old. A fuller investigation of the Crichton Royal Farm sites is presented in Section 5, but no significant difference in *WML* in the wildflower sites was found between 1989 and 1993 (Blake *et al.*, in press). The relatively high values of *WML* in level 1 of both sward type and sward age could therefore be attributed to the sward type rather than sward age. Body size fell steadily with increased intensity of cutting and grazing, but the lowest values were found at level 1 of both inorganic and organic inputs, followed by a rise as input increased.

			Level 0	Level 1	Level 2
WML	**Sward type**	Level 1	n.s.		
		Level 2	p<0.01	p<0.01	
		Level 3	p<0.01	p<0.01	n.s.
	Sward age	Level 1	n.s.		
		Level 2	p<0.05	n.s.	
		Level 3	n.s.	n.s.	p<0.05
	Cutting	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	p<0.01	p<0.05	n.s.
	Grazing	Level 1	n.s.		
		Level 2	p<0.05	n.s.	
		Level 3	n.s.	n.s.	n.s.
	Inorganic input	Level 1	p<0.01		
		Level 2	n.s.	n.s.	
		Level 3	p<0.01	n.s.	n.s.
	Organic input	Level 1	n.s.		
		Level 2	n.s.	n.s.	
		Level 3	p<0.05	n.s.	n.s.

Table 3.7. The significance of the difference between pairs of means of body size (*WML*), for different levels of intensity of the six components of management. See Table 2.1 for explanation of Levels.

3.6 Conclusions

This study of the effects of management practices on the carabid fauna was based on observation, not experiment. It was not possible to introduce controls or eliminate covariance of the parameters. For instance, sward type and sward age must be closely linked, with semi-natural swards being of necessity also old swards. Sites subjected to a high intensity of cutting are almost certain to receive high inputs of inorganic nutrients; those intensively grazed are not likely to be intensively cut. Neither was it possible to obtain reliable quantitative measurements of all of the parameters in all of the sites, since much of the study was retrospective. This being so, the aim was to see whether such imprecise, poor-quality non-quantitative data on management could be related to good-quality, standardised quantitative pitfall catch data to yield useful, ecologically meaningful information.

Several broad conclusions were possible.

Multivariate analysis of the carabid species composition resulted in a division of the sites into low-intensity and moderate-to-high intensity groups. There was also a strong division into sites with low, medium and high moisture levels, with all the high-intensity sites in the medium moisture group. The system of assigning sites to management intensity bands appeared to stand up well, with a few misclassifications explainable by the poor nature of the management data.

By contrast with the poor management data, the good quality of the pitfall catch data was suggested by the high degree of similarity between the two replicates at each site. Z-tests for differences between matched pairs found no significant difference in any of the variables derived from the pitfall data: DECORANA axis scores, log(catch), *S*, residual deviance, *D*, *IRS* or *WML*.

Three different measures of species diversity were examined: species richness, Simpson's diversity index, and the residual deviances of a regression of log(catch) on species richness. Of these, the residual was the best discriminator between management bands, giving the highest K-statistic and showing the clearest trend, changing in a relatively smooth fashion as intensity increased.

Species richness, the simplest measure, performed almost as well as the more complex diversity index, both of them separating the two lower management bands from the three higher ones. Both *S* and *D* seemed to be related more to nutrient inputs than to other components of management.

A new method of expressing the rarity value of a fauna was used, the Individual Rarity Score, which took into account the relative abundances of each species in the catch as well as their known distributions in Scotland. This provides a relatively simple way to calculate rarity scores, and can readily be updated as records improve. Rarity scores were taken from published sources as they stood, rather than being updated by new records produced in this study itself (for instance, *Trechus secalis* at Hule Moss or *Calathus cinctus* at Mersehead). It is preferable that updating of the scores should be done at intervals for the whole fauna at once, rather than piecemeal. The *IRS* decreased significantly across the management bands, clearly separating the two lower bands from the rest.

The average body size of the fauna was estimated by the Weight Median Length, a measure of the median point of the carabid biomass distribution. *WML* varied relatively smoothly with management, decreasing by almost 27% from band 1 to band 5 of management intensity. Silage fields appeared to sustain a fauna of especially small body size. The sward type and age were particularly significant to body size. This suggests that diversity of plant architecture, possibly with a proportion of taller plants, is important for the survival of larger beetles, along with a degree of long-term stability of the habitat. A fuller analysis of *WML* and its relationship with habitat type and environmental variables follows in Section 4 and is dicussed in Blake *et al.* (1994).

In general, the analysis of the carabid faunas of the 55 Scottish locations resulted in a broad division of the sites into two groups, consisting of management bands 1 and 2 in one group with high values of diversity, rarity and body size, and bands 3, 4 and 5 in the other group, with significantly lower values. These results confirm that useful information on habitat quality may be derived from broad-based, qualitative data on management practices.

4. Effects of habitat type and management intensity on the carabid assemblages of grassland, moorland and woodland in north-east England

4.1 Body size

Patterns of body size distribution are of great ecological interest and there is a large amount of literature dealing with the relationships between body size and community structure, both in general and for arthropods or Coleoptera in particular (Hutchinson & MacArthur, 1959; Schoener & Janzen, 1968; van Valen, 1973; Roff, 1981; Peters & Wassenberg, 1983; Gaston & Lawton, 1988a; Maurer & Brown, 1988; Morse *et al.*, 1988; Blackburn *et al.*, 1990, 1993; Lawton, 1990; Loreau, 1992; Currie, 1993; Stork & Blackburn, 1993). However, despite this interest in the ecological role of body size, a search of the literature revealed little quantitative information on how the average body size of carabid assemblages varied between or within different habitats, although the observation was occasionally made that larger species were more abundant in less disturbed habitats (Tietze, 1985; Šustek, 1987; Eyre, 1994).

From the point of view of conservation, particularly of grassland habitats used by breeding wading birds (Charadriiformes), it is interesting to consider whether particular management practices may serve to maximise carabid body size, because of the importance of ground beetles in the diet of many predators, especially birds (Larochelle, 1980). A good supply of large prey is important in the energy budgets of breeding wading birds (Byrkjedal, 1989; Galbraith, 1989;

Beintema *et al.*, 1990), whose best foraging strategy will be to seek a relatively small number of larger prey. The flow of energy through an ecosystem may be concentrated disproportionately in larger individuals (van Valen, 1973) and total arthropod biomass may increase with mean body size even though abundance may fall (Stork & Blackburn, 1993). All of this implies that the availability of energy for predators should increase along with the average body size of their prey. The first aim of this analysis of pitfall catch data from moorland, woodland and grassland sites in north-east England was to determine whether any patterns relating body size to habitat type and management practices could be detected, and to devise a quantitative method of describing them.

4.1.1 Weight median length and habitat type

Data were provided from pitfall trapping projects in north-east England between 1985 and 1991. Sites included coniferous and deciduous woodland, moorland and both improved and unimproved grassland. Sampling took place between April and October, some sites only once and others in two or more successive years. In all cases, lines of nine traps were set and catches pooled to give an annual total for each site. For the purposes of the analysis of body size, the results from repeated samples were combined to give a total of 98 sites: 9 moorland, 39 woodland and 50 grassland. Environmental data available for grassland and moorland sites were: soil density; volumetric soil water content; the proportions of sand and organic matter in the soil; altitude; annual rainfall; vegetation height in centimetres on a scale of 1 to 6 (1-2, 3-5, 6-10, 11-20, 21-50, >50cm); and a management rating on a scale of 1 to 5 (1 the least intensively managed), taking account of the age of the pasture, the intensity and duration of grazing and the level of fertiliser and pesticide inputs (Luff *et al.*, 1990). For woodland sites, the variables measured were: volumetric soil water; organic matter content; altitude; and litter depth. Some data were missing for eight of the ninety-eight sites, so that altitude was the only variable which was measured for all sites.

A mean body length figure for each species in the data set was obtained from the taxonomic literature (Lindroth, 1974). Since the distribution of mean body length was found to be bimodal rather than normal for most sites, the average body length for the site was more appropriately expressed as the median rather than the mean. Values for the Number Median Length (*NML*) and Weight Median Length (*WML*), which is the median point of the biomass distribution, were calculated for each site as described in Section 2.6.

The relationship between *NML* and *WML* is shown in Figure 4.1. For many sites the difference between the two statistics was small, although WML was generally higher, and either *NML* or *WML* could be used as a meaningful measure of body size. At other sites, the two medians diverged widely, especially at small values of *NML*. The higher values of *WML* were due to the presence of relatively small numbers of larger species in the catch. For example, three sites in Figure 4.1 all had *NML* of 9.5mm. One of these had *WML* of 10.6mm and no carabids over 20mm in length, while the other two had *WML*s of 23.1mm and 24.1mm, and 12% and 31% of the catch was over 20mm, respectively. Overall, *WML* was correlated with the proportion of the catch over 20mm ($r_S = 0.699$, $n = 98$, $p < 0.001$) while *NML* was not ($r_S = 0.171$). Weight median length reflected

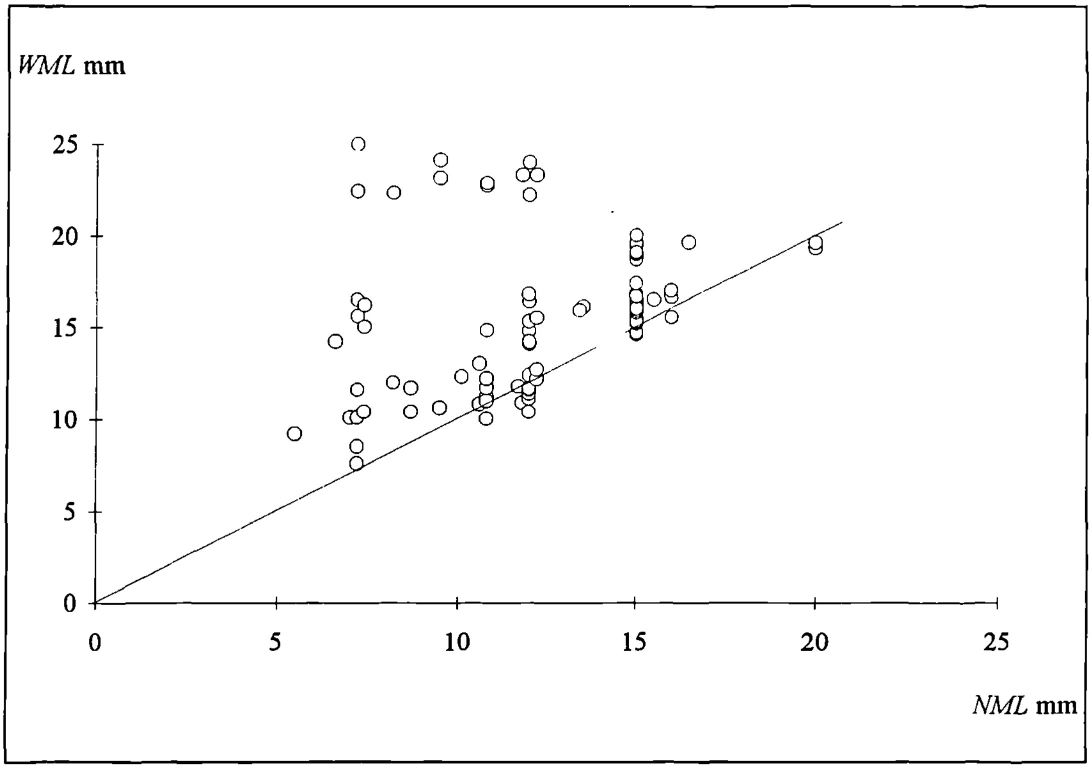

Figure 4.1. The relationship between Number Median Length (*NML*) and Weight Median Length (*WML*) of 98 carabid assemblages in north-east England.

the presence of larger beetles while *NML* did not; it was felt, therefore, that *WML* was more sensitive to changes in the distribution and range of body lengths, and it was taken as the preferred statistic for comparisons between sites.

Weight median length varied according to habitat type (Table 4.1). A significant difference in *WML* was found between grassland and moorland, a very highly significant difference between grassland and woodland, but no significant difference between woodland and moorland. Mean *WML* for grassland sites was 13.4mm, and for woodland and moorland combined, 17.9mm. This meant that the body weight of the median carabid was 28.9mg in grassland, and 62.1mg in wood and moorland, an increase of 115%. The only other correlation which could

Mann-Whitney U-test	**W**	**p**
Grassland: Woodland n = 50 n = 39	2473.5	< 0.001
Grassland:Moorland n = 50 n = 9	1389.5	< 0.05
Moorland: Woodland n = 9 n = 39	920.0	n.s.
Spearman's correlation	r_s	**p**
WML: Habitat type n = 98	0.596	< 0.001

Table 4.1. The relationships of Weight Median Length (*WML*) with habitat types at 50 grassland, 39 woodland and 9 moorland sites. See text for derivation of *WML*.

	r_s	**n**	**p**
WML: Management	-0.629	50	< 0.001
WML: Soil water	-0.434	50	< 0.01
WML: Altitude	-0.341	50	< 0.05
WML: Organic matter	-0.314	50	< 0.05
WML: Sward height	0.464	46	< 0.01
Management: Soil water	0.293	50	< 0.05
Management: Altitude	0.460	50	< 0.01
Management: Sward height	-0.734	46	< 0.001
Soil water: Altitude	0.381	50	< 0.01

Table 4.2. Results of Spearman's rank order correlation tests for correlations between *WML* and environmental variables, at 50 grassland sites. See text for derivation of *WML*. Variables: management intensity on a scale 1 to 5; volumetric soil water content; altitude above sea level; % soil organic matter content; sward height on a scale of 1 to 6.

be sought for the entire data set was between *WML* and altitude, which was not significant.

Spearman's correlation coefficient was derived for *WML* and the four environmental variables measured at woodland sites (soil water, organic matter, altitude and litter depth), when necessary omitting sites where data were incomplete. Only the correlation with organic matter content was significant at $p < 0.05$ ($r_S = 0.366$, $n = 35$). No significant correlations were found between *WML* and any of the environmental variables measured at the moorland sites.

4.1.2 Weight median length and grassland management

Significant Spearman's correlations were found between *WML* and some of the eight environmental variables measured at grassland sites (Table 4.2). The median body size of carabids decreased as management intensity, soil water, organic matter and altitude all increased, and as sward height decreased. However, in this particular dataset, there was a very highly significant correlation of management with altitude; of the 22 sites in management classes 1 and 2 (low intensity), only one was at altitude over 150m, whereas half of the 20 high-intensity sites in classes 4 and 5 were at 240m or over. Soil water, organic matter, altitude, sward height and management levels were all interrelated. It seemed nonetheless that carabid body size was most significantly related to intensity of pasture management, the largest median size occurring at the lowest level of management.

Generalised Linear Interactive Modelling (GLIM - Baker & Nelder, 1978) analysis of all 50 grassland sites found that the coefficient relating *WML* to soil density was not significantly different from zero (Table 4.3), but linear relationships were found with soil water, organic content, and altitude:

WML = 17.04 - (0.073 x volumetric soil water)

WML = 14.71 - (0.046 x organic matter)

WML = 14.73 - (0.011 x altitude)

Constant term	**s.e. of constant**	**Coefficient of slope**	**s.e. of coefficient**	**Variable**
11.87	0.993	1.65	0.98100	Soil density
17.04	1.145	-0.073	0.02170	Water content
14.71	0.520	-0.046	0.01310	Organic matter
14.73	0.621	-0.011	0.00416	Altitude

Table 4.3. GLIM (Generalised Linear Interactive Modelling) analysis of the response of weight median length (*WML*) of carabid assemblages to environmental variables at 50 grassland sites. See text for derivation of *WML*. Variables: Soil bulk density; volumetric soil water content; % soil organic matter content; altitude above sea level

Management band	**1**	**2**	**3**	**4**	**5**
Mean *WML*, mm	15.6	12.1	13.6	13.2	11.1
s.d.	2.83	2.25	2.16	1.54	1.82
n	18	5	7	6	14

Table 4.4. Mean & standard deviation of weight median length (*WML*) of carabid assemblages at 50 grassland sites, by management intensity band. See text for derivation of *WML*. Intensity of management increases from level 1 to 5, as assessed by sward age, grazing regime and artificial inputs. n = number of sites in each management intensity band.

As before, the most significant relationship was that between *WML* and management intensity, giving a decrease in the deviance of the model of 168.6 units. Mean *WML* decreased from 15.6mm at management band 1 to 11.1mm at management band 5 (Table 4.4).

Models were fitted for each of the five management levels interactively with each of the three variables, soil water, organic matter and altitude. In every case, the value of the coefficient of the slope was not significantly different for the five management levels, therefore it was reasonable to re-fit the models with the slopes constrained to be the same for every level. This resulted in five different models for each variable, with the same coefficient of slope but a different constant for each management level. Only the coefficient for organic content was significantly different from zero (Table 4.5), meaning that both soil water and altitude could be neglected when modelling the response of carabid body size to management, but organic matter content must be accommodated by the relationship:

$$WML = C - (0.03 \times \text{organic matter})$$

where C is the constant term appropriate for each of the five management levels (Table 4.6).

Coefficient of slope	**s.e. of coefficient**	**Variable**
-0.036	0.0209	Soil water
-0.030	0.0121	Organic matter
-0.0024	0.00433	Altitude

Table 4.5. Coefficients of slope (c.s.) and the standard error of the coefficient (s.e.), for three variables (volumetric soil water content, % soil organic matter content, altitude above sea level) in the general relationship: *WML* = C + (c.s. x variable), where C is the relevant constant term.

Management intensity band	**Constant term**	**s.e. of constant term**	**Model**
1	16.14	0.563	*WML* = 16.14 - 0.03 x organic
2	12.91	1.105	*WML* = 12.91 - 0.03 x organic
3	14.65	0.989	*WML* = 14.65 - 0.03 x organic
4	13.62	1.030	*WML* = 13.62 - 0.03 x organic
5	12.41	0.833	*WML* = 12.41 -0.03 x organic

Table 4.6. Linear models of carabid weight median length (*WML*) at 50 grassland sites of five different levels of management intensity, as assessed by sward age, grazing regime and artificial inputs, level 5 being the highest intensity. See text for derivation of *WML*. Organic: % soil organic matter content.

4.1.3 Discussion

The general conclusions to be drawn from the foregoing analysis were that carabid body size was greater in woodland or moorland habitats than in grassland, and that within grassland, carabid body size decreased as management intensity increased.

The largest values of *WML* were found in moorland and were in large part due to a high proportion of large *Carabus* species, especially *C. glabratus* and *C. problematicus*. *C. glabratus* occurred only in four moorland and one woodland site and not in any type of grassland, and is important as an indicator species for the moorland habitat type. The distinction between woodland and grassland was also linked to the distribution of *Carabus* species, in this case mainly *C. problematicus* and *C. violaceus*. At least one species of *Carabus*, 24mm or over, occurred on 82% of the woodland sites and on 48% of the grassland sites. These 48% of the grassland sites included 17 of the 23 in management classes 1 and 2 but only 4 of the 20 sites in classes 4 and 5. These four were all upland sites, at altitudes between 240m and 320m. The fauna of the improved grassland sites was dominated almost without exception by *Nebria brevicollis* (12mm) and *Loricera pilicornis* (7.2mm), both highly invasive species. Also common were *Amara communis* (7mm), *Calathus melanocephalus* (7.4mm) and, especially on sites cut for silage, the small *Bembidion aeneum* (4mm) and *Trechus quadristriatus* (3.8mm). The only carabids over 15mm commonly occurring in improved grassland were the very widespread *Pterostichus melanarius* and *P. madidus*. By contrast, *N. brevicollis* and *L. pilicornis* were relatively scarce on unimproved sites, which, besides the large *Carabus* species, also had a greater range of *Pterostichus* species.

