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ASPECTS OF HABITAT SELECTION AND THE INFLUENCE OF BOUNDARIES ON SOME UPLAND INVERTEBRATE COMMUNITIES

Iain Stuart Downie B.Sc. (Paisley)

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I certify that all material in this thesis which is not my own work has been identified and that no material is included for which a degree has previously been conferred on me.

Abstract

Aspects of the distribution and ecology of some surface-dwelling invertebrates were examined on different high-altitude vegetation types in the north Pennines, England. The influence of the boundary between habitats on the invertebrate community was also investigated, and the effects of habitat heterogeneity on invertebrate distribution were discussed.

Spiders and carabids were sampled from the dominant vegetation types on the plateaux of three mountain summits (Cross Fell, Little Dun Fell and Great Dun Fell) in 1991 using pitfall traps. Multivariate methods were used to classify and ordinate the sites based on their fauna and to assess the influence of the local environmental variation on the species distribution. Three spider assemblages were recognised based on their common species composition; two short *Festuca* grassland assemblages and a *Nardus/Eriophorum* assemblage associated with greater vegetation density. The results suggest that variation in the vegetation structure is the major factor influencing spider distribution on the summit plateaux, with slope and soil depth also contributing. The carabids appeared too widely distributed to assign to any specific vegetation types.

The influence of the interface between different vegetation types on the spider and carabid fauna was sampled using pitfall traps in 1992-3. At the boundary between two highly contrasting habitats (sheep pastures and conifer plantations) an edge effect was found in both groups, where species richness was elevated. The major contribution to this increase was the mixing of both pasture and plantation species, species specific to the interface were few. The edge effect at this interface was narrower but larger in spiders than in carabids. At the boundary between two more similar habitats (grazed and ungrazed upland grassland) the edge effect was much reduced, species richness was not elevated, and the level of overlap between habitats was much wider. Edge permeability, structural similarity and altitude were considered the most important factors for the differences between boundaries studied.

It is inferred that in the high altitude invertebrate community most species are widespread crossing boundaries between vegetation types regularly, though some species may have affinities to particular habitats for different aspects of their ecology. The implications that this study has for understanding the effects and impacts of habitat heterogeneity at the landscape level are discussed, such as invertebrate movement patterns, population dynamics and management aspects.

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Chapter 1. General introduction

Habitat heterogeneity and habitat structure are inter-related concepts that refer to variation in pre-existing habitat characteristics in a given area (Hart and Horowitz 1991). All environments show this variation, although the landscape heterogeneity is related to geographical scale. This variation affects the arrangement and selection of organisms for habitats in the physical environment, with organisms selecting their habitats as a result of biotic and abiotic pressures including evolution, competition, climate and physical structure. Southwood (1977) titled his British Ecological Society presidential address "Habitat, the template for ecological strategies?", and suggested that both intra- and inter-habitat variation influenced the adaptational strategies of the organism, outlining the importance of both spatial and temporal habitat characteristics. Each landscape or environment type therefore contains its own characteristic set of organisms, assembled in populations that combine to form the community (Elton 1927, Clapham 1983).

This community composition is one of the fundamental aspects of both biogeography and community ecology. Communities are seldom discrete and may grade continuously in space and time, and species assemblages are not consistent from place to place (Krebs 1985). It is often difficult or impossible to determine where one community ends and the next begins. However, in spite of this continuous variation, separate communities can be identified, as most aspects of species distribution are strongly influenced by the physical environment. Gross variation patterns tend to be controlled by regional differences in the environment, such as climate, and finer patterns are controlled by local heterogeneity within the system (Clapham 1983).

The presence of an environmental gradient is therefore an important limiting factor on the population distribution of any species. Both natural and artificial features, such as changes in soil type, fence placement or even areas of perpetual shade, may induce abrupt boundaries or smooth gradients between vegetation types, and in such situations it may be possible to observe the types of interactions of communities across varying habitats.

Animal community ecology is such an extremely broad ranging subject field that ecologists face a difficult task in studying all the organisms that exist in a particular area; it is more common to study fragments of the whole community (Elton 1949) and concentrate on a single taxonomic group, or perhaps a few groups with key similarities in their ecology. This has led to the specialisation of ecologists into studying specific aspects of each community, which provides a basis for understanding the patterns of the community as a whole. For example, a study of the phylum Arthropoda, whose adaptational success has led to their abundance and diversity in all environments, would be of benefit to both animal and plant ecologists alike, all of whom share an understanding of the importance of biological communities in the balance of the entire ecosystem.

This thesis investigates the habitat preferences of two groups of arthropods: spiders (Araneae) and carabid beetles (Coleoptera: Carabidae) within the invertebrate communities living in upland vegetation types in northern England, and their relationships to various aspects of the physical environment. Both spiders and carabids are represented by a wide range of different species in Britain, and are also readily trapped using simple field sampling techniques. This makes them suitable for both qualitative and quantitative investigations of their community structure, their interactions with the surrounding environment and their relationships between communities.

Spiders are extremely common inhabitants of most terrestrial communities, and are particularly abundant in areas of rich vegetation. As a group, they are generalist predators and have strong dispersal qualities, and they possess a variety of behavioural adaptations for both habitat utilisation and foraging. Studies have uncovered obvious influences of vegetation structure, leaf litter composition, and other aspects of the environment which act upon spider populations (Wise 1993). It is clear the physical structure of environments has an important influence on the distribution and habitat preferences of spider species, directly or indirectly, and ultimately on the composition of spider communities (Coulson and Butterfield 1986, Uetz 1991, Gibson, Hambler and Brown 1992). Biotic factors are important too, interspecific competition accounting for many differences between congeneric species in spatial and temporal distribution (Tretzel 1955).

Carabid beetles occupy a similar feeding niche to spiders, the majority of species are predaceous and surface-dwelling, many species having lost their flight capabilities, or fly spontaneously only on rare occasions (Thiele 1977). Their distribution, like spiders, is similarly controlled by environmental factors such as climate, soil chemistry, the physical structure of the vegetation, and also by biological factors like competition, prey choice and predators (Butterfield and Coulson 1983, Luff *et al.* 1989, McFerran *et al.* 1994a).

The two main objectives of this study are;

1. To observe the variation in spider and carabid species assemblages on sub-montane plateaux habitats as defined by the discrete vegetation types. An attempt will be made to establish the primary causal factors present for this variation.

2. To investigate the influence of boundaries between habitat types on spider and carabid beetle species, examining their distribution and abundance approaching the

interface, and their influence on the adjacent habitats at the edge. Two different types of boundary will be examined, representing both extreme and subtle variation between different habitats.

This sequence of experiments will initially determine if variation in invertebrate species composition of different high altitude vegetation types exists. The extreme boundary situation (hard edge) will show whether any differences in invertebrate distribution exists at the interface between habitats, and the more subtle boundary (soft edge) will provide information on the changes in the species associated with the upland vegetation at their boundaries.

Much of the theory behind biogeography stems from studies on island habitats, based on the fact that they represent replicated natural experiments (Brown and Gibson 1983), where their isolation and varying distances from other habitats result in differences in flora and fauna, from which biogeographers can readily determine the factors that influence the distribution of species. However, islands are not the only cause of isolation (Noonan 1992), many mountains have isolated habitats whose flora or fauna show interesting relationships to those found in other highland areas.

Although relatively small in area and range compared to other alpine areas found throughout the world, the British uplands contain a great variety of landscapes and dependent biotic communities which arise from differences in climate, geology, topography, soils and past-land use (Ratcliffe and Thompson 1988). From a biological point of view, the Cross Fell mountain range is the most important upland massif in England, internationally significant for both the peatland and upland grassland habitats (Ratcliffe 1977). It is one of the largest remaining areas of natural or semi-natural habitat in the country, and therefore represents one of the few opportunities available to study aspects of the biological community in a relatively untouched environment.

The invertebrates associated with this locality represent a unique and under-studied community, providing an ideal natural system for both survey and experimental research. The mosaic of high altitude vegetation types associated with the plateaux of three summits in the north Pennines were sampled for their spider and carabid beetle assemblages in order to observe any differences that exist and the reasons for those variations.

The presence of a boundary between differing but relatively homogeneous habitat types is commonly defined as an ecological transition zone (an ecotone), where there is both a mixture of flora and fauna characteristic of each habitat (Allen and Starr 1982), and also the possibility of species exclusive to that boundary zone. The influence of these characteristics are commonly termed the edge effect (Terrel-Nield 1986). The edge effect may have profound effects on both the physical environment and the species content of habitats, especially close to the interface (Malcolm 1994). Several physical factors contribute to the intensity of the edge effect between habitats, including habitat size and shape, habitat permeability and the sharpness of the boundary (Stamps *et al.* 1987). Any variation in species may be due to both the physical conditions across the transect and the influence of other species present.

The presence and intensity of the edge effect on spider and carabid beetle species across a sharp, extreme ecotone (a sheep pasture - coniferous plantation separated by a fence) will be investigated to provide baseline information on the general interaction of some surface dwelling invertebrates between habitats. This extreme boundary will assess whether or not species of spider and carabid display variation in their distribution between the two habitats, and also assess the influence of the interface.

Once any edge effect relevant to ground-dwelling invertebrates has been established, the same procedures will be applied using a similarly sharp interface but a more subtle or softer ecotone situation, examining the variation in spider and carabid distribution between two sub-montane grassland habitats separated by a fence, where grazing causes differences in the vegetation structure. These two types of habitat are however structurally and climatically more similar than the pasture - plantation transition, and this will provide information relating to the direct influence of habitat permeability on the surface dwelling invertebrates along the transect between the two types of grassland.

The structural modification and progressive fragmentation of natural habitats through human disturbance has increased considerably in recent times (Johnson *et al.* 1981). Therefore the implications that the influence of the interface between the two upland grassland areas has for the variation in species composition and abundance in the discrete sub-montane habitats described earlier are important. This is based on the fact that any invertebrate species assemblage in a given upland habitat island may or may not be directly influenced by the surrounding habitats which could contain a greatly different species assemblage.