The observation that larger *Pterostichus* and *Carabus* species prefer less disturbed habitats is not a new one, and numerous analyses have suggested that carabid assemblages are sensitive to increased intensity of grassland management. Šustek (1987) found that disturbance by urbanisation displaced the carabid body size distribution curve towards smaller size. Tietze (1985) found that, after ten years of intensified management of a grassland in Russia, carabid diversity overall had decreased but large species such as *Carabus* spp. and *P. niger* were especially badly affected. Eyre and Luff (1990) analysed pitfall data from 363 British grassland sites and found intensity of management an important factor affecting species assemblage distribution. Ordination of the carabid assemblages of upland grassland sites in north-east England (Rushton *et al.*, 1989) separated the sites into improved and unimproved groups. Two of the sites in the 'unimproved' group had received artificial inputs but had not been cultivated. *C. problematicus* and *P. niger* were identified as indicators of the unimproved condition.

Eyre (1994) examined pitfall data from 160 grassland, moorland and woodland sites and found a good correlation between species incidence and a disturbance index generated from several environmental variables. Twelve species were associated with high disturbance and had a mean body length of 8.0mm; 24 mid-disturbance species had mean body length 8.2mm; 13 species preferring low-disturbance sites had a mean body length of 13.6mm. From this, it seems that an important factor determining the distribution of large carabids is the degree of disturbance, particularly of the soil. The largest values of *WML* were found in woodland and moorland not because these habitats necessarily sustain a different species assemblage from the surrounding grasslands, but because they suffer less disturbance (Eyre & Luff, 1994).

The question remains as to why disturbance should be more detrimental to larger species of ground beetle than to smaller ones. It may be expected that habitats of low primary productivity would favour smaller body size (Šustek, 1987), but intensively managed grasslands are essentially areas of high primary production in which the primary output is not necessarily available to the higher trophic levels.

Disturbed agricultural ecosystems undergo pronounced fluctuations in their total energy values. Inputs of energy from fertiliser can be very large and virtually instantaneous. Cutting for hay or silage constitutes a catastrophic loss of energy to the system, but even in permanent pasture the extra fertiliser energy is rapidly converted to livestock biomass which is removed from the system at the end of the grazing season. A short-lived energy source favours small body size (Schoener & Janzen, 1968). A fluctuating energy source is more easily exploited by species which are widespread, dispersive and able to sustain wide fluctuations in their population numbers, and such species are more likely to be small (Gaston & Lawton, 1988a). Larger body size implies a longer development time in order to accumulate the larger proportion of community resources referred to by van Valen (1973). Large carabids are predominantly autumn breeders with overwintering larvae (Kegel, 1990), while smaller species often breed in the spring and have fast-growing larvae active in the summer. In addition, adults of some large species may overwinter and breed in a second or subsequent season, while small species seldom do so. A longer life-cycle, particularly a longer larval period, requires a degree of stability of resources over time which is lacking in intensively managed habitats.

Fluctuating resources are more readily utilised by species with a capacity both for rapid growth and for wide dispersal. The development of functional wings is highly variable among the carabids as a whole, some species being monomorphically macropterous, some brachypterous, and others dimorphic as regards wing development. Larger species, in particular almost all *Carabus*, tend to be flightless. Liebherr (1988) found that body size was more likely to increase over evolutionary time in carabid taxa containing brachypterous forms and that large, short-winged taxa tended to be found in stable, favourable habitats. Both den Boer (1970) and Eyre (1994) observed that flightless species were often restricted to localised, stable sites. While large flightless carabids may cover large distances by walking, their dispersal powers are limited in a fragmented landscape which may be a mosaic of cultivation, improved pasture and heath or woodland. Den Boer (1970, 1990) noted that the survival of local carabid populations relied on dispersal, and concluded that the fragmentation of natural habitats would increase the isolation of local groups with low dispersal power and greatly accelerate their extinction.

Habitat type and management level (which together could be represented by disturbance level) were the most important factors affecting *WML*, the only other environmental variable which significantly affected the model being the organic matter content of the soil, which was significant in both woodland and grassland. In woodland, increasing organic matter was linked to increasing WML, while in grassland the correlation was negative. This suggests that soil organic matter is not a determinant of carabid body size *per se,* but is linked in an indirect manner. In woodland, the chief source of organic matter in the soil is likely to be from decaying plant material and it may be that a high organic matter content is an indication of an older, less disturbed woodland, suitable for larger species. In grassland, a major source of organic matter is animal waste, either from grazing livestock or from farmyard manure, and this would constitute a further energy fluctuation in the system, favouring smaller size.

The general result from this analysis, that the degree of disturbance and intensity of grassland management are the most important factors affecting ground beetle body size, has profound implications from the point of view of conservation, especially of wading birds and other species preying on carabids.

The statistic *WML* provides a means of quantitatively describing carabid biomass distribution and could be adapted for other groups or situations. The numerical value of *WML* for any particular site may have little ecological meaning, but changes in *WML* between sites or over time could reveal important trends and patterns in the body size of the fauna.

4.2 Species richness and diversity

The species diversity of the carabid assemblages was described by two parameters: *S*, the species richness, and *D*, the complement of Simpson's index of diversity (Simpson, 1949) as described in Section 2.4. *D* is less sensitive to sample size than *S*, and is influenced by the more abundant species in the sample, while *S* varies between samples according to the number of rarer species taken. A description of diversity should ideally include both components.

Since sampling effort has a bearing on the values of both *S* and *D*, repeated samples in the data set were not combined, giving 61 grassland sites, 11 moorland and 41 woodland.

4.2.1. Habitat type and diversity

A regression of the log-transformed number of individuals taken against the number of species (Fig. 4.2) gave a highly significant linear relationship, Log(catch) = $3.760 + 0.0949S$ ($t = 6.086$, d.f. $=111$). The distance of a particular point from the regression line is indicative of the relative species-richness of the site, in that sites with a high positive residual deviance have fewer species than expected for the sample size, and those with a high negative residual have more species (Luff, in prep.). The 113 sites in the regression appeared to be well distributed on either side, with little distinction between habitat types. Seven of the 11 moorland sites, 20 of the 41 woodland sites and 36 of the 61 grassland sites had negative residuals. However, the ten largest positive residuals (i.e. relatively species-poor assemblages) were all woodland sites. Although the sample size was rather small to reach firm conclusions, the moorland sites

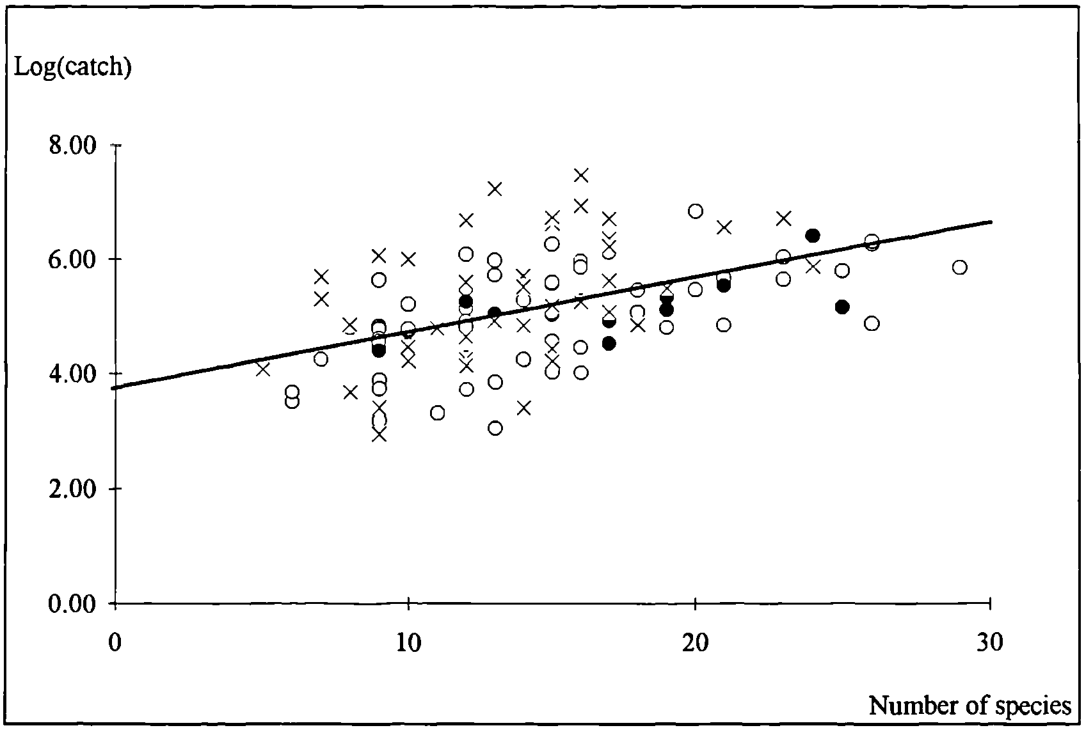

Figure 4.2. Linear regression of the natural logarithm of the number of individuals on the number of species (*S*) taken at 113 sites of three habitat types. The regression equation is: Log(catch) = 3.760 + 0.0949*S*.

○ Grassland

● Moorland

× Woodland

appeared on the whole to deviate less from the regression line than the other sites, possibly suggesting a more uniform community structure.

The woodland sites also had the lowest mean value of *S* (Table 4.7) while moorland had the highest values of both *S* and *D*. Moorland was significantly more species-rich than woodland and more diverse than both woodland and grassland (Table 4.8).

	Grassland n = 61	Moorland n = 11	Woodland n = 41
S	14.5	18.0	13.6
D	0.6819	0.8066	0.6978

Table 4.7. Means of species richness (S) and diversity (D) of the carabid assemblages at 113 sites of three habitat types.

S		Grassland n = 61	Moorland n = 11
	Grassland n = 61		
	Moorland n = 11	3.46/1.985 =1.743	
	Woodland n = 41	0.93/1.505 =0.618	**4.39/1.704 =2.576**
D		Grassland n = 62	Moorland n = 11
	Grassland n = 61		
	Moorland n = 11	**0.125/0.0586 =2.133**	
	Woodland n = 41	0.016/0.0445 =0.360	**0.109/0.0503 =2.167**

Table 4.8. The significance of the difference between pairs of means of species richness (*S*) and diversity (*D*) as tested by t = difference between the means / standard error of the difference. Entries in **bold** are statistically significant.

4.2.2. Grassland management and diversity

The 61 grassland sites had been classified into five management bands according to sward age, grazing and cutting intensity and inputs of fertiliser and pesticides. This classification differed from that applied to the Scottish sites in the present study by taking no account of sward type and by including pesticide applications.

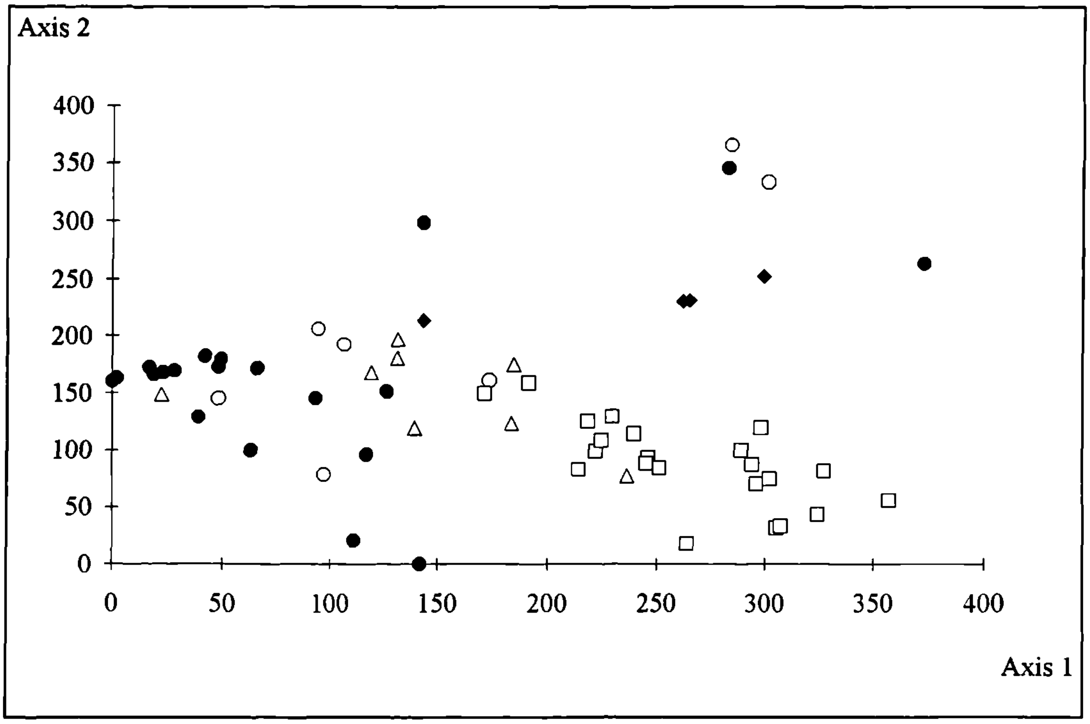

Figure 4.3. The first two axes of the DECORANA ordination of the carabid assemblages of 61 grassland sites in north-east England.

● Management band 1

◆ Management band 2

○ Management band 3

Δ Management band 4

□ Management band 5

The pitfall catch data were transformed to percentages of the total catch for each site and the 61 sites were ordinated by detrended correspondence analysis. Both axes had good explanatory value, with eigenvalues of 0.620 and 0.426 respectively (Appendix 8). The ordination appeared to separate the sites into three groups (Fig. 4.3). The high-intensity band 5 sites were concentrated towards a position high on the first axis and low on the second axis, while the low-intensity band 1 and 2 sites were mostly in the lower half of both axes. From the ordination of the species scores (Appendix 9, Fig. 4.4), this group of sites was associated with species preferring dry conditions. A third group of some seven low-to-moderate intensity sites occupied a relatively high position on both axes and appeared to be associated with species of wetter habitats. The three sites positioned highest on the second axis were Prestwick Carr Marsh (band 1, described as marsh on peat), Prestwick Carr Meadow (band 3, *Juncus* on peat) and Prestwick Carr Pasture (band 3, rough grazing). The second axis was therefore probably related to moisture or to vegetation conditions, while the major axis was more clearly related to management intensity. Classification of the sites by TWINSPAN confirmed the importance of management, one half of the first division containing all 22 band 5 sites, along with nine from bands 2 to 4, and only one from band 1, Preston Carr Marsh. If the second axis is to be interpreted as related to moisture, then intensification of management was associated with drier conditions.

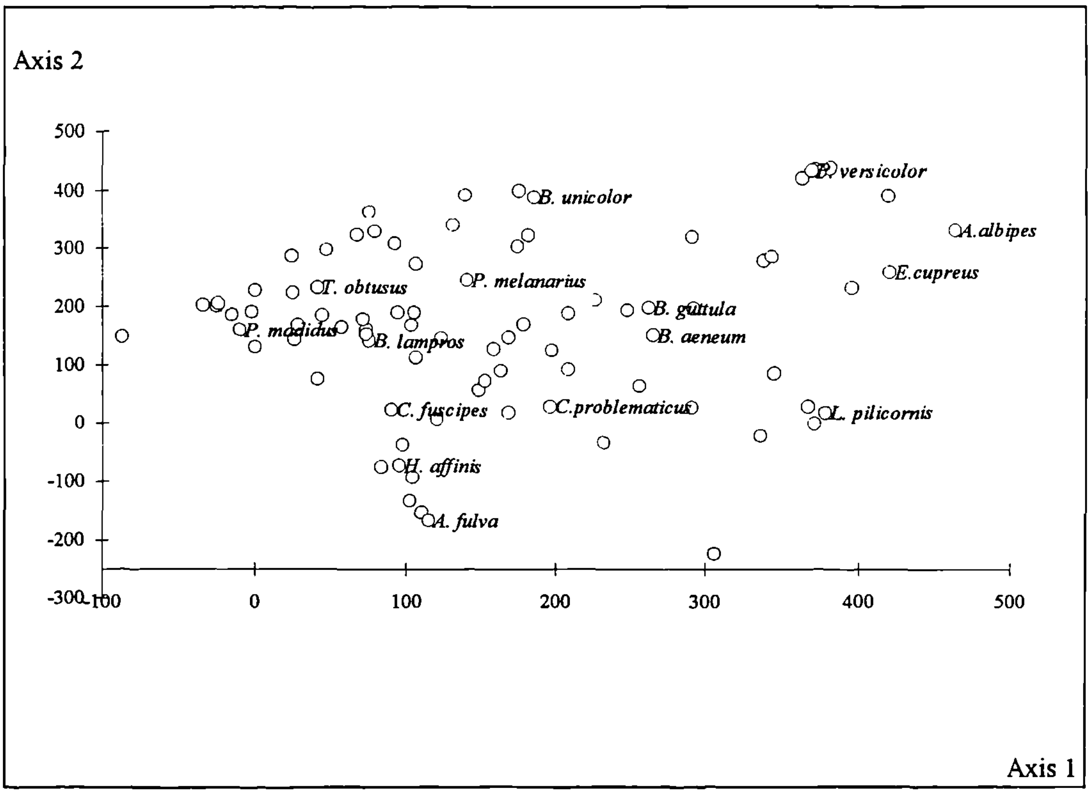

Figure 4.4. DECORANA ordination of the carabid species scores of 61 grassland sites, showing indicator species.

Regression of the natural logarithm of the number of individuals in the catch on the number of species (Fig. 4.5) produced a highly significant linear relationship, log(catch) = 3.645 + 0.0914S (t = 5.398, 59 d.f.). However, there was no clear difference in the size or sign of the residual deviances between management bands, with all bands being more or less evenly scattered on either side of the regression line. There was a suggestion that high-intensity sites were less species-rich, being almost confined to the lower end of the species axis; however, since almost equal numbers were above and below the regression line, this species-poorness was not necessarily indicative of low diversity. This was

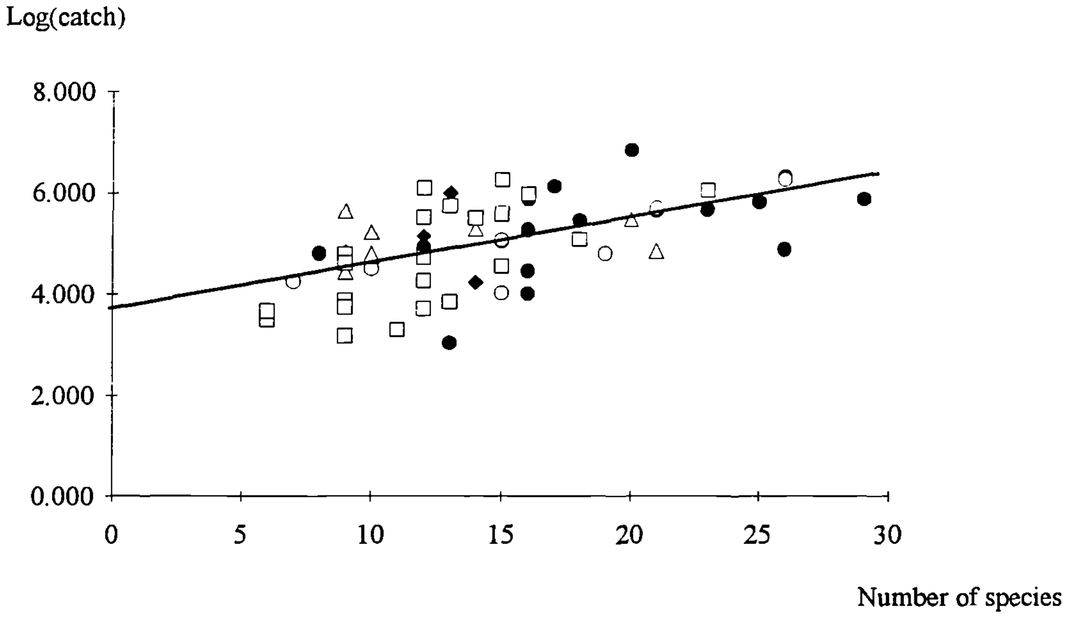

Figure 4.5. Linear regression of the natural logarithm of the number of individuals on the number of species (*S*) taken at 61 grassland sites in 5 management bands.
The regression equation is: Log(catch) = 3.645 + 0.0914*S*.

● Management band 1

◆ Management band 2

○ Management band 3

△ Management band 4

□ Management band 5

	Management band 1 n = 20	Management band 2 n = 4	Management band 3 n = 7	Management band 4 n = 8	Management band 5 n = 22
S	17.6	12.0	16.1	12.9	12.3
D	0.6587	0.7253	0.7244	0.6561	0.6911

Table 4.9. Means of species richness (S) and diversity (D) of the carabid assemblages at 61 grassland sites in 5 management intensity bands.

S		Band 1 n = 20	Band 2 n = 4	Band 3 n = 7	Band 4 n = 8
	Band 1 n = 20				
	Band 2 n = 5	5.6/3.364 =1.665			
	Band 3 n = 7	1.5/2.937 =0.511	-4.1/3.144 =-1.304		
	Band 4 n = 8	4.8/2.859 =1.679	-0.88/3.071 =-0.287	3.3/2.596 =1.271	
	Band 5 n = 22	**5.4/2.485 =2.173**	-0.27/2.726 =-0.099	3.8/2.176 =1.746	0.6/2.071 =0.290
D		Band 1 n = 20	Band 2 n = 4	Band 3 n = 7	Band 4 n = 8
	Band 1 n = 20				
	Band 2 n = 5	-0.066/0.1144 =-0.577			
	Band 3 n = 7	-0.065/0.0998 =-0.651	0.001/0.1069 =0.009		
	Band 4 n = 8	0.002/0.0972 =0.021	0.069/0.1044 =0.661	0.068/0.0882 =0.771	
	Band 5 n = 22	-0.032/0.0845 =-0.379	0.034/0.0927 =0.367	0.033/0.0740 =0.446	-0.035/0.0704 =-0.497

Table 4.10. The significance of the difference between pairs of means of species richness (*S*) and diversity (*D*) as tested by *t* = difference between the means / standard error of the difference. Entries in **bold** are statistically significant.

borne out by examination of the means for the five management bands (Table 4.9), band 5 having a significantly lower mean number of species than band 1, but with no difference in mean values of D (Table 4.10). The low numbers of sites in bands 2, 3 and 4 meant that it would be impossible to reach any meaningful conclusions about their relative values, but in any case there were no significant differences between their means. The relatively high value of S for band 3 was due to two sites, Close House Golf (26 species) and Prestwick Carr Meadow (21 species).

4.2.3. Conclusions

The moorland habitat emerged as quite distinct from both grassland and woodland in terms of its greater species richness and diversity while no differences were found between grassland and woodland. The woodland carabid fauna in Britain may be considered to be a subset of the fauna of surrounding habitats (Eyre & Luff, 1994), which implies that it ought to be impoverished compared with neighbouring habitats. This analysis found that the woodland faunas were certainly species-poor and less diverse compared with moorland, which would be the natural surrounding habitat. By implication, the grassland habitats were also impoverished in comparison with natural conditions.

The species composition of the carabid fauna changed as the intensity of grassland management increased. At the highest level of intensification, there was a significant loss of species richness. The lowest level of management sustained a fauna no less species-rich than the moorland sites (mean S = 17.6 and 18.0 respectively), although less diverse in terms of D (0.6587 and 0.8066). This lower value of D for similar values of S would suggest a less even, more concentrated fauna in low-intensity grassland than in moorland, with dominance by one or a few abundant species. This dominance could be related to increased rates of population growth due to the greater nutrient availability of improved land. In due course, as nutrient input increased further and populations continued to grow, the more competitive species would increase in abundance to the point where competitive exclusion could begin to operate, resulting in the reduced numbers of species found at the highest intensity of management.

5. Effects of sward type and management practices on the carabid assemblages of grassland in southern Scotland

5.1 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.

5.2 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.*, 1994). 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, 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 5.1). 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.

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	-	-	-	-

Table 5.1. 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 (+++).

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 and monthly catches were pooled to give two replicate totals for each site in each year. Species totals were converted to percentages and the sites classified by Two-Way Indicator Species Analysis, TWINSPAN (Hill, 1979b), and ordinated by Detrended Correspondence Analysis, DECORANA (Hill, 1979a). Species nomenclature followed Pope (1977) and the habitat preferences of the species were established from the literature (e.g. Lindroth, 1974; Eyre, 1993 unpublished report).

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 species 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, 1964a) as well as to the size of the area being sampled (Williams, 1943). 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) as described in Section 2.4.

Rarity values of the sites were expressed as the Individual Rarity Score (*IRS*), which was calculated for each assemblage as described in Section 2.5.

A further parameter which was calculated for the carabid fauna of each site was the Weight Median Length, *WML*, (Section 2.6) 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).

5.3 *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. The number of species taken in each set of traps, *S*, was lowest at the unmanaged Caerlaverock and highest in the wildflower swards (Table 5.2). The differences across all three sward types were highly significant (Table 5.3). 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 relatively 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.

Site and Year	***WML***	***S***	***D***	***IRS***
Wildflower swards				
Bungalow Slurry A 1989	14.4	23	0.842	2.12
Bungalow Slurry B 1989	14.4	23	0.856	2.09
Bungalow Slurry A 1993	14.1	23	0.729	2.60
Bungalow Slurry B 1993	14.1	21	0.776	2.70
Bungalow No Slurry A 1989	14.0	21	0.687	1.84
Bungalow No Slurry B 1989	14.0	21	0.693	1.88
Bungalow No Slurry A 1993	14.4	26	0.754	2.41
Bungalow No Slurry B 1993	14.4	24	0.751	2.90
Lochbank One-cut A 1989	14.3	23	0.802	1.79
Lochbank One-cut B 1989	13.7	24	0.819	2.03
Lochbank One-cut A 1993	13.9	21	0.713	2.18
Lochbank One-cut B 1993	13.9	22	0.790	2.01
Lochbank Two-cut A 1989	13.8	22	0.500	1.91
Lochbank Two-cut B 1989	13.9	18	0.640	1.88
Lochbank Two-cut A 1993	14.1	22	0.803	2.06
Lochbank Two-cut B 1993	14.2	21	0.707	2.17
Wet Lochbank A 1989	13.3	25	0.877	3.10
Wet Lochbank B 1989	14.3	24	0.826	2.60
Wet Lochbank A 1993	11.9	18	0.824	2.01
Wet Lochbank B 1993	11.8	25	0.880	2.81
Median	**14.05**	**22.5**	**0.783**	**2.10**
Grasses				
Acrehead Clover A 1989	12.7	20	0.842	2.31
Acrehead Clover B 1989	13.8	17	0.818	2.22
Acrehead Clover A 1993	13.6	20	0.685	3.15
Acrehead Clover B 1993	13.4	19	0.676	3.11
Acrehead Ryegrass A 1989	14.1	21	0.740	2.23
Acrehead Ryegrass B 1989	14.5	23	0.768	1.95
Acrehead Ryegrass A 1993	13.7	20	0.688	3.38
Acrehead Ryegrass B 1993	13.8	23	0.620	3.28
Netherwood Ryegrass A 1989	12.9	17	0.540	1.75
Netherwood Ryegrass B 1989	13.9	20	0.495	1.80
Netherwood Ryegrass A 1993	13.9	19	0.677	2.76
Netherwood Ryegrass B 1993	13.9	22	0.678	2.86
Median	**13.80**	**20.0**	**0.682**	**2.53**
Unmanaged				
Caerlaverock NNR A 1989	17.4	15	0.860	2.00
Caerlaverock NNR B 1989	17.4	15	0.824	1.82
Caerlaverock NNR A 1993	18.6	16	0.879	3.12
Caerlaverock NNR B 1993	17.8	15	0.827	1.57
Median	**17.60**	**15.0**	**0.844**	**1.91**

Table 5.2. Weight Median Length (*WML*) in mm, species richness (*S*), diversity (*D*) and rarity (*IRS*) of the carabid faunas of nine sites (two replicates per site) in 1989 and 1993, along with the median values for each sward type.

	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.

Table 5.3. Summary of results of Mann-Whitney tests for significant differences in median values of body size (*WML*), species richness (*S*), diversity (*D*) and rarity (*IRS*) across three sward types.

	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

Table 5.4. 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.

Ordination of the first two DECORANA axes of the site scores (Appendix 10, Fig. 5.1) 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 with diversity (Table 5.4, p <0.01) and with rarity (p < 0.05) and Axis 2 was correlated with rarity (p < 0.01). No correlations were found between any of the parameters.

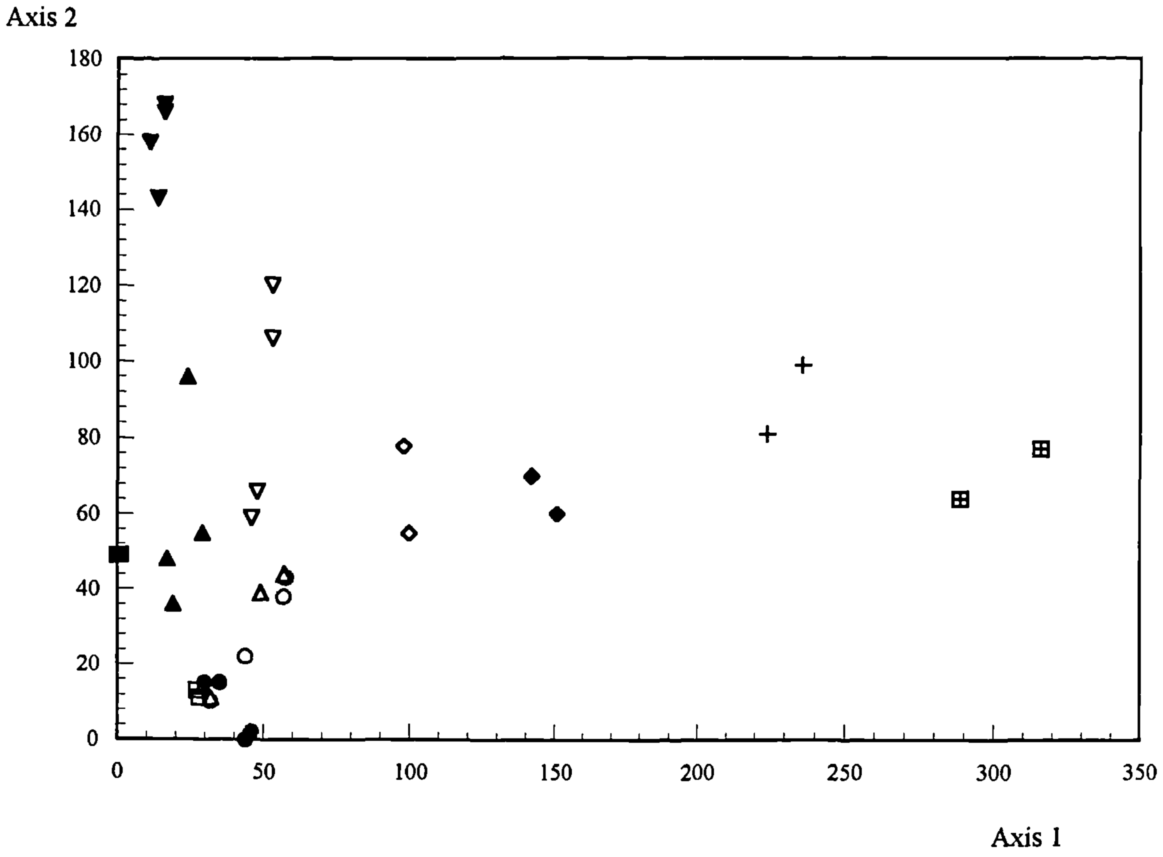

Figure 5.1. DECORANA ordination of nine sites (two replicates per site) in 1989 and 1993. See text and Table 5.1 for details of sites.

▽ Acrehead 89

▼ Acrehead 93

△ Bungalow 89

▲ Bungalow 93

○ Lochbank 89

● Lochbank 93

◇ Wet Lochbank 89

◆ Wet Lochbank 93

□ Netherwood 89

■ Netherwood 93

+ Caerlaverock 89

⊞ Caerlaverock 93

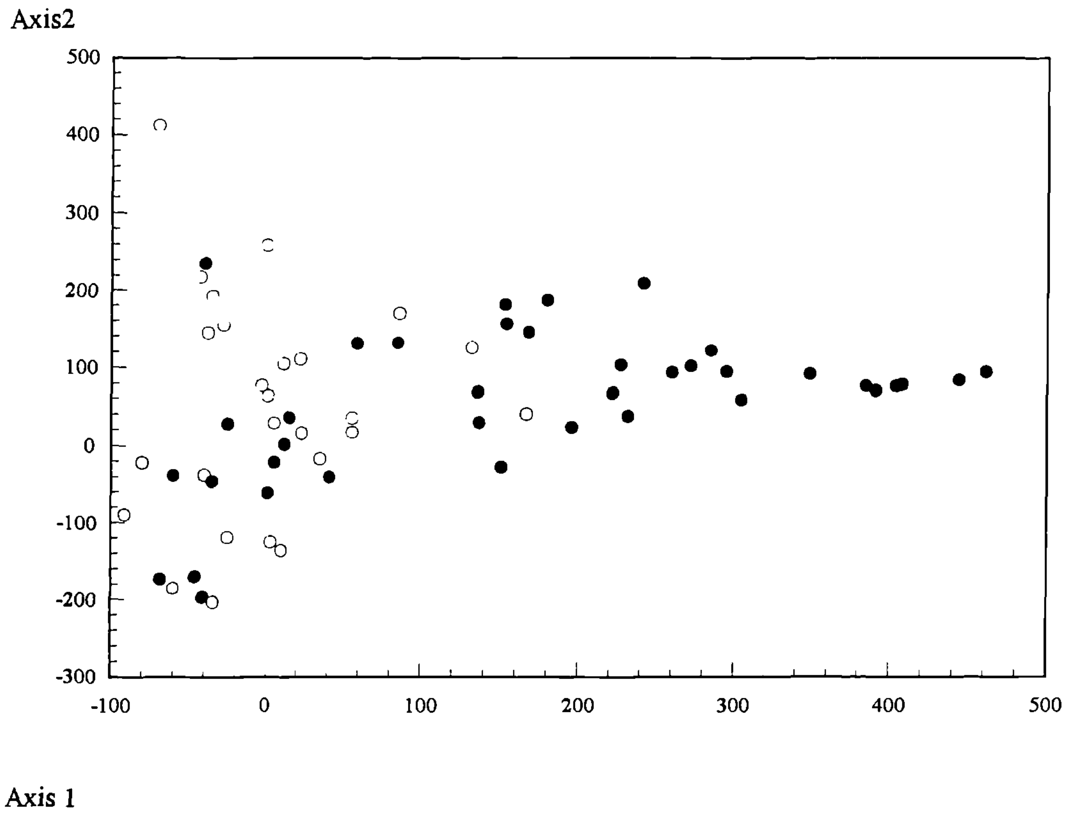

Figure 5.2. DECORANA ordination of the carabid species of nine sites (two replicates per site) in 1989 and 1993. Open symbols - species associated with dry or open habitats; filled symbols - species associated with wet or damp habitats.

In an ordination of the species scores (Appendix 11, Fig. 5.2) 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. 5.1) justified the removal of the extreme outlier Caerlaverock and a fresh analysis of the remaining managed sites (Gauch, 1982b p. 159). This achieved a greater separation on both axes (Appendix 12, Fig. 5.3) and clarified any changes occurring between 1989 and

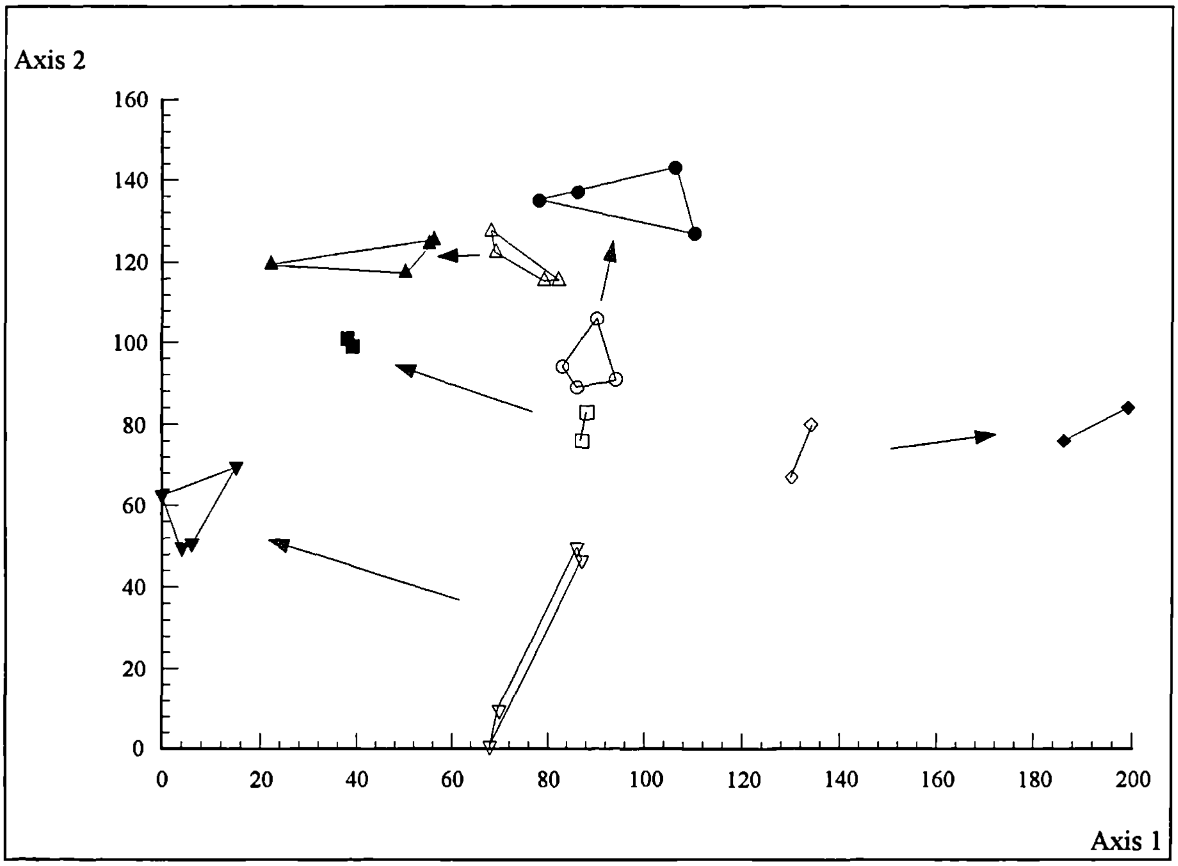

Figure 5.3. DECORANA ordination of eight sites (two replicates per site) in 1989 and 1993, showing changes in position between the two years. See text and Table 5.1 for details of sites.

▽ Acrehead 89

▼ Acrehead 93

△ Bungalow 89

▲ Bungalow 93

○ Lochbank 89

● Lochbank 93

◇ Wet Lochbank 89

◆ Wet Lochbank 93

□ Netherwood 89

■ Netherwood 93

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 substrata. Between 1989 and 1993, all of the managed sites except Lochbank 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. 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 5.2, diversity at Bungalow Meadows fell where slurry was applied, but rose where it was not. Diversity fell at Lochbank One-cut but rose from a very low 1989 level at Lochbank Two-cut. Rarity did increase significantly (Mann-Whitney test, $p < 0.01$).

Changes in the species composition between the two years included an increase in abundance of *B. 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 *A. 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 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 grazing, combined to delay the re-establishment of the original fauna at Acrehead Clover.

5.4 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 (Luff *et al.*, 1989; Eyre *et al.*, 1990; Rushton *et al.*, 1991). 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, 1974; 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.,* 1994). Slurry application may also have been associated with reduced diversity at Bungalow Meadows, but it was not possible to show the significance, if any, 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 (Section 3; 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, 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 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.