There have been many definitions of what represents upland Britain, though as yet there is no consensus or single criterion which satisfy all (Atherden 1992). Altitude is the most widely used measure (Bunce 1987), and gives a useful general overall estimate, however, it does tend to underestimate the area in the north. All the habitats surveyed in this thesis are considered to be upland areas based on their altitude, northerly aspect and land-use type following the proposed limits summarised in Ratcliffe and Thompson (1988). The three pasture-plantation habitats, although all just above 200m, represent the lower altitudinal limit of sampling for invertebrates in this study, but they provided readily accessible areas with similarities in the vegetation to areas much higher in altitude or further north where managed forestry borders typical rough grazing habitats. The exact invertebrate species composition of these lower altitude areas in relation to other higher areas matters little, it is the ecological interactions of the invertebrates within the system being the more important aspect under study.

Chapter 2. General study area

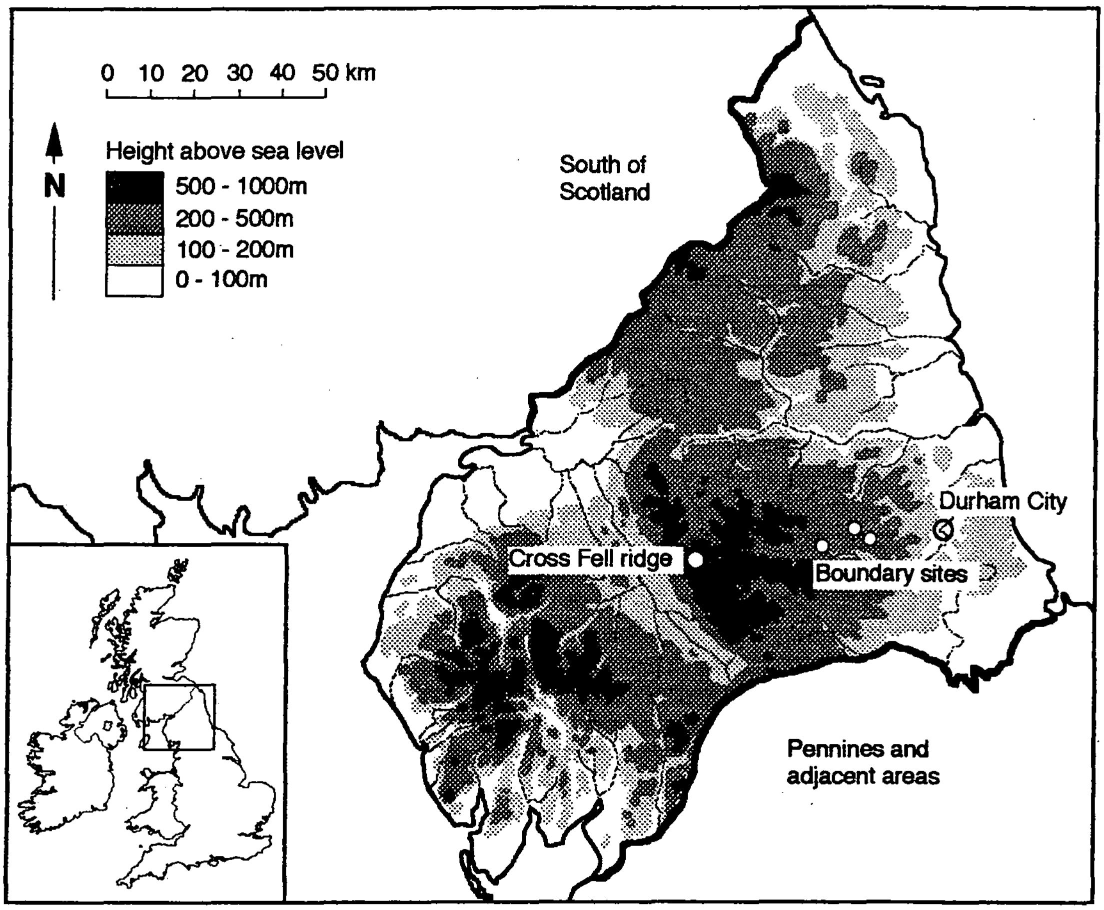
All the sampling areas described in this thesis are located in the north of England, west of Durham City (Figure 2.1). There are two main areas of study; high altitude plateaux habitats and upland pasture/conifer plantation boundary habitats. The high altitude sub-montane plateaux sites are situated at the northern end of the Pennine range in Cumbria (see section 5.2 and 7.2 (plateau boundary site) for detailed descriptions). The upland pasture - plantation boundary sites are all situated in County Durham (see section 6.2 for a detailed description).

The north of England encompasses several counties and is a difficult region to define, but commonly includes the whole of Northumberland, Durham, Cumbria, parts of Lancashire and a little of north Yorkshire (NERC 1978). The chief elements in its topography are the Cheviot Hills and Northumbrian Fells, the northern Pennines, the Cumbrian mountains and Howgill Fells, the Solway Plain and Vale of Eden, and the lowlands of Northumberland and Durham. The main watershed of England, separating east and west-flowing rivers, crosses the Scottish border in the Larriston Fells and the Tyne Gap near Gilsland, thereafter running close to the edge of the west Pennine escarpment until it crosses the Stainmore Gap. The present distribution of high and low land has been strongly influenced by geological factors and the scenery in northern England has also been affected by glacial processes.

Most of the upland areas in England occur in this region, the only exceptions are the Peak district (itself a northern component of the country) and the moorlands of the Devon/Cornwall peninsula which are not nearly as extensive in area or altitude. The uplands therefore represent an important feature of the landscape of England, possessing many unique communities of plant and animal, some not found elsewhere in mainland Britain.

The north of England has been an area of extensive scientific research in many areas of ecology. The extreme variation in the topography and geology from England's highest areas in Cumbria, through the extensive moorland of the north Pennines, to the characteristic Magnesium Limestone sea cliffs of Durham provide researchers with excellent opportunities to study large variation in biology over small geographical distances. The uplands of these areas have been the focus of this research for a number of years. Both the Moor House and the Upper Teesdale National Nature Reserves in the north Pennines are representative of extensive areas of upland Britain. Ecological aspects of Moor House have been studied extensively since 1952 (Heal and Smith 1978, Cragg 1961), as has Upper Teesdale since 1967 (Clapham 1978). The many studies on the flora and fauna have been complemented by long term research on the areas meteorology and the readily accessible high peaks provide ideal conditions for recent studies on the effects of climate change.

Figure 2.1. Map of north of England, showing relative position of sampling areas in relation to Durham City and main topographical features (following NERC 1978). Location as inset.



3.1 Pitfall trapping

The method employed in the collection of the spiders and carabids was pitfall trapping, useful for sampling surface-active animals. They form an inexpensive method of continuous sampling and require little maintenance, and have been used extensively by many investigators (Duffey 1962, Coulson and Butterfield 1986, Turin *et al.* 1991 etc.). However, the usefulness of pitfall traps for collecting the surface - active invertebrate groups has been discussed by many workers (Greenslade 1964a, Obrtel 1971, Luff 1975, Uetz and Unzicker 1976, Baars 1979, Curtis 1980, Halsall and Wratten 1988 and Topping and Sunderland 1992), and there is some debate concerning the pitfall methods suitability for quantitative studies of invertebrate populations. Catches are determined primarily by the numerical density of the invertebrate population at risk and also the level of locomotor activity of the individuals (Greenslade 1964a). The efficiency of the trap is important and this may vary between species, which may show differential susceptibility to trapping according to maturity, size, behaviour and habitat (Curtis 1980). Catches of a single species may vary in different types of ground cover depending on the resistance they present to horizontal movement (Greenslade 1964a), although Halsall and Wratten (1988) found that few differences arose in carabid capture rate when the substrate or trap type was changed in a laboratory situation.

Uetz and Unzicker (1976) compared pitfall traps with quadrat sampling for sampling spiders and gave qualified support for the former method as a suitable means of sampling cursorial spider forms only. Baars (1979) used both field experiments and computer simulations to indicate that continuous pitfall trapping gives reliable relative measures of the sizes of carabid populations. Despite the varied contra-indications to pitfall trapping, the technique is one of the most efficient methods of sampling the surface-active fauna, indeed, probably the best available (Uetz and Unzicker 1976). They sample continuously and are not prone to the problems of spot sampling in time (Topping and Sunderland 1992), thus they have proved to be useful for studying the seasonal and daily variability, the population distribution, the relative abundance in different vegetation types, habitat preference and activity patterns of the species (Thiele 1977).

The pitfall traps used at all sampling sites in this thesis consisted of plastic cups, 70mm in upper diameter, 70mm in depth and 200ml volume, partially filled with a 2% formalin/water solution and detergent to lower the surface tension. Luff (1975) considers plastic cups inferior to glass jars based on the proportion of the catch that escapes, though this was countered by the formalin and detergent solution which wetted and killed specimens which fall in. The arrangement of the pitfall traps varied with the purpose of the experiment and the methods are described in sections 5.3.1 and 6.3.1 for the plateaux and boundary traps respectively.

3.2 Vegetation sampling

Where necessary, the plant community composition of the area sampled was recorded with a 2m by 2m quadrat, the most common size used in the British National Vegetation Classification for sampling mire and grassland vegetation (Rodwell 1991). Each sample was categorised using the computer program TABLEFIT (Hill 1993), which gives the closest NVC code, the type of community, and the degree of similarity to the named type of vegetation.

Vegetation density is considered to have an important influence on the distribution and abundance of invertebrates (Pearson and White 1964, Robinson 1981). Density was assessed using a $0.25m^2$ quadrat placed between each pitfall, within which, five equidistant positions were used to insert a point quadrat pin (a total of 25 points at the plateaux sites and a total of 20 points at the interface sites), measuring the sum number of touches of vegetation in each 10mm height range above the ground. Using this method, higher values indicate a greater density of vegetation. The average gradient of the ground surface was recorded across the pitfall transect using a Suunto Clinometer, where necessary.

3.3 Nomenclature and invertebrate status

Identification of the Araneae was carried out with reference to Roberts (1985-87), Locket and Millidge (1951-53) and Locket *et al.* (1974), and Coleoptera mainly using Joy (1932) and Lindroth (1974). Nomenclature follows Roberts (1985-1987) for the Araneae and Kloet and Hinks (1977) for the Coleoptera. The abbreviated authorities of species are included the first time a binomen is used in the text, except for species of Araneae and Carabidae, where the full authority is included in the appendices relevant to each chapter. Where appropriate, invertebrate species status category definitions follow that of Eversham (1983), where **RDB** applies to species included in the British Red Data Books (Shirt 1987, Bratton 1991). Notable A (**Na**) is used for species which are thought to occur in 30 or fewer 10km squares of the National Grid in Britain. Notable B (**Nb**) species are thought to occur in between 31 and 100km squares of the National Grid.