6. Effects of organic nutrient enrichment

6.1 *Nutrient enrichment by fertiliser application*

Of the 55 locations in the Scottish data set (Section 3; Appendix 1), 21 received applications of inorganic fertiliser and 25 received organic enrichment in the form of slurry, farmyard manure, and/or sewage sludge. Twenty received both kinds of fertilisation, one received only inorganic manure (MUIR94D, a silage field too steeply sloping for slurry tankers), and five received only organic input. These five were wildflower swards at Bungalow Meadows in 1989 and 1993, and three sites on rough grazing on Middleton Moor in 1993, which received poultry manure every two or three years. Nutrient input as part of farm management was found to reduce species richness, diversity and body size (Section 3, Table 3.3). Both inorganic and organic inputs contributed equally to the models of the response of species richness (*S*), diversity (*D*) and body size (*WML*) to management intensity (Section 3, Table 3.2), while rarity (*IRS*) responded only to inorganic input. Consequently, it was difficult to unravel any separate effects of inorganic and organic inputs.

The application of slurry at Bungalow Meadows was associated with a decrease in species richness and diversity between 1989 and 1993, while both *S* and *D* increased at the control site (Table 6.1). The field at Mauchline receiving sewage sludge in addition to slurry and inorganic fertiliser had a marginally higher value of *D*, but the two fields were not strictly comparable since the one receiving sludge was cut for silage while the other was grazed. At Muirkirk, organic input was also associated with slightly higher diversity and lower rarity. These sites at

Site code	Inputs	Log (catch)		*S*		*D*		*IRS*		*WML* mm	
		Replicates		Replicates		Replicates		Replicates		Replicates	
		1	2	1	2	1	2	1	2	1	2
BUNG89A	None	7.093	6.927	21	21	0.687	0.693	1.84	1.88	14.0	14.0
BUNG93A	None	6.807	6.444	26	24	0.754	0.751	2.41	2.90	14.3	14.7
BUNG89C	Slurry	6.468	6.410	23	23	0.842	0.856	2.12	2.09	14.4	14.4
BUNG93C	Slurry	6.632	6.542	23	21	0.729	0.776	2.60	2.70	14.1	14.1
MIDD93G	Poultry manure	4.673	4.673	16	17	0.883	0.843	1.82	1.92	12.1	12.0
MIDD93H	Poultry manure	4.369	5.024	15	20	0.875	0.896	3.43	2.27	17.9	12.1
MIDD93J	Poultry manure	5.303	5.784	20	31	0.829	0.807	1.59	1.62	13.1	12.6
MAUC94B	Slurry + inorganic	5.257	5.606	13	9	0.619	0.623	1.68	1.93	11.3	11.0
MAUC94A	Inorganic + slurry + sewage sludge	5.394	5.533	12	12	0.747	0.721	2.65	1.84	9.5	11.2
MUIR94C	Inorganic + slurry + sewage sludge	5.159	5.371	11	13	0.618	0.617	1.89	1.79	9.1	10.9
MUIR94D	Inorganic	4.575	4.575	9	10	0.615	0.534	2.33	2.04	7.4	7.1

Table 6.1. Values of log (catch) species richness (*S*), diversity (*D*), rarity (*IRS*) and body size (*WML*) at sites receiving different types of nutrient input.

Mauchline and Muirkirk were upland improved land and were quite species-poor. The three silage fields also had carabid assemblages of low body size. It would be unrealistic to attempt any distinction between effects of inorganic and organic input from these data, since diversity was more clearly linked to sward type, broadly increasing in the order: perennial ryegrass - wildflower mixtures - semi-improved rough grazing.

6.2 Natural enrichment by geese

Under natural conditions, grasslands receive nutrient input from the products of decay of plant and animal material. An important source of nutrient may be soluble nitrogen from faeces, such as those of flocks of geese. Large numbers of geese overwinter in Scotland each year, feeding in flocks on grass and arable land. Geese defecate up to 200 times a day, or once every four minutes (Bazely & Jefferies, 1985; Bédard & Gauthier, 1986), the rate depending on the type of vegetation on which they are feeding. Approximately 60% of the nitrogen in goose faeces is in soluble form (Bazely & Jefferies, 1985), the droppings are small, they are scattered evenly throughout the feeding area, and the supply is regularly renewed. While geese may consume a large proportion of the standing crop, the rapid recycling of nitrogen can result in an increase of net primary production of over 100% in nutrient-limited habitats (Bazely & Jefferies, 1985; Ruess *et al.*, 1989). This increase in production is likely to exert an effect on all trophic levels. In order to compare the effects of this natural enrichment with those of artificial fertilisation, in 1993 the carabid assemblages were sampled at six locations, each containing one or two sites used by feeding geese and one which was not.

The six locations (see Appendix 3 for management summary):

1. Lodge of Kelton, Castle Douglas. A dairy farm on the river Dee, with intensively managed pasture eight or nine years old, receiving inorganic nitrogen and cut two or three times a year for silage, then grazed by cattle. Approximately two thousand greylag geese *Anser anser* feed on the fields on Lodge Island throughout the winter months, roosting on the river (P. Norman, pers. comm.). KELT93A1&2: close to a flood pool on Lodge Island.

KELT93B1&2: on a knowe close to the River Dee, on Lodge Island.

KELT93C1&2: control site, farther from the river and not used by geese.

2. Caerlaverock National Nature Reserve. An expanse of unimproved grassland with gorse scrub at the edge of the saltmarsh and adjacent to the Wildfowl & Wetlands Trust Refuge. Grazed by sheep and cattle in the summer. Up to 10,000 Spitzbergen barnacle geese *Branta leucopsis* winter in this area, along with smaller numbers of pink-footed geese *A. brachyrhynchus* (Cranswick & Kirby, 1992).

CAER93D1&2: at the edge of the saltmarsh, close to high-water mark.

CAER93E1&2: a grassy area between the saltmarsh and the improved pasture.

CAER93F1&2: control site, similar to E but not used by geese due to numerous gorse bushes.

3. Middleton Moor, Midlothian. An area of upland rough grazing, receiving organic poultry manure every two or three years but no artificial nitrogen. Grazed by sheep and cattle. Used for feeding and resting by the pink-

footed geese which roost on Fala Flow (October 1991 count 11,362 - Cranswick & Kirby, 1992) and on Gladhouse Reservoir.

MIDD93G1&2: an open area of rough grass.

MIDD93H1&2: a boggy area with rank vegetation.

MIDD93J1&2: control site, similar to G but on a slope close to the road.

4. Islay. Improved grassland at Sanaigmore and Kindrochit in the north-west of the island, close to the RSPB reserve at Loch Gruinart. Grazed by sheep or cattle and two of the three fields cut for silage. Approximately 10,000 Greenland white-fronted geese *A. albifrons flavirostris* and over 20,000 barnacle geese wintered on the island in 1991-2 (Ogilvie, 1992).

ISLA93K1&2: a field at Kindrochit grazed and cut for silage in late summer.

ISLA93L1&2: control site, a field at Kindrochit grazed by cattle.

ISLA93M1&2: field at Sanaigmore grazed by sheep and cut for silage in mid-summer.

5. Vane Farm RSPB Reserve, Loch Leven. Two fields of pasture about six years old, and an unimproved boggy area close to flood pools. The permanent pasture had received N:P:K fertiliser in previous years but no nitrogen was applied in 1993 due to the problems of eutrophication of the loch. Approximately 20,000 pink-footed geese arrive at Loch Leven each autumn (D. Fairlamb, pers. comm.).

VANE93N1&2: A field between the road and the loch, summer grazed by cattle, 'topped' in August but not cut for fodder.

VANE93P1&2: A wet area with *Juncus*, close to a new flood pool. Summer grazed.

VANE93R1&2: control site, as N but close to the road and buildings.

6. Hule Moss, Berwickshire. A small area of rough grassland at the edge of the East Pool and bounded by *Calluna* moor. The moor is managed for grouse by rotational burning, and grazed by sheep. About 12,000 pink-footed geese were present at the main pool in October 1991 (Cranswick & Kirby, 1992).

HULE93S1&2: close to East Pool, lightly used by geese.

HULE93T1&2: control site, farther from the pool, on the banks of a burn.

At each site an estimate of the pattern and degree of usage by geese was made by counting faeces at the first visit in March. A wooden quadrat one-third of a metre square was thrown in a zig-zag pattern across the site, each throw a distance of approximately 1.5 to 2 metres. Both old and fresh droppings wholly or partly within the quadrat were counted. Fifty throws were made to obtain a value for the average number of droppings per square metre (Table 6.2). Standard methods for assessing faecal output involve counts made over a period of time (Bédard & Gauthier, 1986) but this was not possible as the geese returned to their breeding grounds in early spring.

Sward height was measured at the time of trap setting, using an acetate disc, approximately 35mm in diameter and 3mm thick, weighing 225.5g. A metre stick was inserted through a slit in the centre of the disc and the disc allowed to fall vertically down the stick until it came to rest. The height of the underside of the disc above ground level was taken to be the height of the sward (Boorman *et al.*, 1984). This was repeated for a total of twenty-seven measurements for each line of traps, three in the vicinity of each trap. The means and standard deviations

Site	Altitude (m asl)	Faeces per m^2	Sward Height (mm)			Sward type
			March	April	August	
KELT93A	50	1.6	32 (8.8)	112 (25.8)	68 (12.4)	Improved grass - silage
KELT93B	50	5.0	30	147 (20.6)	69 (25.2)	Improved grass - silage
KELT93C	55	0	30	133 (23.7)	45 (14.3)	Improved grass - silage
CAER93D	0	>20	33 (11.6)	39 (16.2)	59 (24.6)	Saltmarsh
CAER93E	0	5.9	30	36 (8.8)	80 (24.4)	Unimproved grass/scrub
CAER93F	0	0	30	38 (12.6)	91 (39.6)	Unimproved grass/scrub
MIDD93G	300	8.6	38 (9.3)	75 (20.5)	80 (36.4)	Rough grazing
MIDD93H	280	5.4	41 (10.1)	72 (25.2)	125 (52.2)	Rough grazing / bog
MIDD93J	320	0	34 (9.2)	48 (11.5)	68 (24.7)	Rough grazing
ISLA93K	45	2.2	30			Pasture
ISLA93L	40	0	30			Pasture
ISLA93M	25	8.3	30			Improved grass - silage
VANE93N	110	6.5	33 (8.9)	36 (8.2)		Pasture
VANE93P	110	12.5	46 (12.4)	68 (28.0)		Wet unimproved grass
VANE93R	115	0	30	38 (9.0)		Pasture
HULE93S	235	1.2	54 (20.5)	50 (16.3)	116 (79.5)	Grass / heather
HULE93T	235	0	58 (36.1)	47 (14.0)	228 (82.5)	Grass / heather

Table 6. 2. Altitude (m above sea level), mean number of goose faeces counted per m^2, sward height (mean & standard deviation) and sward type of 17 sites sampled in 1993. Sward height data were not available for ISLA and VANE later in the season.

of these was calculated (Table 6.2). This method is not considered to be accurate below 30mm, so results of less than this were expressed as 30mm. Where possible, sward height was measured again later in the season.

The cores of soil removed during trap setting were analysed for organic matter content, pH, phosphorus, potassium and magnesium content, and salinity (Table 6.3).

Site	% Loss on Ignition	pH (Water)	Available P (mg/l)	Available K (mg/l)	Extractable Mg (mg/l)	Salinity (mS/cm)
KELT93A	10.0	5.8	14	36	136	0.18
KELT93B	11.6	5.8	125	212	172	0.31
KELT93C	11.7	5.8	90	92	176	0.37
CAER93D	16.8	5.6	16	192	320	0.81
CAER93E	9.9	5.1	8.3	204	144	0.52
CAER93F	10.0	5.0	9.5	140	144	0.49
MIDD93G	15.2	5.2	33	168	212	0.37
MIDD93H	2.3	6.4	8.5	132	296	0.31
MIDD93J	14.7	5.2	14	180	216	0.35
ISLA93K	7.8	5.5	23	52	72	0.14
ISLA93L	11.5	5.3	5.3	120	120	0.19
ISLA93M	24.1	6.4	86	68	324	0.37
VANE93N	11.0	5.5	17	68	160	0.13
VANE93P	18.2	5.1	19	180	136	0.20
VANE93R	4.8	6.5	112	120	200	0.10
HULE93S	17.8	5.8	6.9	104	432	0.13
HULE93T	13.4	5.4	6.1	140	228	0.17

Table 6.3. Soil variables of 17 sites sampled in 1993.

A total of 10,789 ground beetles of 77 species were identified, their abundances converted to percentages and the data ordinated by DECORANA (Hill, 1979a). The ordination on the first two axes (Appendix 13, Fig. 6.1) gave a reasonable separation of the sites with Hule Moss in an extreme position high on the first axis and Caerlaverock saltmarsh high on the second axis. There appeared to be a geographical element in the ordination, since the upland sites were towards the high end of the first axis, the east coast sites were low on the second axis and atlanticity increased upwards on this axis to Islay and Caerlaverock. However, while the uncut field at Islay was close to Caerlaverock, the intensively-managed silage fields of Kelton and Islay were closely associated together, occupying the lowest positions on the major axis. Kelton was also closer on the

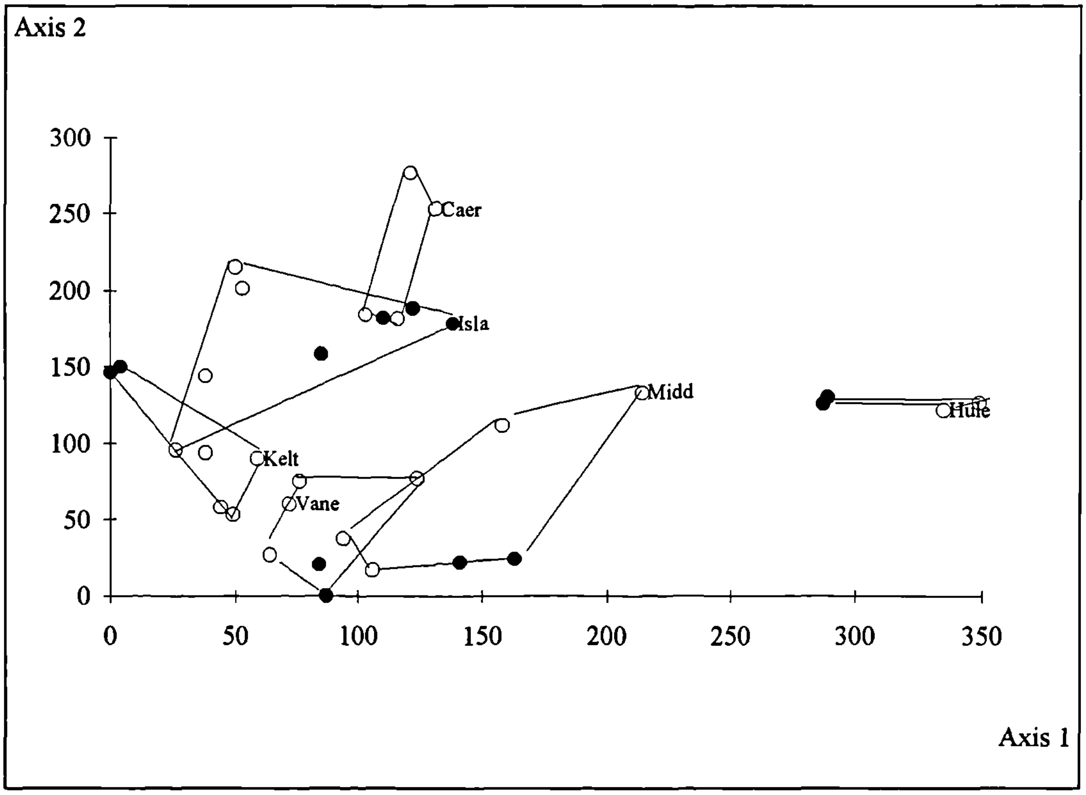

Figure 6.1. The first two axes of the DECORANA ordination of the carabid assemblages of six locations. Open symbols: sites used by feeding geese. Filled symbols: sites not used by geese.

second axis to Vane Farm than to Caerlaverock, suggesting that management was exerting a stronger effect on the fauna than geography or climate. For the most part, the control sites not used by geese (filled symbols in Fig. 6.1) were separated in the ordination from the other sites at the same location. The exception was Caerlaverock, where the control site was indistinguishable from the other site with similar vegetation. Within the data set as a whole, no distinction could be made according to levels of faecal input. Since it was not possible to detect any overall effect on the fauna from the activities of feeding geese, it seems likely that the control sites were distinct for other reasons - reasons which influenced their choice as controls. Except for Caerlaverock, the controls at every location were farther from standing or running water, and closer to human activity. The factors which caused the geese to avoid these sites could also have some influence on the carabid fauna.

Spearman's rank order correlation coefficient (Table 6.4) suggested significant correlations of the DECORANA Axis 1 with altitude and with soil conditions, site score being positively correlated with potassium and magnesium and negatively with available phosphorus. The second axis was correlated negatively with altitude and positively with salinity, hence the high position of Caerlaverock saltmarsh on this axis. Axis 2 was also negatively correlated with phosphorus. No significant correlation was found between ordination position and sward height or goose faeces counts. Goose faeces were not significantly correlated with any other parameter.

Twelve species described as rare or scarce in Scotland were identified, including two Red Data Book Notable A species, and four Notable B (Hyman & Parsons, 1992). Eight of these twelve were found at Caerlaverock, two at Hule Moss, none at Vane Farm, and one apiece at the other three sites. Only one of these scarce species occurred at more than one site (*Blethisa multipunctata* at Kelton and Caerlaverock). Ten species occurred at all six locations: *Agonum fuliginosum*, *A. muelleri*, *Amara plebeja*, *Clivina fossor*, *Loricera pilicornis*, *Nebria brevicollis*, *Pterostichus melanarius*, *P. niger*, *P. strenuus* and *Trechus obtusus*. The catch proportions of five of these were significantly correlated with each other: *A. plebeja*, *C. fossor*, *L. pilicornis*, *N. brevicollis* and *P. melanarius*, all species commonly found in managed habitats. The proportion of *T. obtusus*

	Axis 1	Axis 2	C	pH	P	K	Mg	Sal.	*S*	*D*	*IRS*	*WML*	Alt.	Faec
Axis 1														
Axis 2	0.052													
C	0.073	-0.131												
pH	-0.281	-0.168	-0.129											
P	**-0.718**	**-0.388**	0.082	**0.380**										
K	**0.369**	-0.081	0.189	**-0.444**	-0.045									
Mg	**0.390**	-0.142	**0.446**	**0.444**	-0.008	0.139								
Sal	-0.058	**0.382**	0.235	-0.344	0.034	**0.522**	0.147							
S	**0.645**	-0.079	-0.022	-0.199	-0.357	**0.470**	0.310	0.010						
D	0.253	**-0.387**	-0.040	0.002	-0.064	-0.023	0.262	-0.068	0.234					
IRS	0.017	**0.652**	-0.267	0.061	-0.240	-0.072	-0.004	0.237	0.063	0.127				
WML	**0.460**	-0.259	-0.221	**-0.426**	-0.271	**0.584**	-0.011	0.137	**0.491**	**0.435**	-0.030			
Alt.	**0.379**	**-0.707**	0.094	0.141	0.008	-0.007	**0.364**	**-0.434**	0.155	**0.555**	**-0.395**	0.213		
Faec.	-0.141	0.004	0.340	-0.037	0.254	0.222	0.126	0.313	-0.089	0.019	0.029	-0.090	-0.164	
Sw. ht.	0.289	-0.234	0.068	0.084	-0.139	0.277	0.290	-0.012	0.204	0.325	-0.110	**0.378**	**0.455**	-0.128

Table 6.4 Spearman's rank order correlation matrix of DECORANA axis scores, soil variables, species richness (*S*), diversity (*D*), rarity (*IRS*) body size (*WML*), altitude, number of goose faeces and mean sward height at six locations. Entries in **bold** are statistically significant.

was negatively correlated with those of *C. fossor*, *N. brevicollis* and *P. melanarius*. In the ordination of the species scores (Appendix 14, Fig. 6.2), *T. obtusus* was associated with moorland species high on the first axis.