Chapter 4. A primer on some statistical methods

In this thesis, several descriptive measures are used to quantify the differences in spider and carabid beetle assemblages between habitat types. Two commonly used descriptors are species diversity (which measures the structure and variety of an assemblage), and multivariate analysis (which compares the species content and similarity of several habitats simultaneously). Both these methods are discussed below.

4.1 Species diversity

Species diversity is a measurable characteristic of natural communities which is widely used, and there are essentially two components to this diversity: the number of species, and the structure of the community - the relative abundance of each species (Clapham 1983, Krebs 1985). The simplest measure of diversity is to count the number of species present, referred to as the species richness (S). This method, although straightforward in theory, is difficult to trust in practice as there is usually no distinction between resident, transient, immigrant, common or rare species, and also the numerical structure of the community is completely ignored. The second component of species diversity is that of the heterogeneity or equitability between the numbers of each species.

In any study in population ecology, it is invariably found that a few species are very common, some have medium abundance, and several (sometimes many) are rare, represented by a few individuals. These findings lead to the development of various species abundance models, where the natural variation in the number of common, medium and rare species between communities can be categorised by several different mathematical descriptions of the community (log-normal, gamma, broken-stick, log-series, geometric model, etc.). Reviews of the most commonly described models may be found in Gray (1987), Magurran (1988) and Tokeshi (1993).

However, fitting any of the models described above to real data is fraught with problems (Gray 1987). Data may fit several of the models simultaneously or none at all, and the established goodness-of-fit methods are often of low statistical power (Engen 1978), particularly in communities with relatively small numbers of species (less than 100 species; Tokeshi 1993). Also, in real situations, it is generally impossible to construct a sampling method so that population individuals, regardless of species, have the same chance of being caught. As sample sizes increase, the species therefore will not tend to be sampled in proportions $\mathbf{p} = (p_1, p_2, ..., p_s)$, but in some other proportion, for example $\mathbf{p}^{(m)} = [p_1^{(m)}, p_2^{(m)}, ..., p_s^{(m)}]$, where m refers to the method of sampling. Hence for a given method of sampling, it is the population structure $\mathbf{p}^{(m)}$ and not $\mathbf{p}$ that is to be analysed (Engen, 1978). This concept highlights one of the fundamental flaws of pitfall trap surveys and other relative methods such as interception traps and baited traps (Southwood 1978). Each species sampled may have different individual catch rates, based on activity patterns and also the permeability of the local substrate and vegetation (see section 3.1).

It does seem more sensible to combine the concepts of number of species and relative abundance into a single concept (Peet 1974), and this is more useful for comparing communities from different sites. This concept has been incorporated into the proposal of many indices of diversity which explain various aspects of the community structure. The relation between indices of diversity and species abundance distribution has been studied in detail by several workers (May 1975, Magurran 1988). Unfortunately, there is little agreement on the best diversity measure to use and no index has received the backing of even the majority of workers in the field. However, four indices are widely used, those of species richness (**S**), the log-series α, the Shannon - Weaver index (**H**) and the Simpson index (**D**) (Magurran 1988). The use of **S** has been frequently argued against due to its inability to show the true distribution of the species rather than an even distribution, and its dependence on the area sampled, or the size of the sample (Usher 1983). For these reasons, it will be eliminated in any further discussion, although it is useful as a complementary measure to any index of diversity.

The parametric log-series index α (Fisher *et al.* 1943) represented the first attempt to describe mathematically the relationship between the number of species and the number of individuals of those species, and is described as

$$\mathbf{S} = \alpha \log_e\left(1 + \frac{\mathbf{N}}{\alpha}\right)$$

where **S** equals the number of species, **N** equals the number of individuals and α is the index of diversity. It is the most commonly used statistical model for describing community diversity. It has good discriminant ability between samples, and it is not severely influenced by sample size, demonstrated in Lepidoptera catches (Fisher *et al.* 1943, Taylor 1978, Magurran 1988). The only disadvantage of α is that it is based purely on species richness and the number of individuals (**N**), and takes no account of variation in the equitability of the samples. For example, two samples with equal **S** and **N** may have differences in the species distribution, but using α as a diversity measure will not indicate that this is so. The log-series index works well subject to the assumption that the data measured fit a log-series distribution, unfortunately this is often not the case and generally it does not describe some biological distributions very well (Usher 1983), although Taylor felt that it is a satisfactory measure of diversity, even when the underlying species abundance's do not follow a log series distribution.

Both **H** and **D** are nonparametric indices and make no assumptions as to the fit of the data to a particular distribution model, but they are nevertheless influenced by the proportions of the species present. The Shannon - Weaver index (Shannon and Weaver 1949) is derived from information theory and is the most commonly used of its kind. It is defined as

$$\mathbf{H} = -\sum_{i=1}^{s} (p_i)(\log p_i)$$

where **H** equals the information content or species diversity of the sample, **S** equals the number of species and p_i equals the proportion of the total sample belonging to the $_i$th species.

The Simpson index (Simpson 1949) is the most commonly used dominance measure. It describes the probability of picking two organisms at random that are different species, and is frequently used in its reciprocal form, which describes the probability of picking two organisms that are from the same species. It is defined as

$$\mathbf{D} = \sum_{i=1}^{s} \frac{(n_i(n_i - 1))}{(\mathbf{N}(\mathbf{N} - 1))}$$

where **D** is the species diversity of the sample, **S** equals the number of species, n_i equals the number of individuals in the $_i$th species and **N** equals the total number of individuals. The reciprocal of **D** ensures that the value of the index increases with increasing diversity and also restricts the maximum value of diversity to equal **S**.

One of the most important criteria in choosing the correct index to use is that it is independent of sample size. Taylor (1978) showed that for samples over 1000 individuals of Lepidoptera from light traps, α is statistically independent of **N**, but below this threshold, the independency is suspect. Taylor also demonstrated that both **H** and $^1/_\mathbf{D}$ were more sensitive to sample size than α for Lepidoptera. However when this theory was applied to data from pitfall trap catches of spiders and carabids in this survey, these conclusions were not evident in preliminary trials.

Using data from six trapping areas sampled from April to October 1992 (see section 6.3), ten random sub-samples were taken at each of 80%, 60%, 40% and 20% of the total number of spiders and carabids trapped in each area. All three diversity indices were calculated for these sub-samples and the mean percentage reduction or increase of each index for each sub-sample at each trapping area was calculated (Figure 4.1 and 4.2). In principle, any random sub-sample of a data collection should have fewer species present, but they should represent a similar distribution to the original data, and therefore be independent of sample size. Five out of six trapping areas (three spider and two carabids trap areas) showed similar results, indicating that **H** and $^1/_\mathbf{D}$ were minimally effected by reductions in **N**, while α was considerably affected. At the remaining carabid trapping area (Row B1), **H** and $^1/_\mathbf{D}$ showed results similar to the other rows, while α increased by a small degree. A further ten replicates were performed for Row B1 and similar results were found, suggesting that at this row, the distribution of the species individuals was different to the other rows. Indeed, at this row, there were fewer rare species, only two species with one individual compared to at least seven at the other rows.

The results suggest that for pitfall trap catches of spiders and carabids in this survey, the Simpson index is the most suitable measure of diversity to use, being the least affected by variation in **N**. The Shannon - Weaver index shows similar but consistently greater degrees of variation during reduction of **N**, and the log-series index is adversely influenced by varying **N**. Giavelli *et al.* (1986) have also shown the Simpson index to be almost independent of sample size, while both Yapp (1979) and Usher (1983) prefer using the Simpson index over **H** or α.

In conclusion, there appears to be strong evidence to choose any of the above diversity indices. In most situations, using data from this survey, all three indices showed similar trends along the transect, although the Simpson index provided the best and most reliable measure when related to the size of the sample. When used in conjunction with both the number of individuals and the number of species, Simpson's index provides a useful summary of diversity, because it is easy to understand and calculate, and gives the best method for describing comparisons between several communities of varying distributions. In all subsequent analysis concerning species diversity, the reciprocal of the Simpson index ($^1/_\mathbf{D}$) will be used.

Figure 4.1. Mean percentage deviation (± s.e.) of **H**, $^1/_D$ and α indices from original diversity value using random sub-samples of data at 80%, 60%, 40% and 20% of the total number of individuals of spiders taken at row positions A1, B1 and C1. Ten replicates were used for each sub-sample at each row position.