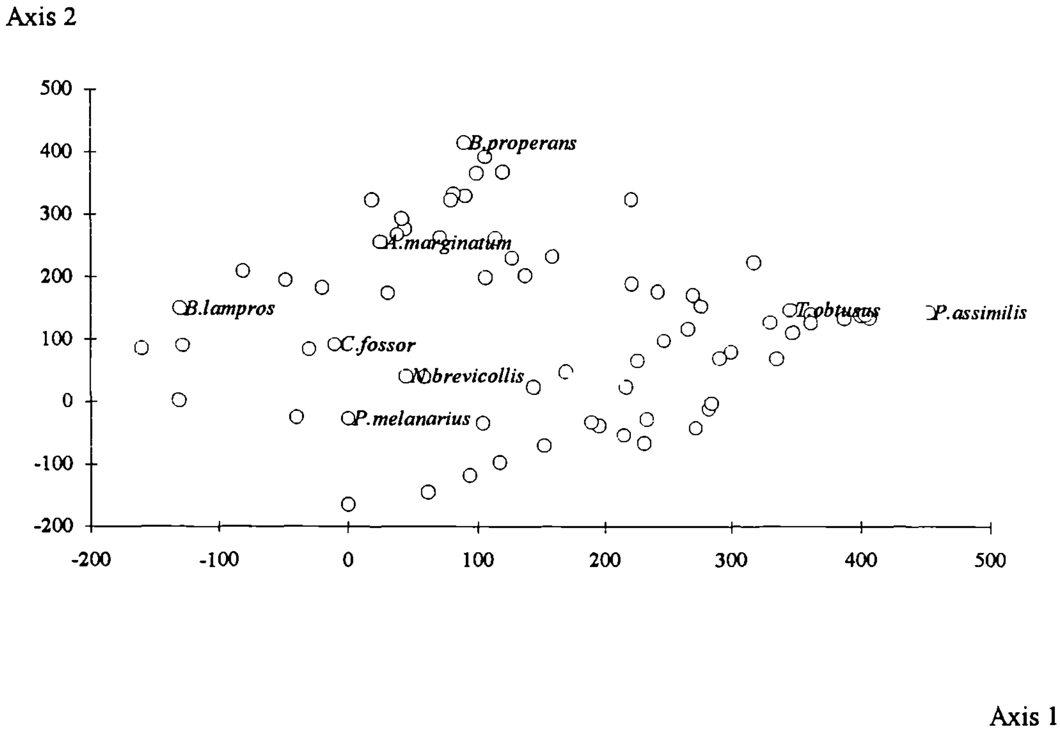

Figure 6.2. The first two axes of the DECORANA ordination of the carabid species of six locations sampled in 1993.

T. obtusus was the only species to show any correlation with the density of goose faeces ($r_S = -0.514$, $p < 0.01$). In a study of the effects of lime application to acidified land in the Loch Fleet catchment area, Foster *et al.* (1995) found that *T. obtusus* was the only carabid beetle in the fauna to respond to the treatment, suggesting a relationship with soil pH or nutrient availability, either directly or through some intermediate factor such as abundance of prey items. In this study, pH was found to be positively correlated with phosphate levels (Table 6.4). The relationship of *T. obtusus* with pH was not significant in itself, but both *Pterostichus niger* and *T. obtusus* varied negatively with soil phosphate levels, while *N. brevicollis* and *P. melanarius* varied positively with phosphate. Since high phosphate levels were only found at those sites which had received inorganic fertiliser in the past (Table 6.3), this could be interpreted as an effect of management intensity, the first two species being detrimentally affected by management, while the second two were favoured by it. Since *T. obtusus* also varied inversely with goose faecal input, it is possible that this species is especially sensitive to nutrient enrichment, possibly being out-competed by some other species which has a faster rate of population growth when nutrient levels are high. However, no other species of similar size to *T. obtusus* was found to be positively correlated with enrichment.

The three improved sites (Kelton, Islay and Vane Farm) had the fewest rare or scarce species, only two among them. *Carabus clatratus*, a Notable A species, was found in the least intensively managed of the Islay sites, a wet field with much *Juncus*, while *B. multipunctata* (Notable B) was found within 40 metres of rank vegetation on the banks of the River Dee at Lodge of Kelton. The dominant species in this group of sites were the widespread and invasive *N. brevicollis, A. muelleri, L. pilicornis* and *P. strenuus.* The geographical difference between Vane Farm and the two western improved sites was reflected in greater numbers of *Amara, Calathus* and *Notiophilus* at Vane Farm, all genera associated with drier habitats.

The forty-one species identified at Caerlaverock included eight scarce or rare in Scotland. This appeared to be the first post-1970 Scottish record for three species, *Agonum nigrum, Bembidion properans* and *Dyschirius luedersi* (Eyre, 1993, unpubl.). Apart from *P. strenuus*, the widespread species typical of intensive management were present in low numbers only. The saltmarsh was dominated by two very small species, *D. globosus* and *B. aeneum.* In all, there were ten species of *Bembidion* and four of *Dyschirius*, with three scarce species in each. Only six of the forty-one species had a mean body size of more than 8mm, and 19 were 6mm or less, so that this fauna was characterised by very small size.

Although the number of species caught was high at Middleton Moor at 41, no one or few species dominated numerically, and total numbers were significantly lower than at any other site, so that the fauna was relatively diverse. *Calathus fuscipes, C. melanocephalus, N. brevicollis, B. unicolor* and *P. strenuus* were all relatively abundant in different lines of traps. *B. biguttatum* was the only scarce species, but *Carabus problematicus* and *C. violaceus*, large species typical of undisturbed habitats, were present in substantial numbers. Both its 'semi-improved' nature and its higher altitude could be factors affecting the separation of Middleton from the other sites in the ordination.

The fauna of Hule Moss was distinct from all others, being essentially an 'edge' fauna of *Calluna* moorland. Typical moorland species found only at Hule Moss were *Bradycellus ruficollis, Carabus arvensis, C. nitens* and *Notiophilus palustris.* The most abundant species were *Patrobus assimilis, Pterostichus*

Site code	Log (catch)		*S*		*D*		*IRS*		*WML* mm	
	Replicates		Replicates		Replicates		Replicates		Replicates	
	1	2	1	2	1	2	1	2	1	2
KELT93A	5.996	5.855	18	16	0.823	0.784	2.05	2.09	11.6	11.5
KELT93B	6.402	6.474	18	15	0.683	0.732	1.62	1.73	12.1	12.1
KELT93C	5.746	5.352	14	13	0.800	0.819	2.49	2.73	8.2	8.4
CAER93D	6.410	6.778	27	30	0.807	0.727	8.16	7.99	10.9	10.5
CAER93E	5.717	5.642	19	24	0.748	0.750	3.15	6.37	15.1	14.2
CAER93F	4.970	4.820	17	22	0.782	0.815	1.76	2.40	16.8	17.0
MIDD93G	4.673	4.673	16	17	0.883	0.843	1.82	1.92	12.1	12.0
MIDD93H	4.369	5.024	15	20	0.875	0.896	3.43	2.27	17.9	12.1
MIDD93J	5.303	5.784	20	31	0.829	0.807	1.59	1.62	13.1	12.6
ISLA93K	4.890	5.403	14	13	0.641	0.485	2.32	2.51	7.9	7.9
ISLA93L	4.304	4.489	16	14	0.767	0.658	2.18	2.39	11.2	9.2
ISLA93M	4.585	5.142	10	9	0.818	0.705	2.63	1.95	8.1	10.0
VANE93N	5.737	5.768	20	17	0.886	0.867	1.98	2.01	12.0	12.0
VANE93P	6.142	4.419	16	18	0.753	0.865	1.77	1.82	12.9	14.3
VANE93R	6.631	6.664	22	21	0.815	0.817	2.11	1.99	12.2	12.2
HULE93S	5.817	6.186	21	20	0.749	0.691	1.68	1.60	10.3	9.9
HULE93T	5.537	5.911	22	33	0.891	0.880	21.27	14.48	13.9	17.3

Table 6.5. Values of log (catch) species richness (*S*), diversity (*D*), rarity (*IRS*) and body size (*WML*) at 17 sites sampled in 1993.

rhaeticus, T. obtusus and *T. secalis*. The dispersive, eurytopic species which dominated the improved sites were all present in only low numbers at Hule Moss.

Species richness was highest at Caerlaverock saltmarsh, part of Middleton Moor and Hule Moss (Table 6.5), and was significantly correlated with Axis 1 score. Diversity (*D*) and rarity (*IRS*) were both correlated with Axis 2 score, *D* negatively and *IRS* positively. Despite the very high values of *IRS* at Hule Moss, rarity was not correlated with Axis 1. Body size (*WML*) was positively correlated with both *S* and *D*, with sward height and with Axis 1 score, the highest values being at Hule Moss and Middleton Moor. Diversity increased and rarity decreased with altitude.

The average carabid body size, as expressed by the *WML*, was correlated with the relative abundance of the largest of the ten common species, *P. niger*, 17.8mm in length ($r_S = 0.598$, $p< 0.01$). Although no effects of nutrient enrichment by goose faecal input on the carabid faunas could be demonstrated, it was apparent that management intensity generally was exerting an effect. The intensively-managed silage fields were low on the major DECORANA axis, with the relatively oligotrophic Hule Moss in the highest position and the moderate-intensity sites intermediate. All of the sites except Hule Moss, Caerlaverock and Vane Farm P received inputs of inorganic or organic fertiliser, the silage fields especially so. Any effects of nutrient input or disturbance by geese proved impossible to detect in a data set containing such variation in management regime.

7. Discussion and conclusions: Carabid beetles and grassland management

The principal aim of this study was to examine the effects of grassland management intensification on various aspects of the carabid fauna, i.e. species composition, diversity, rarity and body size. Two large data sets were available, consisting of 110 sets of pitfall traps in Scotland and 113 in north-east England and collected over a number of years between 1989 and 1994. Apart from the problems inherent in the analysis of pitfall data discussed in Section 1.1, a further difficulty is the natural year by year variation in the composition of ground beetle communities, with sub-populations of each species fluctuating independently both of each other and of neighbouring sub-populations of the same species (den Boer, 1985). This yearly variation is often a major source of variation in a data set (Luff, in prep.,). Only long-term studies at each site can fully address this problem, but in the present study the combination of data from different years went some way towards this. One group of sites at the Crichton Royal Farm, discussed in Section 5, was sampled in two years. The DECORANA ordination of these sites (Figures 5.1 & 5.3) showed the changes in carabid species composition between 1989 and 1993. Had every site changed its ordination position in a roughly similar fashion it would have been difficult to place any interpretation on this other than yearly variation; however, the observation that the unmanaged control sites moved in the opposite direction to the managed sites did suggest that the ordination was reflecting a genuine effect of management.

The first requirement of the study was to establish a system of classification of management intensity, ideally one which was robust, suitable for non-quantitative data and adaptable for use by site managers of any background, whether scientific or not. The resulting classification, summarised in Table 2.1

and Appendix 3, considered six components of management, each of which was divided into four levels of intensity. The scores were additive rather than multiplicative, and unweighted, with no *a priori* assumptions about the relative importance of the various components. If appropriate, additional components such as drainage or pesticide inputs could be included and the range of scores in each of the five management bands adjusted accordingly. Since the aim was to produce a system of scoring management factors only, environmental or 'natural' influences were deliberately excluded - for instance, soil type, moisture, grazing by rabbits etc.

In general, the classification of the grassland sites into five broad management bands was supported by the analyses of species composition, diversity, rarity and body size. To some extent, sites could in fact be described as belonging to one of only two groups - zero or low management, and moderate to high management. The main effects of management appeared to occur on the first introduction of any management whatsoever, suggesting the importance of soil cultivation. In a classification of the ground beetles of 19 upland grassland sites (Rushton *et al.*, 1989), two sites which had been improved by re-seeding without cultivation were associated with the unimproved rather than with the cultivated sites. The TWINSPAN classification of the Scottish sites in this study also emphasised the difference between cultivated and uncultivated sites (Figure 3.1). In arable land, the timing of repeated cultivations will have an influence on the fauna, but in grassland the cultivation operations associated with improvement take place at intervals of several years, ranging from five years or thereabouts in ley rotations to once-only events in upland grazing. Some recovery of the fauna from these effects may be expected in older swards but in this study the only significant difference found between swards over 10 years old and younger ones was that diversity was somewhat higher in the older sward (Table 3.5), although the sample size in this category was admittedly small at eight. Van Dijk (1986) found little re-establishment of the native fauna 12 years after cessation of cultivation, even in the absence of other forms of management, and it may be that with continued management even the oldest swards sustain a carabid fauna different from that of unmanaged habitats. All of the managed sites in this study were degraded in terms of diversity and rarity when compared with the zero management sites, to the extent that differences between the managed sites themselves may have been masked.

The multivariate analysis clearly separated the most intensively managed sites from the least intensively managed in every case, both in the Scottish data set (Figure 3.2) and in the north-east England data set (Figure 4.3). This result was in agreement with that of Eyre *et al.* (1989) who found that both ground beetle and weevil communities were primarily influenced by management. Besides management, moisture was an important determining factor in the ordinations. High management sites tended to be low to intermediate on the axis associated with moisture, while the low intensity sites were split according to whether they were wet or dry. Luff *et al.* (1989) identified moisture and substratum porosity as important determinants of carabid communities, along with altitude. The extreme positions in the TWINSPAN classification (Figure 3.1) and on Axis 2 of the DECORANA ordination (Figure 3.2) were occupied by sites with sandy and peaty soils; however, no clear gradient of soil type was evident between these extreme points. Managed sites tended to be tightly clustered within the ordination, so that no trends within this group could be found. In effect, two very different groups of sites were being ordinated simultaneously and it might have been illuminating to perform the analysis on low- and high-intensity sites separately. In an analysis of intensively managed grasslands, Eyre *et al.* (1990) found that carabid species composition varied with soil moisture and density.

Diversity was described in three ways: by species richness (*S*), by Simpson's diversity index (*D*), and by the residual deviances of the regression of the log-transformed catch on the number of species. Of the three, the residual deviance performed best in terms of distinguishing between management intensity levels, with high intensity sites having more individuals than predicted by the species number - i.e. fewer species for the catch size. The simplest measure of diversity, *S*, performed almost as well as the more complex *D*. A major effect of management seemed to be simple loss of species richness. The main decrease in diversity was between the second and third bands of management intensity, dividing the sites into two groups of low and high intensity. The management component most influencing diversity was nutrient input; sites with no input at all had the highest diversity, but within the sites receiving nutrients, it was highest at intermediate levels of input. A possible explanation for this would be that there were two different suites of species: one suite of slow-growing species in the oligotrophic undisturbed conditions maintaining high diversity by never becoming abundant enough to enter into competition; and another suite of fast-growing invasive species in the managed habitats. At low levels of nutrient input, diversity would be low because of insufficient energy flow in the system for many of these fast-growing species to expand, but presumably too much disturbance for the oligotrophic species. As nutrient input increased, diversity would also rise until the point where the more competitive species became sufficiently abundant to begin excluding others.

It might be expected that the input of organic material would have a somewhat different effect from that of inorganic fertilisation. The analysis of the sites used by grazing geese and of sewage sludge applications (Section 6) attempted to examine this question, but few clear conclusions were possible, due to the difficulty of establishing suitable control sites. Geese are opportunistic feeders and any field not used by them is likely to differ in some way, notably moisture or vegetation conditions, from neighbouring fields which are used. Similarly, farmers who apply sewage sludge are likely to apply it to all of their silage fields. Other studies have found an increase in total biomass of soil invertebrates such as springtails and of the carabid beetles which prey on them in 'biologically' managed fields, i.e. those receiving only organic manure, as opposed to 'conventionally' managed ones receiving inorganic nitrogen. Pimentel & Warneke (1978) concluded that biomass, species richness and diversity of soil arthropods were all increased by the application of organic material, as compared with inorganic or no fertilisation. An increase in availability of prey is likely to be followed by an increase in abundance of carabid beetles, but not necessarily by an increase in their diversity. Hokkanen & Holopainen (1986) noted a large increase in abundance especially of *Pterostichus melanarius* in organic cabbage fields, but there was no significant effect on diversity. Numbers of *Bembidion lampros* and *P. strenuus* were also found to respond to farmyard manure applications (Purvis & Curry, 1984) but again with little effect on diversity. Dritschilo & Erwin (1982) found that the faunas of organically managed plots were more abundant and more species-rich than those of conventional plots but, once more, with no significant difference in any of three diversity indices, leading them to suggest that diversity indices were of limited value as descriptors of community structure. In the present study, however, the complement of Simpson's diversity index was found to discriminate reasonably well between management bands, although not as well as the residual deviance of the regression of log(catch) on species richness. Because of the uncertainties, both theoretical and practical, surrounding the use of diversity indices generally, it is probably preferable to use either the residual or the species richness itself to describe community diversity.

Rarity also fell with increasing management intensity, with the major difference again between bands 1 and 2 and bands 3 to 5. This correspondence of the trends in diversity and rarity suggest that the *IRS* may indeed be a realistic, useful descriptor of the rarity value of a habitat; however, the relationships of *IRS* with individual components of management were not clear, and there were many anomalies in the values. Indices based on distribution lists are always likely to suffer from bias in the records, and it may be that an *IRS* recalculated from updated records at some later date will give more consistent results. It was thought at one point in the analysis that the exclusion of the commonest species from the calculation would give an index more sensitive to the presence of rarities; after all, the presence of ubiquities conveys no information. However, this seemed rather arbitrary, it needlessly complicated a concept attractive largely for its simplicity, and it raised the problem that the various indices calculated for a sample (*S, D, IRS, WML*) would be based on species lists of different lengths. Some way of quantifying rarity is necessary in habitat assessments, and the *IRS*, taking into account the abundances of the species, seems to be a useful step forward.

The downward trend in body size as management intensified was very clear in both the Scottish and the English data sets, with values of 15.6mm at band 1 and 11.1mm at band 5 in England, and 15.3mm and 11.2mm respectively in Scotland. Mean moorland and woodland *WML* in England was 17.9mm; the only values over 16mm in the Scottish grassland data set were sites in management bands 1 and 2. This degree of similarity in the results from two data sets geographically separated and based on somewhat different species lists suggests that some confidence can be placed in the *WML* as a descriptor of average body size. In terms of individual components of management, body size responded negatively to all types of intensification, but was especially related to sward type and age, suggesting a relationship, perhaps, with vegetation structure as well as with nutrient status and disturbance. Siepel (1990) found that the body size of foliage-active Coleoptera was greater in unfertilised mown grasslands than in unfertilised grazed ones, but in either case decreased with increasing fertiliser applications. There were no unfertilised mown sites in the present study, but it was found that carabid body size was inversely related to both grazing and cutting, with the lowest values at the highest level of cutting when, inevitably, fertiliser inputs were also high. Siepel surmised that the negative relationship of body size with fertilisation was due to increased disturbance favouring small, colonising species, even though his results showed that the body size decrease was mostly because of loss of larger species rather than increased abundance of small ones (although there was a certain increase in the latter). Larger species certainly appear to be poor tolerators of disturbance, but smaller species may have a wider tolerance; Eyre (1994) classified 49 species according to the degree of disturbance with which they were associated and found only two species over 15mm in length tolerated high disturbance. These were *Pterostichus melanarius*, a species found to be associated with intensive management in this study, and *Carabus nemoralis*, the only species of *Carabus* found in moderately intensive sites. The use of the *WML* to describe body size emphasises the rôle of larger species; a drop in *WML* suggests a loss of large individuals not compensated for by an increase in small ones. The decrease in body size on moving from moorland to grassland habitats was to a great extent mediated by the loss of species of the genus *Carabus*, and the high *WML* at the lowest level of grassland management was partly due to a greater abundance of *Pterostichus niger*. The decline to band 5 of management intensity could not be related so readily to any one or few species. It may be concluded that the decline in body size with management intensification was related to the requirement of larger species for a more stable, less disturbed habitat.