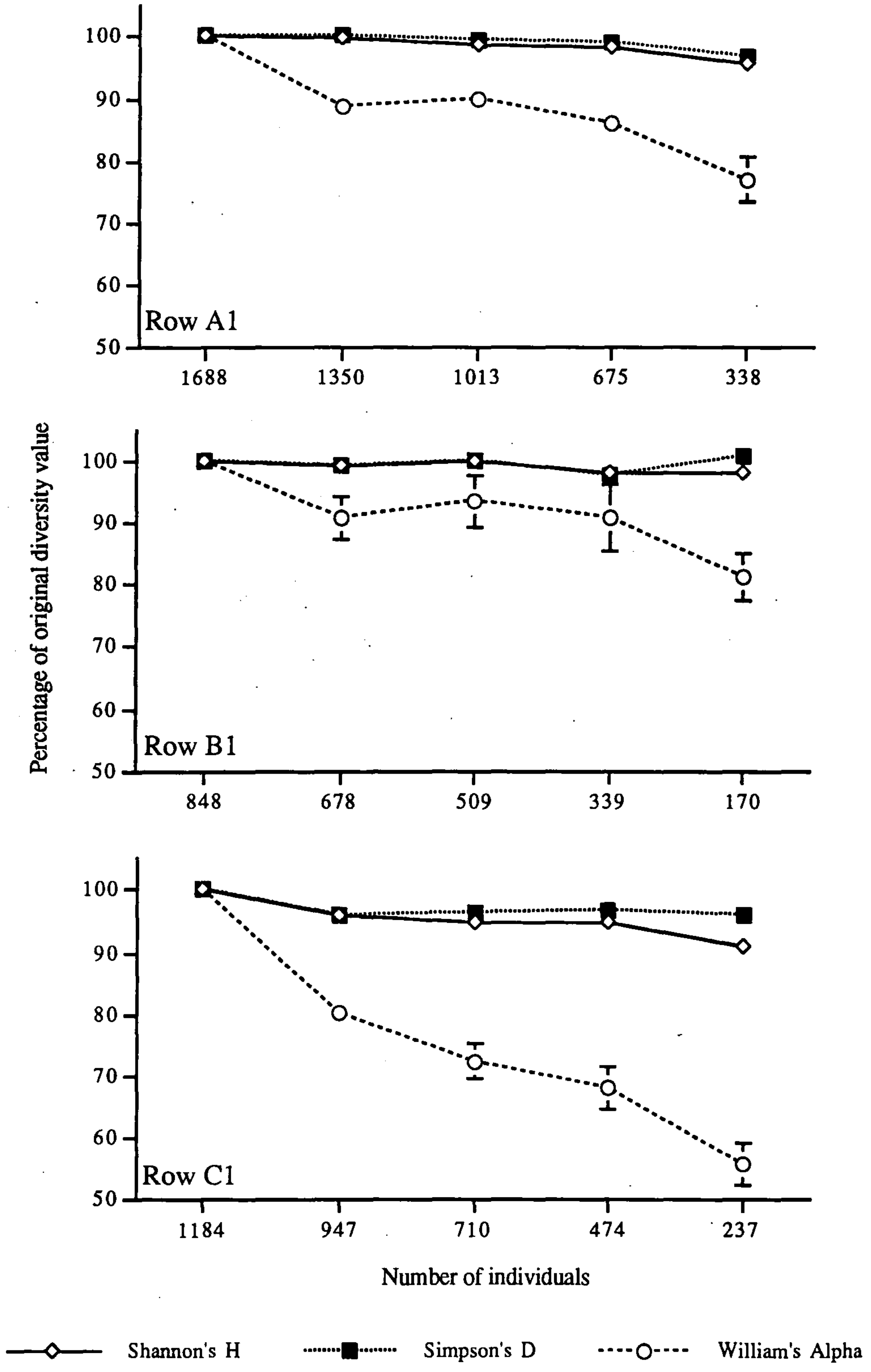
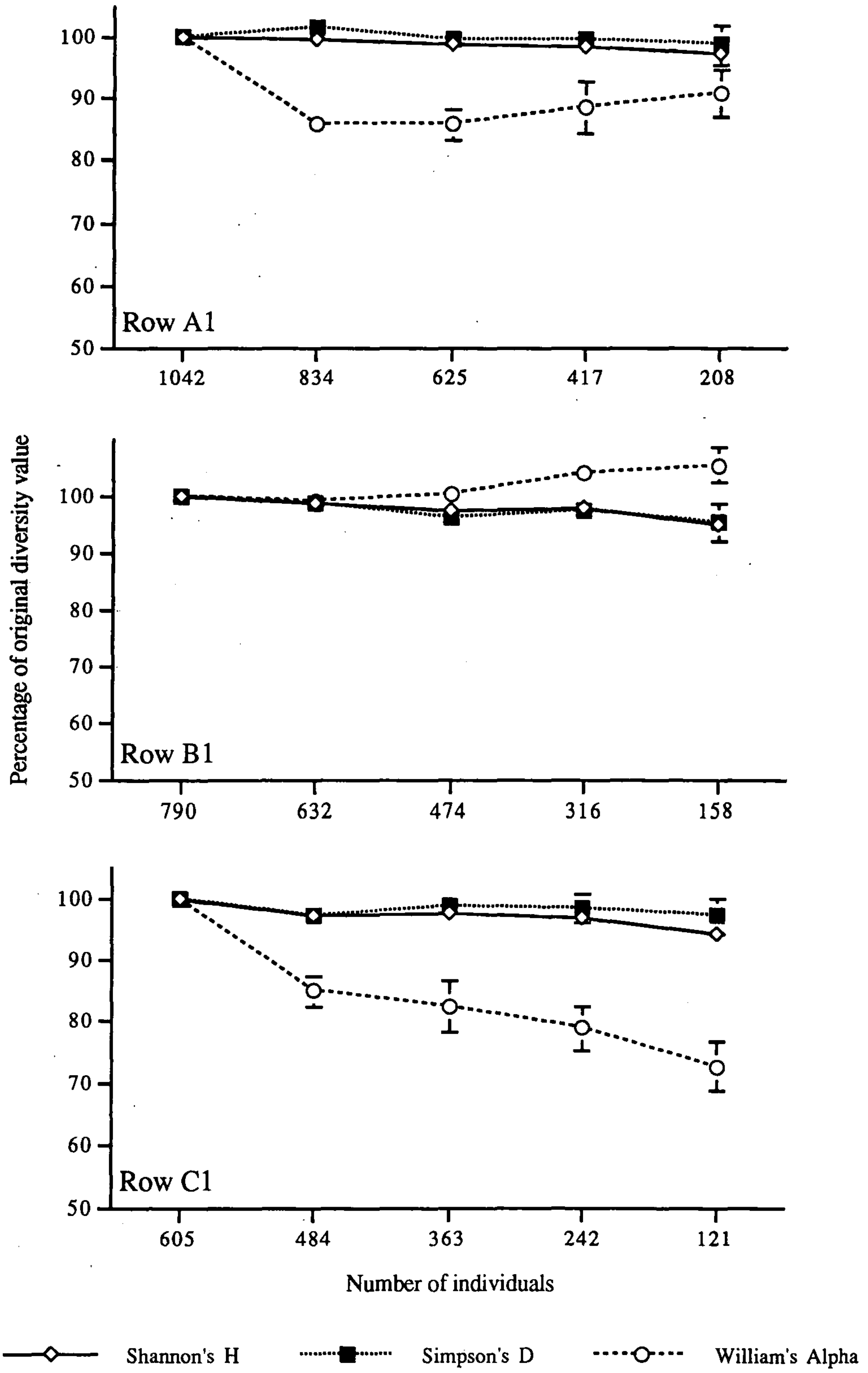


Figure 4.2. Mean percentage deviation (± s.e.) of **H**, $^{1}/_{D}$ and α indices from original diversity value using random sub-samples of data at 80%, 60%, 40% and 20% of the total number of individuals of carabids taken at row positions A1, B1 and C1. Ten replicates were used for each sub-sample at Rows A1 and C1, 20 were used at Row B1.



4.2 Multivariate methods

Several techniques of multivariate analysis were used throughout this study, including both classification and ordination methods. Both these procedures represent the primary methods of clarifying relationships among taxonomic and ecological samples in community ecology. Both methods have been used frequently by ecologists and their application has been reviewed by several workers (Gauch and Whittaker 1981, Gordon 1987, James and McCulloch 1990).

Classification in community ecology may be described as the activity of dividing a group of species into a smaller number of groups in such a way that species in the same class are similar to one another, and dissimilar to species in other classes (Gordon 1987). However several different methods or clustering strategies are now available, largely due to the recent rapid development of computing capabilities, the most common techniques include non-hierarchical and hierarchical; polythetic and monothetic; divisive and agglomerative methods.

Non-hierarchical clustering techniques separate samples or species into a number of clusters but specify no structure interrelating the clusters, and hence may be rejected in favour of hierarchical techniques, which define relationships among the clusters, and therefore provide more detailed information. Monothetic techniques separate on the basis of presence or absence of a single sample or species at each site, while polythetic methods partition clusters on the basis of more than one (usually all) samples or species. Polythetic methods are considered the best techniques for community samples as they can use the data as fully as possible (Gauch and Whittaker 1981), and hence monothetic methods may also be rejected.

Perhaps the most important choice and therefore the most difficult method to choose is between divisive and agglomerative techniques. Divisive methods begin with all species in a single cluster and divide them, usually into two, then further divide these groups until a sensible number of classes have developed based on the ecologist's knowledge and subjective correlation with the environmental variation. In contrast, agglomerative methods begin with the individual samples or species, and join these into larger clusters until a single cluster contains all samples or species. Within both these techniques, there are several different strategies, which can and generally do produce different classifications of the same data set, making it more difficult to chose between them. Several papers have attempted to make evaluations of different techniques, notably Lambert and Williams (1966) and Gauch and Whittaker (1981).

For the purposes of this study, two possible classification methods were proposed initially. Cluster Analysis is an agglomerative polythetic technique which has a variety of common clustering algorithms, such as complete linkage, average linkage and single linkage (Gordon 1987). The measure used during Cluster Analysis may also vary, but one of the most commonly employed is Sørensen's Index of Similarity (Sørensen 1948). Clusters are formed based on the similarity in species content of different samples. However, Sørensen's Index is based on presence/absence data and allows no distinction between specimens represented by a single occurrence or by a large number of individuals. To compensate, a modified form of Sørensen's Index may be used, which adds extra weight to the more abundant species, achieved by introducing an extra 'pseudospecies' for species with large occurrences of individuals (e.g. more than 29 individuals at any one site following Butterfield and Coulson 1983, Coulson and Butterfield 1986). Several pseudospecies may even be used for highly abundant species.

A widely used alternative method is Two-way Indicator Species Analysis (TWINSPAN, Hill 1979a), a divisive polythetic technique which incorporates the ordination method of reciprocal averaging (Hill 1973) to divide the data set. This method also incorporates the use of pseudospecies to add weight to the more common species, but it also uses indicator species that are preferential to one side or other of the division. Another advantage of this method is that both the samples and the species may be classified.

Gauch and Whittaker (1981) examined both techniques (including the variety of clustering algorithms in Cluster Analysis) using both simulated and real data. Their results suggest that two-way indicator species analysis is usually the best, but that there are cases in which other techniques may be complementary. They suggest that the "...usually better results and greater robustness of TWINSPAN are mainly due to the emphasis on the overall data structure rather than preoccupation with details". Lambert *et al.* (1973) also state that "polythetic-divisive methods have theoretical advantages in that all the available information is used to make the critical topmost divisions". Another important consideration is the experimental question posed initially, which may concern classification of the overall data or might emphasise details of individual sample comparisons. Kent and Ballard (1988) outline an extensive list of authors who recommend TWINSPAN as the best numerical classification method available at present.

Both techniques (TWINSPAN and Cluster Analysis) were tested using spider and carabid data from pitfall traps on different habitat types on summit plateaux in the north Pennines during 1991. Similar classification groupings were produced by both methods using the data available. In conclusion, the hierarchical, divisive polythetic, method of two-way indicator species analysis was the primary classification method used in this thesis following the preferences in the literature. However, a useful rationale is that 'parts of the classification that are in agreement using two or more methods are unlikely to be purely artefacts of a particular clustering strategy and more likely to represent genuine structure in the data' (Gordon 1987). Based on this concept, complementary analyses of any data examined were performed using Cluster Analysis, following the same criteria as Butterfield and Coulson (1983), as comparison with their work is an important consideration in investigating the community structure of spider and carabid communities in north England. Due to the secondary nature of cluster analysis as a classification technique in this study, the results will not be shown, only the similarity or dissimilarity to the results of TWINSPAN will be discussed. Cluster analysis is used in certain situations in this study to measure similarities along transects (Chapters 6 and 7).

As with classification methods, there are several indirect ordination methods which are commonly used in community ecology, including Principal Components Analysis, Reciprocal Averaging (or correspondence analysis) and Detrended Correspondence Analysis (hereafter referred to as PCA, RA and DCA respectively). Ordination methods use community data to produce axes of variation which show the similarities of samples based on their species content by their relative positions on those axes. The choice of ordination method to use is an easier one than that required for the choice of classification methods. Each method described above generally represents part of a succession in ordination methods beginning with PCA, then the development of RA and the subsequent introduction of DCA. PCA has been widely used from its introduction in 1966, but it is not now recommended due to distortion in the analysis termed "the arch effect" (Gauch *et al.* 1977). RA also suffers from this distortion, and as such, DCA was introduced as the detrending component counters this distortion in the analysis. As a method, correspondence analysis is very important as it provides the basis for most developments in ordination methods since 1970 (Kent and Coker 1992). It is also at the heart of TWINSPAN, probably the most widely used classification method.

Based on the development of these methods, the ordination technique used in this thesis was Detrended Correspondence Analysis. It uses similar methods to TWINSPAN, the classification method used, as well as being the most up to date technique available. Gauch (1982) and Rushton (1987) consider DCA a suitable method for the ordination of ecological data, and Kent and Coker (1992) agreed that DCA was as good if not better than most indirect ordination methods.

A further lateral development of DCA has been the introduction of Canonocal Correspondence Analysis or CCA (ter Braak 1988). This method has the advantage of distributing the samples and species along the ordination axes in light of known environmental variables by imposing the extra restriction that the axes be linear combinations of the environmental variables (using multiple regression methods), a technique referred to as either Direct or Constrained ordination. This technique is useful in assessing whether the species distribution is explained by the variables collected including their relative importance, or by others not recorded. CCA was also used in this study.

Both ordination methods produce diagrams in which points represent samples or species in ordination space, and using CCA, vectors represent the direction and relative influence of the environmental variables relating to the samples or species.

4.3 Logarithmic transformation of data

Throughout the analyses included in this thesis several common statistical tests were performed, and logarithmic transformations of the data were carried out where necessary. However, in the presentation of the results throughout the thesis, the original data have been maintained, including arithmetic means and their associated standard errors. This was regarded to be more understandable in the reading of the results, and in no way altered the outcome or significance of the analyses.

5.1 Introduction

The growing interest in the conservation of natural habitats and their related flora and fauna has led to an increased demand on biologists to provide sound, objective information on the detailed ecology of these areas. The British uplands, covering a substantial though sparsely populated area, are an important and complex component of the British countryside (Gimingham 1988), and are therefore of high public interest as a recreational and leisure feature.

The uplands of Britain show close ecological affinities to those of Scandinavia and may be regarded as insular, oceanic outliers of these ranges (Ratcliffe 1977), with biota limited by the isolation of Britain as an island and the relatively small area (MacArthur and Wilson 1967).

The mountain flora is poor compared with that of the continental ranges, some widespread and characteristic species being scarce (*Oxytropis campestris* (L.)) or absent (*Ranunculus glacialis* L.) here. On the other hand, no continental mountains have a comparable extent of vegetation dominated by *Calluna vulgaris* (L.) or *Juncus squarrosus* L., and the abundance of ferns with a strong Atlantic distribution (such as *Hymenophyllum wilsonii* Hooker) and bryophytes (especially *Racomitrium lanuginosum* Brid.) is also unparalleled except perhaps in south-west Norway and the Faroes. The extent of blanket mire in the British uplands is another unique feature, and although it is sometimes loosely compared to the Arctic tundra, this is not an accurate description. The British hill country is in addition one of the main European strongholds of birds such as the Peregrine Falcon (*Falco perigrinus* Tunstall), Golden Eagle (*Aquila chrysaëtus* L.) (Ratcliffe 1977) and the Red Grouse (*Lagopus lagopus scoticus* (Lath.)).

A variety of factors, operating at distinctly different time scales, have shaped the British uplands. These scales may vary from thousands of years on a geological scale to one or two hundred years in ecological succession, or to just a decade or two in terms of recent management activities. At whatever time scale a process is studied, the upland communities are dynamic, responding to changes in climate, successional age or management activity. It is the degree of predictability of these changes that indicates how much is understood about the ecology of the uplands (Thompson and Usher 1988).

Mountain plateaux are one of Britain's largest natural habitats, and comprise a resource nearest to that found in unspoilt Arctic/Alpine areas. The high altitude, shallow infertile soils and severe climate, however, render the plateaux vulnerable to both natural and human induced damage (Thompson *et al.* 1987). In recent years they have been subjected to increasingly high impacts from recreation and grazing by sheep (*Ovis aries*). These factors have a major effect on the structure of both the vegetation and fauna present. The plant communities are nearly always short and prostrate, and some animals are restricted to these areas due to their dependence on the vegetation or special physical features. Good examples are provided by the invertebrates which form an important part of the food source of many equally specialised vertebrates. Coulson and Butterfield (1985) collected more than twenty rare species of invertebrates from peat and upland grassland communities in northern England, highlighting the unique nature of these areas on a national scale, so special consideration must be given to the increased isolation and rarity/relict potential of the mountain summit plateaux. Aspects of mountain wildlife have been studied in considerable detail in Britain, as have the effects of several different types of disturbance (for a comprehensive list of studies, see Thompson and Brown (1992)).

Altitude has a substantial effect on invertebrate community composition, and in turn influences the structure of the upland food web (Coulson 1988). Although the invertebrate species composition of these areas possess a high degree of rare and exclusive forms, the number of species is relatively few compared to lowland and forest communities, but they are characterised by a great abundance of individuals of these species (Mani 1968). In many cases the numbers form at least as high a biomass of soil and litter fauna as that of many lowland soils (Coulson and Whittaker 1978).

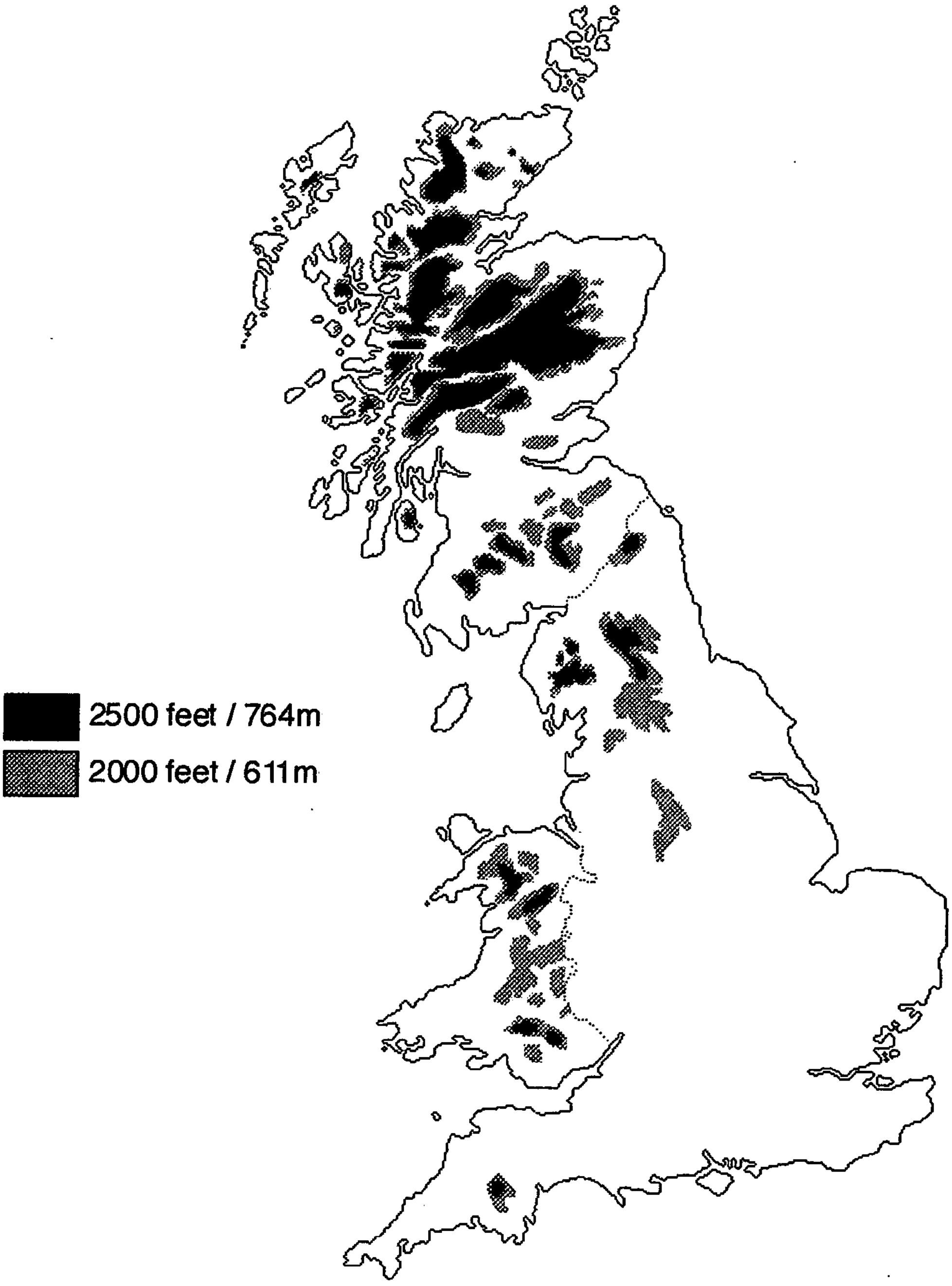
Two of the major invertebrate predator groups in the uplands are spiders and carabids (Coulson and Whittaker 1978), but there has been little attention and few studies on their distribution at the community level. Cherrett (1964) described the spiders from a series of habitats on the Moor House National Nature Reserve in Cumbria, and showed that many Lycosidae and Linyphiidae species were habitat specific. Coulson and Butterfield (1986) identified several spider communities on peat and grasslands in the north of England and suggested that their distribution was determined primarily by the vegetation "architecture". They also found an increase in the proportion of Linyphiidae species with increasing altitude. Otto and Svensson (1982) studied ground-living spider communities along altitudinal and vegetation gradients in western Norway and suggested that mountain spiders in temperate regions are mostly widely distributed and easily dispersed. They also found a decrease in size of spider at higher altitudes. Both Uetz (1991) and Wise (1993) give reviews of studies on spider distribution and factors controlling their habitat selection.