Different observers critically examining a habitat or an ecosystem will each take something different from it, depending on their point of view. The entomologist, the botanist, the ornithologist, the agriculturalist and conservationist each has their own idea of what environmental goods a site has to offer. Yet each one ought to be interested in the nature of the carabid beetle fauna of the habitat.

The entomologist, of course, is interested in the beetles for their own sake as an object of study, but also for what they tell about the health and nature of the invertebrate community generally. The response of the carabid fauna to environmental change may be seen as a readily measurable indication of the response of other taxa. If, as this study has shown, intensification of grassland management results in a less diverse carabid fauna of smaller body size, adapted to dry conditions and dominated by a few abundant species, then there is a likelihood of these trends applying to the insects and other invertebrates generally.

To the botanist, the environmental goods of a habitat consist of its botanical diversity and productivity. However, any efforts to manipulate or conserve botanical content should also consider the effects on wildlife in general and invertebrates in particular, without assuming that high invertebrate diversity will necessarily follow from high botanical diversity. The result of this study, that more diverse wildflower swards were associated with a more diverse carabid fauna than grass swards, but with a different species composition from that of undisturbed herb-rich grassland, should be of interest to the botanist.

The ornithologist, both academic and amateur, is interested in the ability of a habitat to support populations of overwintering or breeding birds. The carabid fauna is important to many species of bird in its rôle as a source of prey. By reducing the average body size of the carabid beetles, even though total abundance may increase, there is a danger that intensification of grassland management may reduce the value of this food source to foraging birds.

The prime concern of the agriculturalist has traditionally been productivity, but with the need to reduce over-production and the growing emphasis on environmental issues in the public mind has come an awareness of agricultural land as habitat in its own right. The usefulness of carabid beetles as predators of pest species has long been known, and many agriculturalists recognise the benefit of providing refugia for them in the form of uncultivated strips or headlands. The loss of larger species with intensification could be detrimental to the control of some pests such as slugs, but the increase in abundance of many smaller carabids is probably related to increased numbers of springtails, aphids and Diptera on which the beetles prey. Because of its transient nature, some types of managed land, particularly arable land, may support a carabid fauna of high diversity and rarity value and while these assemblages may not be 'natural' they are no less interesting for that.

To the conservationist, the environmental goods of a habitat are easily defined in the terms of a list of criteria: diversity, rarity, naturalness, typicalness.....etc. But if easily defined, these criteria may not be easily quantified, and quantification is necessary so that in the face of limited resources different sites can be evaluated and decisions on conservation management taken in an objective manner. Quantification requires a survey of organisms present, including invertebrates. Pitfall trapping remains the most reliable, cost-effective method of surveying surface-active invertebrates over a period of time, and the indices of diversity and rarity used in this study appear to be related to grassland management practices in a sensible, ecologically meaningful way.

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Appendix 1. Pitfall trapping locations in central and southern Scotland.

Site code	Location	Year	Habitat type	Altitude	O.S. ref.
ACRE89A	Acrehead, Crichton, Dumfries	1989	Improved grassland	20m	NX9873
ACRE89C	Acrehead, Crichton, Dumfries	1989	Improved grassland	20m	NX9873
ACRE93A	Acrehead, Crichton, Dumfries	1993	Improved grassland	20m	NX9873
ACRE93C	Acrehead, Crichton, Dumfries	1993	Improved grassland	20m	NX9873
AUCH90F	Auchalton Meadows, Ayrshire	1990	Unimproved grassland	160m	NS3303
AUCH90G	Auchalton Meadows, Ayrshire	1990	Unimproved grassland	160m	NS3303
BUNG89A	Bungalow Meadows, Crichton, Dumfries	1989	Improved grassland	60m	NX9974
BUNG89C	Bungalow Meadows, Crichton, Dumfries	1989	Improved grassland	60m	NX9974
BUNG93A	Bungalow Meadows, Crichton, Dumfries	1993	Improved grassland	60m	NX9974
BUNG93C	Bungalow Meadows, Crichton, Dumfries	1993	Improved grassland	60m	NX9974
CAER89A	Caerlaverock Castle, Dumfriesshire	1989	Unimproved grassland	<10m	NY0265
CAER93A	Caerlaverock Castle, Dumfriesshire	1993	Unimproved grassland	<10m	NY0265
CAER93D	Caerlaverock, Dumfriesshire	1993	Saltmarsh	<10m	NY0665
CAER93E	Caerlaverock, Dumfriesshire	1993	Unimproved grassland	<10m	NY0666
CAER93F	Caerlaverock, Dumfriesshire	1993	Unimproved grassland	<10m	NY0565
CAIR90C	Cairn Hill, Ayrshire	1990	Unimproved grassland	230m	NX1793
CAIR90D	Cairn Hill, Ayrshire	1990	Unimproved grassland	235m	NX1793
CAIR90E	Cairn Hill, Ayrshire	1990	Unimproved grassland	235m	NX1793
FEOC90H	Feoch Meadows, Ayrshire	1990	Unimproved grassland	140m	NX2682
FEOC90J	Feoch Meadows, Ayrshire	1990	Unimproved grassland	140m	NX2682
HULE93S	Hule Moss, Berwickshire	1993	Wet moorland	235m	NT7149
HULE93T	Hule Moss, Berwickshire	1993	Wet moorland	235m	NT7149
ISLA93K	Kindrochit.Islay, Hebrides	1993	Improved grassland	45m	NR2368
ISLA93L	Kindrochit.Islay, Hebrides	1993	Improved grassland	40m	NR2368
ISLA93M	Sanaigmore.Islay, Hebrides	1993	Improved grassland	25m	NR2470
KELT93A	Kelton, Castle Douglas, Kirkcudbrightshire	1993	Improved grassland	50m	NX7361
KELT93B	Kelton, Castle Douglas, Kirkcudbrightshire	1993	Improved grassland	50m	NX7361

Appendix 1. continued

KELT93C	Kelton, Castle Douglas, Kirkcudbrightshire	1993	Improved grassland	55m	NX7460
LOCH89A	Lochbank, Crichton, Dumfries	1989	Improved grassland	50m	NX9974
LOCH89C	Lochbank, Crichton, Dumfries	1989	Improved grassland	50m	NX9974
LOCH89E	Lochbank, Crichton, Dumfries	1989	Improved grassland	50m	NX9974
LOCH93A	Lochbank, Crichton, Dumfries	1993	Improved grassland	50m	NX9974
LOCH93C	Lochbank, Crichton, Dumfries	1993	Improved grassland	50m	NX9974
LOCH93E	Lochbank, Crichton, Dumfries	1993	Improved grassland	50m	NX9974
MACA90A	Macawston, Ayrshire	1990	Improved grassland	30m	NS2004
MACA90B	Macawston, Ayrshire	1990	Improved grassland	30m	NS2004
MAUC94A	Mauchline, Ayrshire	1994	Improved grassland	130	NS5030
MAUC94B	Mauchline, Ayrshire	1994	Improved grassland	125	NS5030
MERS94A	Mersehead, Kirkcudbright	1994	Improved grassland	<10m	NX9355
MERS94B	Mersehead, Kirkcudbright	1994	Improved grassland	<10m	NX9355
MERS94C	Mersehead, Kirkcudbright	1994	Arable	<10m	NX9356
MERS94D	Mersehead, Kirkcudbright	1994	Sand dunes	<10m	NX9155
MIDD93G	Middleton, Midlothian	1993	Rough grazing	300m	NT3555
MIDD93H	Middleton, Midlothian	1993	Rough grazing	280m	NT3555
MIDD93J	Middleton, Midlothian	1993	Rough grazing	320m	NT3655
MUIR94C	Muirkirk, Ayrshire	1994	Improved grassland	230	NS6628
MUIR94D	Muirkirk, Ayrshire	1994	Improved grassland	240	NS6628
NETH89A	Netherwood, Crichton, Dumfries	1989	Improved grassland	50m	NX9872
NETH93A	Netherwood, Crichton, Dumfries	1993	Improved grassland	50m	NX9872
SHEW90L	Shewalton Sandpits, Ayrshire	1990	Reclaimed sandpits	10m	NS3237
SHEW90M	Shewalton Sandpits, Ayrshire	1990	Reclaimed sandpits	10m	NS3237
SHEW90N	Shewalton Sandpits, Ayrshire	1990	Reclaimed sandpits	20m	NS3237
VANE93N	Vane Farm, Loch Leven, Fife	1993	Improved grassland	110m	NT1598
VANE93P	Vane Farm, Loch Leven, Fife	1993	Unimproved wet grassland	110m	NT1599
VANE93R	Vane Farm, Loch Leven, Fife	1993	Improved grassland	115m	NT1599

Appendix 2. Checklist of species of carabid beetle taken in 110 sets of pitfall traps in central and southern Scotland.

Cicindela campestris Linnaeus
Cychrus caraboides (Linnaeus)
Carabus arvensis Herbst
Carabus clatratus Linnaeus
Carabus granulatus Linnaeus
Carabus nemoralis O.F. Müller
Carabus nitens Linnaeus
Carabus problematicus Herbst
Carabus violaceus Linnaeus
Leistus ferrugineus (Linnaeus)
Leistus fulvibarbis Dejean
Leistus rufescens (Fabricius)
Nebria brevicollis (Fabricius)
Nebria salina Fairmaire & Laboulbène
Notiophilus aquaticus (Linnaeus)
Notiophilus substriatus Waterhouse
Notiophilus biguttatus (Fabricius)
Notiophilus germinyi Fauvel
Notiophilus palustris (Duftschmid)
Blethisa multipunctata (Linnaeus)
Elaphrus cupreus Duftschmid
Elaphrus riparius (Linnaeus)
Loricera pilicornis (Fabricius)
Dyschirius globosus (Herbst)
Dyschirius luedersi Wagner
Dyschirius nitidus (Dejean)
Dyschirius politus (Dejean)
Dyschirius salinus Schaum
Clivina fossor (Linnaeus)
Broscus cephalotes (Linnaeus)
Patrobus assimilis Chaudoir
Patrobus atrorufus (Ström)
Trechus obtusus Erichson
Trechus quadristriatus (Schrank)
Trechus rubens (Fabricius)
Trechus secalis (Paykull)
Trechus micros (Herbst)
Asaphidion flavipes (Linnaeus)
Bembidion lampros (Herbst)
Bembidion properans Stephens
Bembidion bipunctatum (Linnaeus)
Bembidion varium (Olivier)
Bembidion bruxellense Wesmael
Bembidion femoratum Sturm
Bembidion tetracolum Say
Bembidion quadrimaculatum (Linnaeus)
Bembidion schueppeli Dejean
Bembidion minimum (Fabricius)
Bembidion obtusum Serville
Bembidion harpaloides Serville
Bembidion aeneum Germar
Bembidion biguttatum (Fabricius)
Bembidion guttula (Fabricius)
Bembidion unicolor Chaudoir
Pogonus chalceus (Marsham)
Stomis pumicatus (Panzer)
Pterostichus adstrictus Eschscholtz
Pterostichus aethiops (Panzer)
Pterostichus cupreus (Linnaeus)
Pterostichus diligens (Sturm)
Pterostichus madidus (Fabricius)
Pterostichus melanarius (Illiger)
Pterostichus minor (Gyllenhal)
Pterostichus niger (Schaller)
Pterostichus nigrita (Paykull)
Pterostichus rhaeticus Heer
Pterostichus strenuus (Panzer)
Pterostichus vernalis (Panzer)
Pterostichus versicolor (Sturm)
Abax parallelepipedus (Piller & Mitterpacher)
Calathus cinctus Motschulsky
Calathus erratus C.R.Sahlberg
Calathus fuscipes (Goeze)
Calathus melanocephalus (Linnaeus)
Calathus micropterus (Duftschmid)
Calathus mollis (Marsham)
Calathus piceus (Marsham)
Laemostenus terricola (Herbst)
Synuchus nivalis (Panzer)
Olisthopus rotundatus (Paykull)
Agonum albipes (Fabricius)
Agonum assimile (Paykull)
Agonum dorsale (Pontoppidan)
Agonum fuliginosum (Panzer)
Agonum marginatum (Linnaeus)
Agonum muelleri (Herbst)
Agonum nigrum Dejean
Agonum piceum (Linnaeus)
Agonum viduum (Panzer)
Amara aenea (Degeer)
Amara apricaria (Paykull)
Amara aulica (Panzer)
Amara bifrons (Gyllenhal)
Amara communis (Panzer)
Amara familiaris (Duftschmid)
Amara fulva (O.F.Müller)
Amara lunicollis Schiödte
Amara ovata (Fabricius)
Amara plebeja (Gyllenhal)
Amara similata (Gyllenhal)

Appendix 2. continued

Amara tibialis (Paykull)
Harpalus rufipes (Degeer)
Harpalus affinis (Schrank)
Harpalus latus (Linnaeus)
Harpalus rubripes (Duftschmid)
Harpalus tardus (Panzer)
Anisodactylus binotatus (Fabricius)
Trichocellus cognatus (Gyllenhal)
Trichocellus placidus (Gyllenhal)
Bradycellus harpalinus (Serville)
Bradycellus ruficollis (Stephens)
Badister bipustulatus (Fabricius)
Dromius linearis (Olivier)
Metabletus foveatus (Fourcroy)

Appendix 3. Calculation of management intensity bands.

Site code	Sward type	Sward age	Cutting	Grazing	Inorganic inputs	Organic inputs	Total score	Management intensity band
ACRE89A	2	3	1	2	2	3	13	4
ACRE89C	3	3	0	3	3	2	14	4
ACRE93A	2	2	1	2	2	3	12	4
ACRE93C	3	2	0	3	3	2	13	4
AUCH90F	0	0	0	1	0	0	1	1
AUCH90G	0	0	0	1	0	0	1	1
BUNG89A	1	3	1	2	0	0	7	3
BUNG89C	1	3	1	2	0	3	10	3
BUNG93A	1	2	1	2	0	0	6	2
BUNG93C	1	2	1	2	0	3	9	3
CAER89A	0	0	0	0	0	0	0	1
CAER93A	0	0	0	0	0	0	0	1
CAER93D	0	0	0	2	0	0	2	1
CAER93E	0	0	0	2	0	0	2	1
CAER93F	0	0	0	2	0	0	2	1
CAIR90C	0	0	0	3	0	0	3	2
CAIR90D	0	0	0	3	0	0	3	2
CAIR90E	0	0	0	3	0	0	3	2
FEOC90H	0	0	0	2	0	0	2	1
FEOC90J	0	0	0	2	0	0	2	1
HULE93S	0	0	0	1	0	0	1	1
HULE93T	0	0	0	1	0	0	1	1
ISLA93K	2	2	1	2	1	1	9	3
ISLA93L	2	1	0	2	1	1	7	3
ISLA93M	3	2	2	2	3	2	14	4
KELT93A	3	2	3	2	3	3	16	5
KELT93B	3	2	3	2	3	3	16	5
KELT93C	3	2	3	2	3	3	16	5

Appendix 3. continued

Site code	**Sward type**	**Sward age**	***Cutting***	**Grazing**	**Inorganic inputs**	**Organic inputs**	**Total management score**	**Management intensity band**
LOCH89A	1	3	1	2	0	0	7	3
LOCH89C	1	3	2	2	0	0	8	3
LOCH89E	1	3	1	2	0	0	7	3
LOCH93A	1	2	1	2	0	0	6	2
LOCH93C	1	2	2	2	0	0	7	3
LOCH93E	1	2	1	2	0	0	5	2
MACA90A	2	1	0	3	0	0	6	2
MACA90B	2	1	0	3	0	0	6	2
MAUC94A	3	2	2	2	3	3	15	5
MAUC94B	3	2	0	3	2	1	11	4
MERS94A	1	2	0	3	1	1	8	3
MERS94B	1	2	0	3	1	1	8	3
MERS94C	3	3	3	0	3	3	15	5
MERS94D	0	0	0	0	0	0	0	1
MIDD93G	1	0	0	2	0	2	5	2
MIDD93H	1	0	0	2	0	2	5	2
MIDD93J	1	0	0	2	0	2	5	2
MUIR94C	3	2	3	2	3	3	16	5
MUIR94D	3	2	3	2	3	0	13	4
NETH89A	3	3	3	2	3	3	17	5
NETH93A	3	2	3	2	3	3	16	5
SHEW90K	1	2	0	0	0	0	3	2
SHEW90M	0	1	0	0	0	0	1	1
SHEW90N	1	2	0	0	0	0	3	2
VANE93N	3	2	0	2	2	2	11	4
VANE93P	0	0	0	1	0	0	1	1
VANE93R	3	2	0	2	2	2	11	4

Appendix 4. The first two axes of the DECORANA ordination of the carabid assemblages of 110 sites in central and southern Scotland. Sample (site) scores.

Site code	**Axis 1 Eigenvalue .551**		**Axis 2 Eigenvalue .479**	
	Replicates		**Replicates**	
	1	2	1	2
ACRE89A	46	40	202	200
ACRE89C	50	48	213	210
ACRE93A	0	3	205	207
ACRE93C	5	9	210	214
AUCH90F	243	261	111	75
AUCH90G	227	213	207	226
BUNG89A	50	45	217	217
BUNG89C	64	66	211	210
BUNG93A	45	32	226	226
BUNG93C	39	44	231	237
CAER89A	166	181	135	117
CAER93A	255	243	65	80
CAER93D	172	152	186	180
CAER93E	151	165	172	184
CAER93F	158	170	135	143
CAIR90C	247	239	220	191
CAIR90D	238	247	298	257
CAIR90E	268	306	141	139
FEOC90H	284	268	75	118
FEOC90J	297	295	26	100
HULE93S	336	344	17	0
HULE93T	294	293	41	57
ISLA93K	100	93	161	151
ISLA93L	134	181	168	126
ISLA93M	95	82	193	203
KELT93A	76	68	184	196
KELT93B	73	66	202	205
KELT93C	41	34	181	180
LOCH89A	36	40	220	212
LOCH89C	72	71	213	218
LOCH89E	86	86	183	182
LOCH93A	86	73	232	226
LOCH93C	77	85	223	227
LOCH93E	129	129	153	170
MACA90A	96	92	179	176
MACA90B	95	83	172	174
MAUC94A	68	65	185	178
MAUC94B	101	87	185	189
MERS94A	48	105	235	196
MERS94B	101	95	240	242
MERS94C	44	49	246	236
MERS94D	268	294	378	396
MIDD93G	129	158	240	261
MIDD93H	245	194	104	149
MIDD93J	202	172	256	242
MUIR94C	66	67	190	190
MUIR94D	61	60	186	180
NETH89A	34	32	218	217
NETH93A	13	15	231	239
SHEW90L	347	306	395	372
SHEW90M	204	221	219	278
SHEW90N	315	270	366	313
VANE93N	111	104	216	216
VANE93P	89	140	229	171
VANE93R	122	143	242	272

Appendix 5. The first two axes of the DECORANA ordination of the carabid assemblages of 110 sites in central and southern Scotland. Species scores.