Among the small number of studies on communities of upland Carabidae are those of Butterfield and Coulson (1983), who studied carabid communities on peat and upland grasslands in northern England. They identified eight community types and the species which characterise them, suggesting moisture content was the factor controlling the distribution of species. Pearson and White (1964) sampled surface active arthropods in moorland country in north Wales, and concluded that the structure of the vegetation rather than the species composition is the most important factor influencing carnivores. Refseth (1980) commented on the use of carabid communities in southern Norway for biological classification, considering them a valuable contribution to existing habitat classification systems. Thingstad (1987) used pitfall trapping to sample the carabid fauna of alpine and sub-alpine habitats in northern Norway and showed that the carabid beetles are under the influence of the same abiotic factors as the vegetation. Cardenas and Bach (1989) studied the effects of environmental factors on carabid beetles on mountains in Spain, showing some species are influenced by microclimate, while others are influenced by soil content and type.

Most workers showed that distribution of both spiders and carabids in the uplands is dependent on a number of factors, such as soil moisture, plant structure (Cherrett 1964, Coulson and Butterfield 1986) and prey distribution (Cherrett 1964, Otto and Svensson 1982 and Thingstad 1987).

The proportion of land in Britain which is classed as mountainous (above 611m, Ratcliffe and Thompson 1988) is only 2.5%, and less than 0.2% of this total occurs in England (Figure 5.1). This study concerns invertebrates from the largest upland area in England, the north Pennines (Figure 2.1). The aim of this chapter is to present and compare sub-montane spider and carabid communities living in different vegetation types, between April and October 1991, on three summit fell top areas in the northern Pennines, using classification and ordination techniques for identifying the habitat preferences. An attempt has been made to identify the major environmental variables that influence spider and carabid distribution within this altitudinal zone (above 800m).

Figure 5.1. Distribution of land in Britain above 611m and 764m.



5.2 Study Area

The three summit areas (Figure 5.2) used for this study lie towards the northern end of the Pennine range. The fell tops are Little Dun Fell (842m Ordnance Datum, National Grid Reference NY 704330), Great Dun Fell (848m NY 711322) and Cross Fell (893m NY 688345). Both Little Dun Fell and Great Dun Fell plateaux are relatively small, (approximately 0.2km^2 and 0.4km^2 above 800m respectively), whilst the relatively flat summit of Cross Fell covers almost 2km^2. All three fell tops are composed of a massive bedded, medium to coarse-grained yellow sandstone, known as the Dun Fell Sandstone (Hornung 1974, Turner 1984), covered by a mosaic of peat and mineral soils.

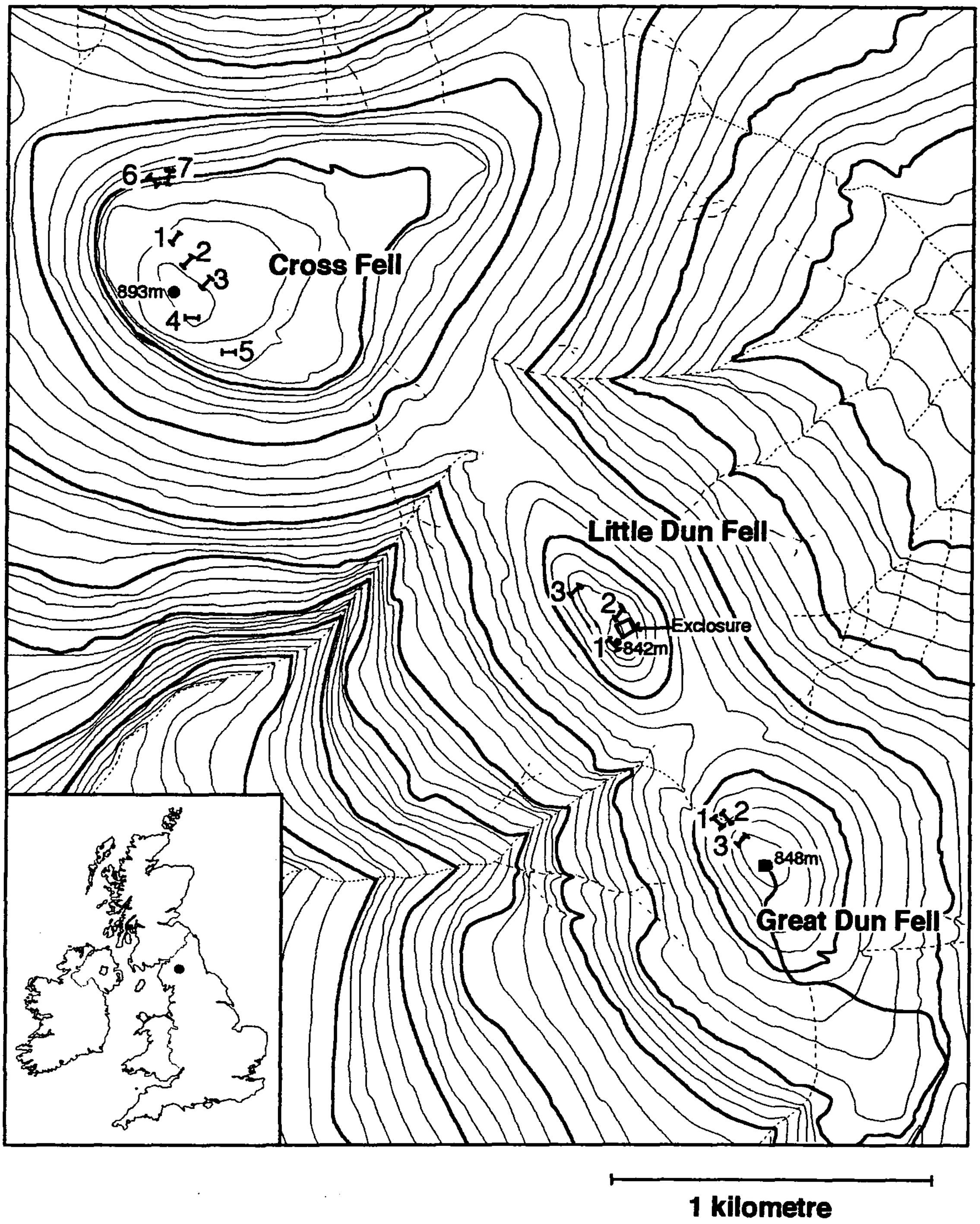
With increasing altitude, woodland becomes sparser and trees become stunted. Grasslands become shorter and heather more compact in its growth form. At about 600m altitude the grass abundance is reduced by an increase in the numbers of small sedges and mosses, and the heather becomes scarce. This is accompanied by an increase in the area of bare rock exposed. These changes are attributable to the harsh, near arctic climatic conditions, and are readily observable on the higher Pennine peaks.

However, it has not always been so. Turner (1984) concluded that during the climatic optimum of the post-glacial period there was no reason why trees should not have become established on these Pennine fell tops, and indeed has demonstrated this had been the case. From 5000 years Before Present the warm climate began to deteriorate, the forests gradually began to break down and eventually gave way to peat forming communities over the entire fell tops. Following this most of the peat began to erode, exposing the pavement and gave rise to the present day *Festucetum* and patches of *Juncus squarrosus* which overlay the now podzolised original forest soil.

The present climate has left a considerable area at altitudes well above the tree line (approx. 600m with present grazing pressure, (Pigott 1978)). Manley (1942) gives a general summary of the climate of this area based on many years observations; "We therefore form a conception of an excessively windy and pervasively wet autumn, a very variable and stormy winter with long spells of snow-cover, high humidity and extremely bitter wind, alternating with brief periods of rain and thaw. April has a mean temperature little above freezing-point and sunny days in May are offset by cold polar air; while the short and cloudy summer is not quite warm enough for the growth of trees. Throughout the year indeed the summits are frequently covered in cloud".

In a ten year study on Dun Fell, Chandler and Gregory (1976) found that for approximately two-thirds of the time, visibility is less than 200m, and it is estimated

Figure 5.2. Map of study area showing position of 13 sampling sites at Cross Fell, Little Dun Fell and Great Dun Fell, Cumbria. Contours are at 10m intervals, bold contours indicate 50m intervals. Exclosure indicated on Little Dun Fell (see section 7.2). Location as inset.



that there are minima temperatures for every month of the year below 0°C (Manley 1943). The climate and other meteorological aspects have been well studied for both Moor House NNR. (Heal and Smith 1978) and Dun Fell (Manley 1942, 1943). A comparison with other areas at different altitudes and latitudes is shown in Table 5.1.

A fall in air temperature with altitude is one of the most familiar features of the climate of mountains, demonstrated by the frequent persistence of snow cover. The physical explanation is the decrease in atmospheric pressure with increasing altitude, so that air moving upwards expands and cools (Pigott 1978). This cooling or "adiabatic lapse rate" is usually about 1°C for each 100m increase in altitude (about 0.67 - 0.8°C per 100m for air saturated with water vapour). Lapse rates of around 0.7 are evident in Britain based on the mean July temperature for several locations in Table 5.1. British mountains on the whole are only of moderate size but they lie near the sea and cross the path of the strong Atlantic breezes from the west (Pearsall 1950). For this reason, wind, clouds and rain play a large part in the weather conditions, demonstrated by the lapse rates obtained above.

Table 5.1. Mean January and July temperatures for five meteorological stations in the United Kingdom, showing their altitude and latitude. Adapted from Pearsall (1950).