Species	**Axis 1** **Eig. .551**	**Axis 2** **Eig. .479**
Abax parallelepipedus (Piller & Mitterpacher)	270	48
Agonum albipes (Fabricius)	-31	183
Agonum assimile (Paykull)	-37	192
Agonum dorsale (Pontoppidan)	-36	240
Agonum fuliginosum (Panzer)	285	24
Agonum marginatum (Linnaeus)	208	373
Agonum muelleri (Herbst)	59	135
Agonum nigrum Dejean	156	228
Agonum piceum (Linnaeus)	-5	128
Agonum viduum (Panzer)	-27	308
Amara aenea (Degeer)	188	386
Amara apricaria (Paykull)	-46	250
Amara aulica (Panzer)	193	287
Amara bifrons (Gyllenhal)	151	379
Amara communis (Panzer)	211	354
Amara familiaris (Duftschmid)	12	280
Amara fulva (O.F.Müller)	303	429
Amara lunicollis Schiödte	316	367
Amara ovata (Fabricius)	-81	255
Amara plebeja (Gyllenhal)	123	203
Amara similata (Gyllenhal)	-65	211
Amara tibialis (Paykull)	343	449
Anisodactylus binotatus (Fabricius)	-33	260
Asaphidion flavipes (Linnaeus)	-19	316
Badister bipustulatus (Fabricius)	311	405
Bembidion aeneum Germar	96	168
Bembidion biguttatum (Fabricius)	207	93
Bembidion bipunctatum (Linnaeus)	183	100
Bembidion bruxellense Wesmael	83	311
Bembidion femoratum Sturm	-58	302
Bembidion guttula (Fabricius)	59	197
Bembidion harpaloides Serville	194	96
Bembidion lampros (Herbst)	-68	225
Bembidion minimum (Fabricius)	170	243
Bembidion obtusum Serville	57	120
Bembidion properans Stephens	293	422
Bembidion quadrimaculatum (Linnaeus)	59	331
Bembidion schueppeli Dejean	-20	198
Bembidion tetracolum Say	29	314
Bembidion unicolor Chaudoir	289	50
Bembidion varium (Olivier)	152	177
Blethisa multipunctata (Linnaeus)	196	95
Bradycellus harpalinus (Serville)	334	432
Bradycellus ruficollis (Stephens)	420	-98
Broscus cephalotes (Linnaeus)	327	442
Calathus cinctus Motschulsky	357	459
Calathus erratus C.R.Sahlberg	424	472
Calathus fuscipes (Goeze)	279	409
Calathus melanocephalus (Linnaeus)	241	346
Calathus micropterus (Duftschmid)	349	-7

Appendix 5. continued

Calathus mollis (Marsham)	362	461
Calathus piceus (Marsham)	-68	228
Carabus arvensis Herbst	341	107
Carabus clatratus Linnaeus	226	70
Carabus granulatus Linnaeus	245	66
Carabus nemoralis O.F. Müller	161	288
Carabus nitens Linnaeus	392	-47
Carabus problematicus Herbst	317	357
Carabus violaceus Linnaeus	342	30
Cicindela campestris Linnaeus	446	478
Clivina fossor (Linnaeus)	24	170
Cychrus caraboides (Linnaeus)	284	333
Dromius linearis (Olivier)	253	423
Dyschirius globosus (Herbst)	226	178
Dyschirius luedersi Wagner	147	240
Dyschirius nitidus (Dejean)	152	177
Dyschirius politus (Dejean)	375	466
Dyschirius salinus Schaum	170	243
Elaphrus cupreus Duftschmid	274	45
Elaphrus riparius (Linnaeus)	254	404
Harpalus affinis (Schrank)	202	386
Harpalus latus (Linnaeus)	320	347
Harpalus rubripes (Duftschmid)	387	420
Harpalus rufipes (Degeer)	19	281
Harpalus tardus (Panzer)	407	422
Laemostenus terricola (Herbst)	226	410
Leistus ferrugineus (Linnaeus)	-72	256
Leistus fulvibarbis Dejean	-34	220
Leistus rufescens (Fabricius)	305	356
Loricera pilicornis (Fabricius)	52	163
Metabletus foveatus (Fourcroy)	443	476
Nebria brevicollis (Fabricius)	96	219
Nebria salina Fairmaire & Laboulbène	368	345
Notiophilus aquaticus (Linnaeus)	358	420
Notiophilus biguttatus (Fabricius)	160	266
Notiophilus germinyi Fauvel	355	102
Notiophilus palustris (Duftschmid)	320	24
Notiophilus substriatus Waterhouse	153	312
Olisthopus rotundatus (Paykull)	354	34
Patrobus assimilis Chaudoir	398	-48
Patrobus atrorufus (Ström)	297	75
Pogonus chalceus (Marsham)	330	449
Pterostichus adstrictus Eschscholtz	327	200
Pterostichus aethiops (Panzer)	352	70
Pterostichus cupreus (Linnaeus)	-147	181
Pterostichus diligens (Sturm)	353	2
Pterostichus madidus (Fabricius)	242	262
Pterostichus melanarius (Illiger)	-6	227
Pterostichus minor (Gyllenhal)	310	26
Pterostichus niger (Schaller)	257	63
Pterostichus nigrita (Paykull)	245	59
Pterostichus rhaeticus Heer	375	-40
Pterostichus strenuus (Panzer)	158	179
Pterostichus vernalis (Panzer)	144	161

Appendix 5. continued

Pterostichus versicolor (Sturm)	327	31
Stomis pumicatus (Panzer)	112	97
Synuchus nivalis (Panzer)	257	88
Trechus micros (Herbst)	31	163
Trechus obtusus Erichson	352	-20
Trechus quadristriatus (Schrank)	163	239
Trechus rubens (Fabricius)	279	227
Trechus secalis (Paykull)	390	-80
Trichocellus cognatus (Gyllenhal)	389	-52
Trichocellus placidus (Gyllenhal)	208	77

Appendix 6. Calculated parameters of 55 locations (2 replicates each) in central and southern Scotland.
Band: management intensity band. Log (catch): logarithm of the number of carabid beetles. *S*: number of species.
Residual: residual of the linear regression of log (catch) on *S*. *D*: Simpson's diversity index. *IRS*: individual rarity score.
WML: weight median length. See Section 2 for calculation of management band, *D*, *IRS* and *WML*.

Site code	Band	Log (catch)		*S*		Residual		*D*		*IRS*		*WML* mm	
		Replicates		Replicates		Replicates		Replicates		Replicates		Replicates	
		1	2	1	2	1	2	1	2	1	2	1	2
AUCH90F	1	5.984	5.525	27	20	-0.458	-0.321	0.850	0.783	6.11	6.53	16.9	10.8
AUCH90G	1	6.775	7.241	24	21	0.594	1.305	0.700	0.550	4.12	3.20	14.8	14.1
CAER89A	1	4.317	4.605	15	15	-1.111	-0.821	0.860	0.824	2.00	1.82	17.4	17.4
CAER93A	1	5.493	5.352	16	15	-0.025	-0.081	0.879	0.827	3.12	1.57	18.6	17.8
CAER93D	1	6.410	6.778	27	30	-0.028	0.091	0.807	0.727	8.16	7.99	10.9	10.5
CAER93E	1	5.717	5.642	19	24	-0.047	-0.546	0.748	0.750	3.15	6.37	15.1	14.2
CAER93F	1	4.970	4.820	17	22	-0.629	-1.198	0.782	0.815	1.76	2.40	16.8	17.0
FEOC90H	1	4.898	5.165	15	21	-0.531	-0.775	0.833	0.894	5.04	5.00	17.2	17.4
FEOC90J	1	3.892	4.344	9	9	-1.038	-0.588	0.753	0.696	2.00	3.26	15.4	17.0
HULE93S	1	5.817	6.186	21	20	-0.115	0.339	0.749	0.691	1.68	1.60	10.3	9.9
HULE93T	1	5.537	5.911	22	33	-0.478	-1.031	0.891	0.880	21.27	14.48	13.9	17.3
MERS94D	1	6.045	6.735	32	29	-0.807	0.125	0.617	0.788	5.94	9.45	12.1	12.1
SHEW90M	1	4.489	4.078	20	15	-1.361	-1.351	0.885	0.839	4.45	3.70	22.6	23.6
VANE93P	1	6.142	4.419	16	18	0.625	-1.263	0.753	0.865	1.77	1.82	12.9	14.3
BUNG93A	2	6.807	6.444	26	24	0.456	0.254	0.754	0.751	2.41	2.90	14.3	14.7
CAIR90C	2	5.945	5.464	26	25	-0.404	-0.810	0.912	0.891	5.11	4.45	15.5	13.8
CAIR90D	2	6.105	6.342	22	23	0.082	0.238	0.655	0.794	3.59	5.83	12.7	14.2
CAIR90E	2	5.565	5.366	24	24	-0.626	-0.816	0.895	0.887	3.98	3.81	13.1	11.9
LOCH93A	2	6.258	5.948	22	21	0.242	0.015	0.803	0.707	2.06	2.17	14.1	14.2
LOCH93E	2	5.587	5.226	18	25	-0.093	-1.040	0.824	0.880	2.01	2.81	11.9	11.8

Appendix 6. continued

Site code	Band	Log (catch)		*S*		Residual		*D*		*IRS*		*WML*	
		Replicates		Replicates		Replicates		Replicates		Replicates		Replicates	
		1	2	1	2	1	2	1	2	1	2	1	2
MACA90A	2	6.538	6.504	20	16	0.689	0.985	0.803	0.832	3.27	3.87	11.7	11.6
MACA90B	2	6.560	6.611	22	25	0.542	0.340	0.867	0.833	3.70	3.16	11.6	10.8
MIDD93G	2	4.673	4.673	16	17	-0.845	-0.929	0.883	0.843	1.82	1.92	12.1	12.0
MIDD93H	2	4.369	5.024	15	20	-1.061	-0.831	0.875	0.896	3.43	2.27	17.9	12.1
MIDD93J	2	5.303	5.784	20	31	-0.551	-0.993	0.829	0.807	1.59	1.62	13.1	12.6
SHEW90L	2	6.335	5.826	30	23	-0.349	-0.272	0.668	0.786	6.20	6.09	11.0	11.4
SHEW90N	2	5.112	5.011	14	23	-0.238	-1.092	0.788	0.884	18.20	11.85	17.9	17.8
BUNG89A	3	7.093	6.927	21	21	1.155	0.995	0.687	0.693	1.84	1.88	14.0	14.0
BUNG89C	3	6.468	6.410	23	23	0.368	0.308	0.842	0.856	2.12	2.09	14.4	14.4
BUNG93C	3	6.632	6.542	23	21	0.528	0.605	0.729	0.776	2.60	2.70	14.1	14.1
ISLA93K	3	4.890	5.403	14	13	-0.458	0.136	0.641	0.485	2.32	2.51	7.9	7.9
ISLA93L	3	4.304	4.489	16	14	-1.215	-0.858	0.767	0.658	2.18	2.39	11.2	9.2
LOCH89A	3	6.576	5.765	22	18	0.562	0.087	0.500	0.640	1.91	1.88	13.8	13.9
LOCH89C	3	6.639	5.919	23	24	0.538	-0.266	0.802	0.819	1.79	2.03	14.3	13.7
LOCH89E	3	6.246	6.240	25	24	-0.020	0.054	0.877	0.826	3.10	2.60	13.3	14.3
LOCH93C	3	6.489	6.604	21	22	0.555	0.582	0.713	0.790	2.18	2.01	13.9	13.9
MERS94A	3	7.382	6.726	20	23	1.529	0.628	0.500	0.652	1.26	1.60	13.3	11.6
MERS94B	3	7.048	6.824	32	28	0.193	0.298	0.776	0.739	2.01	2.02	11.9	12.0
ACRE89A	4	6.501	6.662	20	17	0.649	1.061	0.842	0.818	2.31	2.22	12.7	13.8
ACRE89C	4	6.389	6.159	21	23	0.455	0.058	0.740	0.768	2.23	1.95	14.1	14.5
ACRE93A	4	6.308	6.182	20	19	0.459	0.413	0.685	0.676	3.15	3.11	13.6	13.4
ACRE93C	4	6.073	6.315	20	23	0.219	0.218	0.688	0.620	3.38	3.28	13.7	13.8
ISLA93M	4	4.585	5.142	10	9	-0.432	0.212	0.818	0.705	2.63	1.95	8.1	10.0

Appendix 6. continued

Site code	Band	Log (catch)		*S*		Residual		*D*		*IRS*		*WML*	
		Replicates		Replicates		Replicates		Replicates		Replicates		Replicates	
		1	2	1	2	1	2	1	2	1	2	1	2
MAUC94B	4	5.257	5.606	13	9	-0.004	0.682	0.619	0.623	1.68	1.93	11.3	11.0
MUIR94D	4	4.575	4.575	9	10	-0.358	-0.442	0.615	0.534	2.33	2.04	7.4	7.1
VANE93N	4	5.737	5.768	20	17	-0.111	0.171	0.886	0.867	1.98	2.01	12.0	12.0
VANE93R	4	6.631	6.664	22	21	0.612	0.725	0.815	0.817	2.11	1.99	12.2	12.2
KELT93A	5	5.996	5.855	18	16	0.317	0.345	0.823	0.784	2.05	2.09	11.6	11.5
KELT93B	5	6.402	6.474	18	15	0.717	1.039	0.683	0.732	1.62	1.73	12.1	12.1
KELT93C	5	5.746	5.352	14	13	0.402	0.086	0.800	0.819	2.49	2.73	8.2	8.4
MAUC94A	5	5.394	5.533	12	12	0.210	0.350	0.747	0.721	2.65	1.84	9.5	11.2
MERS94C	5	6.267	6.465	28	29	-0.252	-0.145	0.869	0.881	3.38	3.67	11.0	9.7
MUIR94C	5	5.159	5.371	11	13	0.064	0.106	0.618	0.617	1.89	1.79	9.1	10.9
NETH89A	5	6.806	6.836	17	20	1.211	0.989	0.540	0.495	1.75	1.80	12.9	13.9
NETH93A	5	6.981	7.112	19	22	1.213	1.092	0.677	0.678	2.76	2.86	13.9	13.9

Appendix7. The significance of the difference between pairs of means of species richness (*S*), diversity (*D*), rarity (*IRS*) and body size (*WML*) as tested by *t* = difference between the means÷ standard error of the difference. Entries in **bold** are statistically significant. See Table 2.1 for explanation of Levels.

			Level 0	Level 1	Level 2
S	**Sward type**	n	34	34	12
		Level 1 n=34	-0.5/2.095 =-0.239		
		Level 2 n=12	3.6/2.403 =1.498	**4.1/1.722 =2.381**	
		Level 3 n=30	**4.2/2.080 =2.019**	**4.7/1.231 =3.818**	0.6/1.703 =0.352
	Sward age	n	38	8	46
		Level 1 n=8	2.5/2.562 =0.976		
		Level 2 n=46	2.6/1.903 =1.366	0.1/2.045 =0.049	
		Level 3 n=18	-1.2/2.141 =-0.560	-3.7/2.269 =-1.631	**-3.8/1.484 =-2.561**
	Cutting	n	64	22	8
		Level 1 n=22	-0.1/1.744 =-0.057		
		Level 2 n=8	4.2/2.298 =1.828	4.3/2.192 =1.962	
		Level 3 n=16	**3.8/1.877 =2.024**	**3.9/1.744 =2.236**	-0.4/2.298 =-0.174
	Grazing	n	14	10	66
		Level 1 n=10	-0.5/3.299 =-0.152		
		Level 2 n=66	3.1/2.914 =1.064	**3.6/1.802 =2.000**	
		Level 3 n=20	-0.3/3.078 =-0.098	0.2/2.057 =0.097	**-3.4/1.356 =-2.507**
	Inorganic input	n	68	8	10
		Level 1 n=8	1.4/2.221 =0.630		
		Level 2 n=10	3.6/2.064 =1.744	2.2/2.457 =0.900	
		Level 3 n=24	**4.6/1.642 =2.802**	3.2/2.115 =1.513	1.0/1.950 =0.513
	Organic input	n	60	10	16
		Level 1 n=10	2.9/2.210 =1.312		
		Level 2 n=16	2.0/1.945 =1.028	-0.9/2.182 =-0.412	
		Level 3 n=24	2.6/1.781 =1.460	-0.3/2.037 =-0.147	0.6/1.747 =0.343

Appendix 7. continued

			Level 0	Level 1	Level 2
D	**Sward type**	n	34	34	12
		Level 1 n=34	0.026/0.0384 =0.676		
		Level 2 n=12	0.054/0.0450 =1.201	0.028/0.0337 =0.832	
		Level 3 n=30	0.076/0.0390 =1.951	0.050/0.0251 =1.990	0.022/0.0342 =0.642
	Sward age	n	38	8	46
		Level 1 n=8	-0.008/0.0470 =-0.170		
		Level 2 n=46	**0.078/0.0349 =2.234**	**0.086/0.0375 =2.292**	
		Level 3 n=18	0.052/0.0393 =1.324	0.060/0.0416 =1.441	-0.026/0.0272 =-0.954
	Cutting	n	64	22	8
		Level 1 n=22	0.44/0.0328 =1.341		
		Level 2 n=8	0.020/0.0432 =0.462	-0.024/0.0412 =-0.582	
		Level 3 n=16	**0.086/0.0353 =2.436**	0.042/0.0328 =1.280	0.066/0.0432 =1.526
	Grazing	n	14	10	66
		Level 1 n=10	0.043/0.0638 =0.674		
		Level 2 n=66	0.063/0.0563 =1.118	0.020/0.0348 =0.574	
		Level 3 n=20	0.059/0.0595 =0.992	0.016/0.0398 =0.402	-0.004/0.0262 =-0.153
	Inorganic input	n	68	8	10
		Level 1 n=8	**0.141/0.0402 =3.509**		
		Level 2 n=10	0.028/0.0374 =0.750	**-0.113/0.0445 =-2.542**	
		Level 3 n=24	**0.086/0.0297 =2.900**	-0.055/0.0383 =-1.438	0.058/0.0353 =1.644
	Organic input	n	60	10	16
		Level 1 n=10	**0.134/0.0391 =3.428**		
		Level 2 n=16	-0.024/0.0344 =-0.698	**-0.158/0.0386 =-4.093**	
		Level 3 n=24	0.042/0.0315 =1.333	**-0.092/0.0360 =-2.553**	**0.066/0.0309 =2.136**

Appendix 7. continued

			Level 0	Level 1	Level 2
IRS	**Sward type**	n	34	34	12
		Level 1 n=34	1.75/1.112 =1.574		
		Level 2 n=12	2.05/1.300 =1.577	0.30/0.973 =0.308	
		Level 3 n=30	**2.61/1.126 =2.318**	0.86/0.726 =1.184	0.56/0.990 =0.566
	Sward age	n	38	8	46
		Level 1 n=8	1.16/1.424 =0.815		
		Level 2 n=46	1.50/1.057 =1.419	0.34/1.137 =0.300	
		Level 3 n=18	2.25/1.190 =1.891	1.09/1.261 =0.864	0.75/0.825 =0.909
	Cutting	n	64	22	8
		Level 1 n=22	1.81/0.965 =1.876		
		Level 2 n=8	2.07/1.272 =1.627	0.26/1.212 =0.214	
		Level 3 n=16	1.90/1.038 =1.830	0.09/0.965 =0.093	-0.17/1.272 =-0.134
	Grazing	n	14	10	66
		Level 1 n=10	-0.44/1.707 =-0.258		
		Level 2 n=66	**3.24/1.507 =2.150**	**3.68/0.932 5 =3.946**	
		Level 3 n=20	2.71/1.592 =1.702	**3.15/1.064 =2.960**	-0.53/0.701 =-0.756
	Inorganic input	n	68	8	10
		Level 1 n=8	2.09/1.264 =1.653		
		Level 2 n=10	1.88/1.175 =1.600	-0.21/1.398 =-0.150	
		Level 3 n=24	1.76/0.934 =1.884	-0.21/1.203 =-0.175	-0.12/1.109 =-0.108
	Organic input	n	60	10	16
		Level 1 n=10	**2.39/1.181 =2.024**		
		Level 2 n=16	**2.12/1.040 =2.038**	-0.27/1.166 =-0.232	
		Level 3 n=24	**1.99/0.952 =2.090**	-0.40/1.089 =-0.367	-0.13/0.934 =-0.139

Appendix 7. continued

			Level 0	Level 1	Level 2
WML	**Sward type**	n	34	34	12
		Level 1 n=34	1.4/0.924 =1.515		
		Level 2 n=12	**3.7/1.080 =3.426**	**2.3/0.809 =2.842**	
		Level 3 n=30	**3.7/0.936 =3.951**	**2.3/0.604 =3.810**	0
	Sward age	n	38	8	46
		Level 1 n=8	0.3/1.283 =0.234		
		Level 2 n=46	**2.3/0.953 =2.413**	2.0/1.024 =1.953	
		Level 3 n=18	0.8/1.073 =0.746	0.5/1.136 =0.440	**-1.5/0.744 =-2.018**
	Cutting	n	64	22	8
		Level 1 n=22	0.7/0.873 =0.802		
		Level 2 n=8	2.1/1.150 =1.826	1.4/1.097 =1.276	
		Level 3 n=16	**3.0/0.939 =3.194**	**2.3/0.873 =2.635**	0.9/1.150 =0.783
	Grazing	n	14	10	66
		Level 1 n=10	2.2/1.673 =1.315		
		Level 2 n=66	**3.0/1.477 =2.031**	0.8/0.914 =0.875	
		Level 3 n=20	3.0/1.561 =1.922	0.8/1.043 =0.767	0
	Inorganic input	n	68	8	10
		Level 1 n=8	**3.7/1.060 =3.491**		
		Level 2 n=10	1.9/0.986 =1.928	-1.8/1.173 =-1.534	
		Level 3 n=24	**3.1/0.784 =3.954**	-0.6/1.010 =-0.594	1.2/0.931 =1.289
	Organic input	n	60	10	16
		Level 1 n=10	**3.4/1.075 =3.163**		
		Level 2 n=16	1.5/0.946 =1.585	-1.9/1.061 =-1.791	
		Level 3 n=24	**2.0/0.867 =2.308**	-1.4/0.991 =-1.413	0.5/0.850 =0.588

Appendix 8. The first two axes of the DECORANA ordination of the carabid assemblages of 61 grassland sites in north-east England. Sample (site) scores.