			Mean Temperature °C	
	Altitude (m)	Latitude	January	July
Ben Nevis	1366	56° 45'	-5	5
Dun Fell	848	54° 40'	-2	10
Moor House	571	54° 40'	1	12
Braemar	345	57° 0'	2	13
Fort William	9	56° 45'	4	14

Fell top plateaux habitats are unique in their isolation and therefore usually possess a variety of undisturbed physical features which are distinctive. Solifluction hummocks, measuring up to 2m in diameter and 0.3m high, arise as a consequence of the alternate freezing and drying of the soil waters where vegetation cover is heterogeneous, the denser patches buffer the ground from frost, while the freezing of surrounding ground causes iced material to move under the vegetated patch, forcing it upwards to form the beginnings of a small hummock (Thompson *et al* 1987). These features are common on the larger area plateau of Cross Fell. Also on Cross Fell are well developed "stone-stripes" in which there are alternate parallel bands of large stones and fine compact sandy soil (Pigott 1978).

On drier ground above 600m the replacement of montane *Calluna* heath by *Vaccinium myrtilis* L. heath and acidic grasslands has been almost complete, and indeed, in the sampling area, above 820m, *Calluna* is absent. Replacement of *Vaccinium* heaths by grasses has occurred widely in the montane zone. *Festuca ovina* L. or *Deschampsia flexuosa* (L.) communities are more extensive on dry ground. Sparse and dwarfed *Vaccinium* persist, especially in rocky places, as with the creeping *Galium saxatile* L. On wetter ground, and areas of extended snow cover, *Nardus stricta* L. appears and rises to dominance, with the smaller and less competitive species of grass reduced in abundance, while on the more water-logged and gleyed soils *Juncus squarrosus* typically takes over from the *Nardus*. In areas where peat soil is present, generally eroded into 'haggs', the dominant vegetation is primarily *Eriophorum vaginatum* L. and *E. angustifolium* Honckeny.

On the highest tops, especially the large summit plateau of Cross Fell, the grass communities merge into a type dominated by *Racomitrium lanuginosum*. This is the most widespread summit bryophyte community, occurring northwards from north Wales (Ratcliffe 1977), and is indicative of acid soils. Much of the ground on the Cross Fell plateaux is subject to solifluction and *Racomitrium* occupies the crest of the hummocks, whilst the intervening depressions are mostly grass covered (with some *Vaccinium*), which gives a distinctive vegetational pattern (Ratcliffe 1978). The Pennine heaths are far less *Racomitrium* dominated than their more northern counterparts in the Scottish Highlands, and are best described as *Racomitrium-Festuca* or *Racomitrium-Deschampsia* communities (Ratcliffe 1977, Thompson *et al.* 1987). The high amounts of grass in the Pennine types occur as a direct result of the high grazing pressures from sheep.

Due to the inclusion of both Great Dun Fell and Little Dun Fell in the Moor House National Nature Reserve, and the close proximity of Cross Fell (a Site of Special Scientific Interest, approximately 1km outside the NNR boundary), the vegetation of the summit areas have been well documented (Welch 1967, Eddy *et al.* 1969, Ratcliffe 1977 and Rawes 1981).

5.2.1. Sampling sites

Thirteen sites were sampled, encompassing all the principle fell top vegetation communities, from all three summits (Figure 5.2). The site characteristics are summarised in Table 5.2, and are described below. Plates 1 and 2 show an area of *Eriophorum* mire (site CF2) and a typical *Carex-Racomitrium-Festuca* heath (site CF3).

Cross Fell 1, (CF1). A *Festuca ovina* grassland occurring just off the main plateau on the north side. *F. ovina* and other associated grasses comprised 75% of the cover, whilst sedges such as *Eriophorum angustifolium* and *Carex bigelowii* Torrey ex Schweinitz had a 10% cover. The remaining vegetation was composed of mosses and lichens in small quantities. The soil on this site possessed an organic matter content of 45%.

Cross Fell 2, (CF2). An area of ombrogenous bog on the main plateau, approximately 40m by 20m, with *Eriophorum vaginatum* (with *E. angustifolium* present) tussocks dominating (70%). *F. ovina* and *Polytrichum commune* L. were also present. The soil had a 90% organic content.

Cross Fell 3, (CF3). A *Racomitrium lanuginosum-Festuca ovina* community of about 20% and 50% cover respectively. This site was also on the main plateau, on stony ground influenced by solifluction. *P. commune* and *Deshampsia flexuosa* were also moderately abundant (10% each). Organic content of the soil was 39%

Cross Fell 4, (CF4). *Racomitrium lanuginosum-Festuca heath* (60%), very similar to CF3 with respect to solifluction hummocks, and on the main plateau, also with *D. flexuosa* (10%) and *Vaccinium myrtilis* L. (7%). *P. commune* was also present, though not abundant (4%). Soil organic content was 78%.

Cross Fell 5, (CF5). *Carex bigelowii* dominated (45%) grassland with 40% F. ovina. This site was on the south side, on a shallow slope off the plateau. It was relatively small in area (18m by 5m) and surrounded by *Juncus squarrosus* and peat haggs. The rest of the vegetation was composed of broad leaved grasses (5%), mosses (5%), *V. myrtilis* (scattered) and lichens. Soil organic content of 81%.

Cross Fell 6, (CF6). *Nardus stricta* dominated (60%), with 15% *P. commune*, and the presence of *E. angustifolium*, *D. flexuosa*, *J. Squarrosus*, *Galium saxatile*, *Carex* spp., *Agrostis capillaris* L. and *Sphagnum* spp. This was a snow-bed community where snow lies until mid May. Soil organic content was 84%.

Cross Fell 7, (CF7). *Nardus stricta-Polytrichum commune* complex (60%), with *G. saxatile* at 15% abundance. *F. ovina*, *A. capillaris*, *C. bigelowii* and *D. flexuosa* are also present. Occurrences of *Rumex acetosella* L., *Carex echinata* Murray, *Carex flacca* Schreber and *Stellaria* sp. in small numbers. A snow-bed community, with prolonged snow lie, until June. Organic content of soil was 82%.

Little Dun Fell 1, (LDF1). *Festuca ovina* grassland, with 80% dominance (with broad leaved grasses present). Moss was about 6% and *V. myrtilis* about 4%. The rest is mostly *E. angustifolium*, with *G. saxatile* and lichens. This site was on the west face of the smaller fell top (cf. Cross Fell), and was very exposed. Soil organic content of 75%.

Little Dun Fell 2, (LDF2). *Festuca ovina* grassland (70%) with 10% *Campylopus flexuosus* (L.) moss and 6% *P. commune* cover, the rest *V. myrtilis, A. capillaris, E. angustifolium, C. bigelowii* and lichens, in smaller proportions than LDF1. Soil organic content of 30%, less exposed on the east of the summit.

Little Dun Fell 3, (LDF3). *Festuca ovina* grassland, of 80% including *F. vivipara* (L.) and broad leaved grasses. *P. commune* had 10% abundance and *E. angustifolium* was present (3%). Lichens, *Galium* and *Vaccinium* were also present. This site was on the north face of Little Dun Fell and had a soil organic content of 55%.

Great Dun Fell 1, (GDF1). *Eriophorum* dominated, with *E. vaginatum* (70%) and *E. angustifolium* (10%). Also *A. capillaris, P. commune, D. flexuosa* and *J. squarrosus* (5% each) occurred throughout the site. *C. bigelowii* was present, though scattered. An organic content of 84%.

Great Dun Fell 2, (GDF2). Mineral grassland with 30% bare ground and 30% *Poa annua* L. There were small hummocks with *N. strica* and *P. commune* present (20%), the rest was made up of *E. vaginatum, G. saxatile, F. ovina, A. capillaris* and *D. flexuosa.* This area was directly next to GDF1 and was regularly flooded by a close spring. It had a soil organic content of 30%.

Great Dun Fell 3, (GDF3). *Festuca ovina* grassland, 70% *Festuca ovina* and 8% *A. capillaris. Polytrichum* had 10% abundance, and the rest was bare soil, rock, *G. saxatile, V. myrtilis* and lichen cover. With a soil organic content of 22%, this site was at the highest altitude on Great Dun Fell, adjacent to the Radar Station at the summit.

Plate 1. *Eriophorum* mire (site CF2).

Plate 2. *Carex-Racomitrium-Festuca* heath (site CF3).

Table 5.2. The location and characteristics of the 13 fell-top sites sampled during 1991. Cross Fell sites are CF1 - 7, Little Dun Fell sites LDF1 - 3 and Great Dun Fell sites GDF1 - 3. National Vegetation Classification code (NVC, Rodwell 1991) and coefficient of similarity are included (see text).

Site	Grid Reference	Altitude (m)	Vegetation type	NVC Code	Similarity to NVC (%)
CF1	NY 686346	884	*Festuca-Agrostis-Rumex* grassland	U1b	57
CF2	NY 687345	886	*Eriophorum vaginatum* mire	M20a	70
CF3	NY 689344	890	*Carex-Racomitrium* moss heath	U10a	64
CF4	NY 688342	890	*Carex-Racomitrium* moss heath	U10a	75
CF5	NY 691342	880	*Carex-Racomitrium* moss heath	U10b	58
CF6	NY 686349	850	*Nardus-Galium* grassland	U5	63
CF7	NY 687349	850	*Nardus-Galium* grassland	U5	73
LDF1	NY 705329	840	*Festuca-Agrostis-Rumex* grassland	U1b	55
LDF2	NY 705331	840	*Festuca-Agrostis-Rumex* grassland	U1b	57
LDF3	NY 703333	820	*Festuca-Agrostis-Rumex* grassland	U1	51
GDF1	NY 709324	820	*Eriophorum vaginatum* mire	M20a	73
GDF2	NY 709325	820	*Nardus-Galium* grassland	U5	40
GDF3	NY 709323	840	*Festuca-Agrostis-Rumex* grassland	U1	67

5.3 Methods

5.3.1 Pitfall traps on the Pennine plateaux

At each of the north Pennine plateaux sites, six pitfall traps were used, arranged in a straight line at 2m intervals. This formation increased trap independence and reduced sampling error, with each trap's efficiency being minimally affected by the others (Luff 1975). Where the habitat type was considered a patch surrounded by different vegetation, the trap line was placed, as far as possible, at the centre. Thus edge effects were kept to a minimum. Sampling was carried out from 11 April to 21 October 1991, the traps emptied every 14 days.