Site no.	Band	Axis 1 Eig.0.620	Axis 2 Eig. 0.426
1	1	143	298
2	1	373	263
3	1	117	96
4	1	42	182
5	1	66	171
6	1	17	172
7	1	49	179
8	1	63	99
9	1	126	151
10	1	0	160
11	1	2	163
12	1	48	173
13	1	142	0
14	1	111	20
15	1	28	169
16	1	23	168
17	1	283	345
18	1	39	129
19	1	93	145
20	1	19	166
21	2	143	213
22	2	265	231
23	2	299	252
24	2	262	230
25	3	106	192
26	3	48	145
27	3	94	206
28	3	301	333
29	3	97	78
30	3	284	365
31	3	173	161
32	4	131	181
33	4	22	149
34	4	236	77
35	4	131	197
36	4	139	119
37	4	184	175
38	4	183	124
39	4	119	168
40	5	229	129
41	5	327	81
42	5	296	70
43	5	239	114
44	5	222	99
45	5	214	83
46	5	264	18
47	5	246	93

Appendix 8. continued

48	5	251	84
49	5	171	150
50	5	224	108
51	5	218	125
52	5	302	74
53	5	305	31
54	5	245	88
55	5	307	33
56	5	324	43
57	5	357	55
58	5	289	99
59	5	298	119
60	5	191	159
61	5	294	87

Appendix 9. The first two axes of the DECORANA ordination of the carabid assemblages of 61 grassland sites in north-east England. Species scores.

Species	Axis 1 Eig. 0.620	Axis 2 Eig. 0.426
Abax parallelepipedus (Piller & Mitterpacher)	-25	200
Agonum albipes (Fabricius)	463	331
Agonum dorsale (Pontoppidan)	94	189
Agonum fuliginosum (Panzer)	291	321
Agonumgracile (Sturm)	367	29
Agonum moestum (Duftschmid)	381	438
Agonum muelleri (Herbst)	345	86
Agonum obscurum (Herbst)	79	329
Agonum piceum (Linnaeus)	363	421
Agonum thoreyi Dejean	419	391
Amara aenea (Degeer)	73	160
Amara apricaria (Paykull)	248	195
Amara aulica (Panzer)	26	143
Amara bifrons (Gyllenhal)	168	19
Amara communis (Panzer)	131	342
Amara eurynota (Panzer)	106	274
Amara familiaris (Duftschmid)	158	128
Amara fulva (O.F.Müller)	110	-154
Amara lunicollis Schiödte	148	57
Amara ovata (Fabricius)	71	178
Amara plebeja (Gyllenhal)	336	-21
Amara praetermissa (Sahlberg)	44	185
Amara similata (Gyllenhal)	-15	186
Amara tibialis (Paykull)	123	146
Asaphidion flavipes (Linnaeus)	178	171
Badister bipustulatus (Fabricius)	0	228
Bembidion aeneum Germar	265	151
Bembidion biguttatum (Fabricius)	139	393
Bembidion bruxellense Wesmael	208	93
Bembidion guttula (Fabricius)	292	197
Bembidion lampros (Herbst)	75	141
Bembidion monticola Sturm	306	-224
Bembidion obtusum Serville	47	298
Bembidion quadrimaculatum (Linnaeus)	-15	186
Bembidion tetracolum Say	395	233
Bembidion unicolor Chaudoir	175	400
Bembidion varium (Olivier)	106	274
Bradycellus harpalinus (Serville)	103	169
Bradycellus verbasci (Duftschmid)	120	7
Calathus fuscipes (Goeze)	90	24
Calathus melanocephalus (Linnaeus)	152	73
Carabus granulatus Linnaeus	371	437
Carabus nemoralis O.F. Müller	0	131
Carabus problematicus Herbst	196	29
Carabus violaceus Linnaeus	28	169

Appendix 9. continued

Cicindela campestris Linnaeus	102	-133
Clivina fossor (Linnaeus)	208	189
Cychrus caraboides (Linnaeus)	24	288
Dromius linearis (Olivier)	25	224
Dromius notatus Stephens	83	-76
Dyschirius politus (Dejean)	115	-167
Elaphrus cupreus Duftschmid	420	260
Harpalus affinis (Schrank)	104	-93
Harpalus latus (Linnaeus)	-87	149
Harpalus rubripes (Duftschmid)	95	-73
Harpalus rufipes (Degeer)	73	152
Harpalus tardus (Panzer)	97	-37
Leistus ferrugineus (Linnaeus)	-2	191
Leistus rufescens (Fabricius)	75	363
Loricera pilicornis (Fabricius)	378	19
Nebria brevicollis (Fabricius)	256	65
Nebria salina Fairmaire & Laboulbène	232	-33
Notiophilus aquaticus (Linnaeus)	57	164
Notiophilus biguttatus (Fabricius)	163	91
Notiophilus germinyi Fauvel	-34	202
Notiophilus palustris (Duftschmid)	41	75
Notiophilus substriatus Waterhouse	92	309
Patrobus assimilis Chaudoir	371	0
Patrobus atrorufus (Ström)	226	212
Pterostichus adstrictus Eschscholtz	291	28
Pterostichus aethiops (Panzer)	168	149
Pterostichus cristatus (Dufour)	67	323
Pterostichus diligens (Sturm)	338	279
Pterostichus madidus (Fabricius)	-10	160
Pterostichus melanarius (Illiger)	140	246
Pterostichus minor (Gyllenhal)	374	431
Pterostichus niger (Schaller)	105	190
Pterostichus nigrita (Paykull)	343	286
Pterostichus strenuus (Panzer)	181	323
Pterostichus vernalis (Panzer)	174	305
Pterostichus versicolor (Sturm)	369	434
Stomis pumicatus (Panzer)	-24	205
Synuchus nivalis (Panzer)	106	112
Trechus micros (Herbst)	262	199
Trechus obtusus Erichson	41	233
Trechus quadristriatus (Schrank)	197	126
Trechus secalis (Paykull)	185	390

Appendix 10. The first two axes of the DECORANA ordination of the carabid assemblages of nine sites (two replicates per site) at Crichton Royal farm and Caerlaverock in 1989 and 1993. Sample (site) scores.

Site and Year	**Axis 1 Eig. 0.524**	**Axis 2 Eig. 0.181**
Bungalow Slurry A 1989	49	39
Bungalow Slurry B 1989	57	44
Bungalow Slurry A 1993	19	36
Bungalow Slurry B 1993	17	48
Bungalow No Slurry A 1989	32	11
Bungalow No Slurry B 1989	29	14
Bungalow No Slurry A 1993	29	55
Bungalow No Slurry B 1993	24	96
Lochbank One-cut A 1989	57	38
Lochbank One-cut B 1989	58	43
Lochbank One-cut A 1993	44	0
Lochbank One-cut B 1993	46	2
Lochbank Two-cut A 1989	32	10
Lochbank Two-cut B 1989	44	22
Lochbank Two-cut A 1993	35	15
Lochbank Two-cut B 1993	30	15
Wet Lochbank A 1989	98	78
Wet Lochbank B 1989	100	55
Wet Lochbank A 1993	151	60
Wet Lochbank B 1993	142	70
Acrehead Clover A 1989	53	120
Acrehead Clover B 1989	53	106
Acrehead Clover A 1993	16	166
Acrehead Clover B 1993	16	168
Acrehead Ryegrass A 1989	46	59
Acrehead Ryegrass B 1989	48	66
Acrehead Ryegrass A 1993	14	143
Acrehead Ryegrass B 1993	11	158
Netherwood Ryegrass A 1989	28	11
Netherwood Ryegrass B 1989	27	13
Netherwood Ryegrass A 1993	1	49
Netherwood Ryegrass B 1993	0	49
Caerlaverock NNR A 1989	236	99
Caerlaverock NNR B 1989	224	81
Caerlaverock NNR A 1993	316	77
Caerlaverock NNR B 1993	289	64

Appendix 11. The first two axes of the DECORANA ordination of the carabid assemblages of nine sites (two replicates per site) at Crichton Royal Farm and Caerlaverock in 1989 and 1993. Species scores.

Species	**Axis 1**	**Axis 2**
	Eig. .524	**Eig. .181**
Abax parallelepipedus (Piller & Mitterpacher)	385	75
Agonum assimile (Paykull)	-60	-38
Agonum dorsale (Pontoppidan)	5	28
Agonum fuliginosum (Panzer)	136	68
Agonum muelleri (Herbst)	0	257
Agonum nigrum Dejean	168	145
Amara aenea (Degeer)	1	63
Amara apricaria (Paykull)	11	104
Amara aulica (Panzer)	-25	-120
Amara bifrons (Gyllenhal)	-3	76
Amara communis (Panzer)	10	-137
Amara familiaris (Duftschmid)	35	-17
Amara lunicollis Schiödte	132	125
Amara ovata (Fabricius)	-91	-90
Amara plebeja (Gyllenhal)	86	169
Amara similata (Gyllenhal)	-60	-185
Amara tibialis (Paykull)	56	17
Anisodactylus binotatus (Fabricius)	-46	-170
Asaphidion flavipes (Linnaeus)	-40	234
Badister bipustulatus (Fabricius)	-38	143
Bembidion aeneum Germar	241	208
Bembidion biguttatum (Fabricius)	168	145
Bembidion bruxellense Wesmael	1	-61
Bembidion guttula (Fabricius)	153	181
Bembidion lampros (Herbst)	-43	216
Bembidion obtusum Serville	167	40
Bembidion tetracolum Say	59	130
Bembidion unicolor Chaudoir	305	57
Blethisa multipunctata (Linnaeus)	461	92
Calathus fuscipes (Goeze)	-40	-38
Calathus melanocephalus (Linnaeus)	56	35
Calathus piceus (Marsham)	-35	-46
Carabus granulatus Linnaeus	404	75
Carabus nemoralis O.F. Müller	137	29
Clivina fossor (Linnaeus)	180	187
Cychrus caraboides (Linnaeus)	295	94
Dromius linearis (Olivier)	-35	191
Dyschirius globosus (Herbst)	260	93
Elaphrus cupreus Duftschmid	391	69
Elaphrus riparius (Linnaeus)	168	145
Harpalus affinis (Schrank)	-80	-22
Harpalus rufipes (Degeer)	22	110
Laemostenus terricola (Herbst)	3	-125
Leistus ferrugineus (Linnaeus)	-68	-173
Leistus fulvibarbis Dejean	15	35

Appendix 11. continued

Leistus rufescens (Fabricius)	285	121
Loricera pilicornis (Fabricius)	85	131
Nebria brevicollis (Fabricius)	41	-40
Notiophilus biguttatus (Fabricius)	-28	153
Notiophilus substriatus Waterhouse	23	16
Pterostichus cupreus (Linnaeus)	-70	412
Pterostichus diligens (Sturm)	444	82
Pterostichus madidus (Fabricius)	-25	27
Pterostichus melanarius (Illiger)	5	-22
Pterostichus minor (Gyllenhal)	461	92
Pterostichus niger (Schaller)	232	37
Pterostichus nigrita (Paykull)	272	101
Pterostichus rhaeticus Heer	408	77
Pterostichus strenuus (Panzer)	222	66
Pterostichus vernalis (Panzer)	227	102
Pterostichus versicolor (Sturm)	-41	-197
Stomis pumicatus (Panzer)	196	23
Synuchus nivalis (Panzer)	-34	-204
Trechus micros (Herbst)	154	156
Trechus obtusus Erichson	151	-28
Trechus quadristriatus (Schrank)	12	1
Trichocellus placidus (Gyllenhal)	349	90

Appendix 12. The first two axes of the DECORANA ordination of the carabid assemblages of eight sites (two replicates per site) at Crichton Royal Farm in 1989 and 1993. Sample (site) scores.

Site and Year	**Axis 1 Eig. 0.269**	**Axis 2 Eig. 0.118**
Bungalow Slurry A 1989	68	128
Bungalow Slurry B 1989	69	123
Bungalow Slurry A 1993	56	126
Bungalow Slurry B 1993	55	125
Bungalow No Slurry A 1989	82	116
Bungalow No Slurry B 1989	79	116
Bungalow No Slurry A 1993	50	118
Bungalow No Slurry B 1993	22	120
Lochbank One-cut A 1989	90	106
Lochbank One-cut B 1989	94	91
Lochbank One-cut A 1993	110	127
Lochbank One-cut B 1993	106	143
Lochbank Two-cut A 1989	83	94
Lochbank Two-cut B 1989	86	89
Lochbank Two-cut A 1993	86	137
Lochbank Two-cut B 1993	78	135
Wet Lochbank A 1989	130	67
Wet Lochbank B 1989	134	80
Wet Lochbank A 1993	199	84
Wet Lochbank B 1993	186	76
Acrehead Clover A 1989	68	0
Acrehead Clover B 1989	70	9
Acrehead Clover A 1993	4	49
Acrehead Clover B 1993	6	50
Acrehead Ryegrass A 1989	87	46
Acrehead Ryegrass B 1989	86	49
Acrehead Ryegrass A 1993	15	69
Acrehead Ryegrass B 1993	0	62
Netherwood Ryegrass A 1989	88	83
Netherwood Ryegrass B 1989	87	76
Netherwood Ryegrass A 1993	38	101
Netherwood Ryegrass B 1993	39	99

Appendix 13. The first two axes of the DECORANA ordination of the carabid assemblages of 17 sites (two replicates per site) sampled in 1993. Sample (site) scores.

Site code	**Axis 1 Eig. 0.611**	**Axis 2 Eig. 0.312**
KELT93A1	59	90
KELT93A2	38	94
KELT93B1	44	58
KELT93B2	49	53
KELT93C1	4	150
KELT93C2	0	146
CAER93D1	131	252
CAER93D2	121	276
CAER93E1	103	184
CAER93E2	116	181
CAER93F1	110	182
CAER93F2	122	188
MIDD93G1	94	37
MIDD93G2	106	17
MIDD93H1	214	133
MIDD93H2	158	112
MIDD93J1	163	24
MIDD93J2	141	22
ISLA93K1	53	201
ISLA93K2	50	215
ISLA93L1	85	158
ISLA93L2	138	178
ISLA93M1	38	144
ISLA93M2	26	96
VANE93N1	76	75
VANE93N2	72	60
VANE93P1	64	27
VANE93P2	124	77
VANE93R1	84	20
VANE93R2	87	0
HULE93S1	335	122
HULE93S2	349	127
HULE93T1	289	130
HULE93T2	287	126

Appendix 14. The first two axes of the DECORANA ordination of the carabid assemblages of 17 sites sampled in 1993. Species scores.

Species	**Axis 1** **Eig. .611**	**Axis 2** **Eig. .312**
Agonum albipes (Fabricius)	-128	91
Agonum assimile (Paykull)	-160	85
Agonum dorsale (Pontoppidan)	-131	2
Agonum fuliginosum (Panzer)	276	153
Agonum marginatum (Linnaeus)	19	322
Agonum muelleri (Herbst)	25	255
Agonum nigrum Dejean	100	364
Agonum piceum (Linnaeus)	-48	194
Amara aenea (Degeer)	-81	209
Amara aulica (Panzer)	0	-164
Amara bifrons (Gyllenhal)	152	-70
Amara communis (Panzer)	44	275
Amara familiaris (Duftschmid)	-40	-25
Amara lunicollis Schiödte	127	230
Amara plebeja (Gyllenhal)	144	23
Asaphidion flavipes (Linnaeus)	90	414
Bembidion aeneum Germar	91	329
Bembidion biguttatum (Fabricius)	242	175
Bembidion bipunctatum (Linnaeus)	114	261
Bembidion bruxellense Wesmael	94	-118
Bembidion guttula (Fabricius)	59	40
Bembidion harpaloides Serville	137	202
Bembidion lampros (Herbst)	-130	150
Bembidion minimum (Fabricius)	80	322
Bembidion properans Stephens	90	414
Bembidion tetracolum Say	31	174
Bembidion unicolor Chaudoir	270	170
Bembidion varium (Olivier)	90	414
Blethisa multipunctata (Linnaeus)	-30	84
Bradycellus ruficollis (Stephens)	399	138
Broscus cephalotes (Linnaeus)	120	367
Calathus fuscipes (Goeze)	117	-97
Calathus melanocephalus (Linnaeus)	195	-39
Calathus micropterus (Duftschmid)	335	69
Carabus arvensis Herbst	451	144
Carabus clatratus Linnaeus	221	188
Carabus granulatus Linnaeus	71	262
Carabus nemoralis O.F. Müller	217	23
Carabus nitens Linnaeus	406	135
Carabus problematicus Herbst	282	-12
Carabus violaceus Linnaeus	300	80
Clivina fossor (Linnaeus)	-10	91
Cychrus caraboides (Linnaeus)	291	69
Dyschirius globosus (Herbst)	221	323
Dyschirius luedersi Wagner	82	331
Dyschirius nitidus (Dejean)	90	414
Dyschirius salinus Schaum	80	322
Elaphrus cupreus Duftschmid	266	116
Elaphrus riparius (Linnaeus)	106	391

Appendix 14. continued

Harpalus rufipes (Degeer)	38	267
Leistus rufescens (Fabricius)	317	223
Loricera pilicornis (Fabricius)	169	48
Nebria brevicollis (Fabricius)	45	41
Nebria salina Fairmaire & Laboulbène	189	-33
Notiophilus aquaticus (Linnaeus)	284	-2
Notiophilus biguttatus (Fabricius)	231	-67
Notiophilus germinyi Fauvel	347	111
Notiophilus palustris (Duftschmid)	361	126
Notiophilus substriatus Waterhouse	-20	182
Patrobus assimilis Chaudoir	403	140
Patrobus atrorufus (Ström)	272	-43
Pterostichus adstrictus Eschscholtz	217	23
Pterostichus diligens (Sturm)	330	128
Pterostichus madidus (Fabricius)	215	-54
Pterostichus melanarius (Illiger)	0	-27
Pterostichus niger (Schaller)	247	97
Pterostichus nigrita (Paykull)	158	232
Pterostichus rhaeticus Heer	387	134
Pterostichus strenuus (Panzer)	106	199
Pterostichus vernalis (Panzer)	42	292
Synuchus nivalis (Panzer)	226	64
Trechus micros (Herbst)	62	-145
Trechus otusus Erichson	345	148
Trechus quadristriatus (Schrank)	233	-29
Trechus secalis (Paykull)	361	140
Trichocellus cognatus (Gyllenhal)	361	126
Trichocellus placidus (Gyllenhal)	104	-35