5.3.2 Variables sampled

Plant composition and vegetation density measurements were taken at each site using the methods outlined in section 3.2. The mean soil depth was also recorded for each site. Five soil samples, using a trowel to a depth of approximately 100mm (less if the base rock was near the surface and stone volume was too high), were extracted from each of the sites. The vegetation, litter layer and the top 10mm of soil were removed and the remaining soil was used to obtain pH measurements, organic content and moisture content. All samples were taken in July 1991.

The use of a soil corer was not suitable as in montane plateaux areas the top soil horizon is extremely thin. In quantitative terms the stone content in these upper horizons can exceed 40% by volume. The orientation of the stones within the profile is also significant; the nature of the sandstone is such that it fragments to produce slab-like pieces and in upper parts of the profile these are orientated with their long axes close to the vertical (Hornung, 1974) making sampling difficult.

From these soil samples, pH measurements were obtained for each site, using 10g of untreated soil mixed with 25ml of 0.01M $CaCl_2$ (White 1987). Moisture content was obtained by dry weight, and organic content was obtained by loss on ignition at 500°C for three hours in a muffle furnace. The percentage organic content was obtained by dividing the weight lost on ignition by the weight of the dry soil and multiplied by 100. Details of soil characteristics, vegetation density and slope at each site are given in Table 5.3.

5.3.3 Community parameters

For each of the sites the mean number of individuals, species richness and diversity of the spiders and carabids were measured. The means was obtained from six traps at each site over the whole season. Species richness was obtained from the number of species which occurred at the site. Species diversity was calculated using the reciprocal form of Simpson's index, (an adaptation of "the probability of picking two organisms at random that are different species", Simpson 1949). The reciprocal method ensures that the value of the index increases with increasing diversity (Magurran 1988). For a fuller description see Section 4.1.

Although there are several different indices of species diversity, there is little difference in the end result (Krebs 1985), and Simpson's Index has been used as it is almost independent of sample size (Giavelli *et al.* 1986). If the sampling efficiency is uniform at all sites, then species richness and diversity measures used together to make useful between site comparisons in community analysis studies.

The similarity between the species content of the fell tops was assessed using Sørensen's Index (Sørensen 1948);

$$\mathbf{I} = \frac{\mathbf{2j}}{\mathbf{a+b}}$$

where **a** is the number of species trapped on fell top **A**, **b** is the number of species from fell top **B** and **j** represents the number of joint occurrences. The results may be converted to a percentage if required.

5.3.4 Multivariate methods

Multivariate techniques have been used frequently to study the relationships between invertebrates and environmental variables (Rushton *et al.* 1987, Bauer 1989). The sites were classified according to the similarities of the spider and carabid species composition and abundance of their fauna. Classification was assessed using the divisive polythetic method of Two-way indicator species analysis (TWINSPAN, Hill 1979a). A polythetic divisive classification technique, TWINSPAN was used to produce an ordered table of the common species occurring in each assemblage. TWINSPAN first produces a classification of the samples according to the species composition, and uses this to obtain a classification of the species according to their ecological preferences. The two classifications are then used together to obtain an ordered two-way table that expresses the species' synecological relations (Hill 1979a). A modification of Sørensen's Index was also used to classify the sites using Cluster Analysis using Average Linkage (an agglomerative method as opposed to divisive). The introduction of pseudospecies allowed some measure of abundance as opposed to presence/absence (species were assigned a pseudospecies if they had an abundance of 30 or more individuals at one or more sites; see Butterfield and Coulson (1983) for a full description). The results of this method are discussed but not presented (see section 4.2).

The sites were then ordinated using Detrended Correspondence Analysis (DCA in CANOCO, ter Braak, 1988). Two dimensional plots (ordinations) were produced to show the relative similarities of samples based on their spider or carabid beetle fauna by their relative positions on gradient axes. Samples close together are similar in species composition; those dissimilar are far apart.

Canonical correspondence analysis was used as a combination of ordination and multiple regression (ter Braak 1988), using CANOCO (Canonical Community Ordination) which is an extension of DECORANA (Hill 1979b). The advantage of this form of ordination is that the axes are chosen in the light of known environmental variables by imposing the extra restriction that the axes be linear combinations of the environmental variables (Direct Gradient Analysis). This technique produces an ordination diagram in which points represent samples or species and vectors (arrows) represent environmental variables. This gives a graphical summary of the weighted averages of all sites with respect to environmental variables. Only the directions and relative lengths of the arrows convey information (ter Braak 1986), so they can be adjusted accordingly and still show the relative influence of the environmental variable present. CANOCO can also test statistically whether the species are related to the supplied environmental variables, using the Monte Carlo permutation test (Hope 1968). Section 4.2 discusses the reasons for using the above multivariate methods. All species of spider and carabid recorded from each site were incorporated in all methods of analysis and weighted according to logarithmic abundance categories, which helped account for variability in the efficiency of the pitfall traps between different habitat types.

Table 5.3. Environmental variables for 13 fell top sites in the north Pennines during 1991. All variables sampled July 1991.

Site	pH	Organic content (%)	Water content (%)	Soil depth (mm)	Slope (degrees)	Vegetation density			Density total
						0-20mm	21-40mm	>41mm	
CF1	4.1	45	45	130	2	134	36	4	174
CF2	3.9	90	77	>300	1	151	68	47	266
CF3	4.3	39	59	130	1	123	23	-	146
CF4	4.1	78	76	40	1	134	16	1	151
CF5	4.1	81	59	90	6	123	34	1	157
CF6	4.4	84	78	>300	11	196	120	159	475
CF7	4.2	82	62	>300	12	138	91	52	281
LDF1	3.9	75	55	60	1	146	8	-	154
LDF2	4.3	30	28	60	6	117	9	-	126
LDF3	4.3	55	50	>300	3	99	4	-	103
GDF1	4.7	84	79	>300	8	145	64	111	410
GDF2	4.8	30	68	>300	6	72	4	-	76
GDF3	4.5	22	46	170	9	128	3	-	131

5.4 Results

Between 11 April and 31 October 1991, 5921 individual spiders (Araneae) from 56 species (including immatures) and 3690 carabid beetles (Coleoptera: Carabidae) from 22 species were taken in pitfall traps from 13 sites on Cross Fell, Little Dun Fell and Great Dun Fell in the north Pennines, England. Table 5.4 shows the overall distribution of numbers of species at the three fell tops, and their characteristics.

Table 5.4. The faunistic characteristics of the three north Pennine fell top areas based on the 56 spider species and 22 carabid species found during 1994. Numbers of species occurring and number of species exclusive to each fell top. (Figures in parentheses indicate percentage of the total number of species of spider or carabid recorded).

	Cross Fell	Little Dun Fell	Great Dun Fell
Spiders (n = 56)			
Total number of species	46 (82%)	39 (70%)	39 (70%)
Number of exclusive species	10 (18%)	3 (5%)	5 (9%)
Carabids (n = 22)			
Total number of species	14 (64%)	13 (59%)	20 (91%)
Number of exclusive species	1 (5%)	1 (5%)	6 (27%)

Species which were exclusive to a particular fell top were uncommon, and their abundance at these sites tended to be low. As a consequence of this low occurrence, the species compositions of the three fell tops were apparently similar. All three fell tops showed high similarity values of both spider and carabid species using Sørensen's Index, as outlined in Table 5.5 (all comparisons > 70% similarity).

Table 5.5. Similarity matrices based on Sørensen's Index for the three fell top areas for both spiders and carabids during 1991.

		Cross Fell	Little Dun Fell
Spiders	Little Dun Fell	0.80	
	Great Dun Fell	0.75	0.82
Carabids	Little Dun Fell	0.81	
	Great Dun Fell	0.76	0.73

The majority of the species of spider belonged to the family Linyphiidae (84% of the 56 species recorded), 7% belonged to Lycosidae and the rest were Thomisidae (4%), Clubionidae (2%), Hahniidae (2%) and Theridiidae (2%). Over 98% of all individuals trapped were linyphiids. The total numbers of individuals of each species of both spider and carabid captured at each site are given in Appendices 1a and 1b respectively, along with their full Latin names. Downie *et al.* (1994) provides a detailed summary of most of the invertebrates taken in the pitfall traps at each of the sub-montane plateaux sites.

5.4.1 Differences in composition and diversity between sites

Tables 5.6 and 5.7 summarise the mean number of individuals, species and the species diversity per trap for the spiders and carabids trapped at all 13 sites respectively, illustrated in Figures 5.3, 5.4 and 5.5. The mean species richness of the spider catches at each site did not vary significantly ($F_{12,65} = 1.9$, ns). Only site GDF2 had a mean outside the 11-15 species range. However, the mean numbers of individuals captured did vary significantly ($F_{12,65} = 7.1$, $p < 0.001$). This suggests that the structure of the species distribution was different between sites. The inverse of Simpson's Index was used to measure the variation in diversity per trap based on six traps at each site over the whole sampling period. Site LDF3 had the highest mean number of individuals (122 ± 10 s.e.), yet the diversity of the species composition was the lowest (2.6 ± 0.2). This was due to the dominance of *Erigone promiscua*, which accounted for over 60% of the total catch at that site. In comparison, site CF7 had the highest mean diversity at 7.6 ± 0.4 and a relatively low mean number of individuals (45 ± 5). The dominant species trapped at CF7 was *Centromerita bicolor*, which contributed only 15% of the total catch at that site.

The mean species richness of the carabid catches per trap at each site did however vary significantly ($F_{12,65} = 11.0$, $p < 0.001$), and again site GDF2 had the lowest mean value. The mean numbers of carabid individuals captured at each site also varied significantly ($F_{12,65} = 11.0$, $p < 0.001$), again suggesting that the structure of the species distribution was different between sites. The diversity measurements showed different results to those of the spiders ($r = 0.09$, df = 11, ns). Site CF5 had the highest mean number of individuals (81 ± 8) and the highest mean number of species (9 ± 1), there was also a relatively high mean diversity measurement (4.4 ± 0.2) indicating a fairly even spread of the species taken. The lowest mean diversity was found at site CF4, where *Nebria gyllenhali* contributed to over 78% of the carabid specimens trapped. Highest mean diversity measurements were found at sites CF1 and GDF3, where the dominant species were *N. gyllenhali* and *Notiophilus germinyi* (34% and 28% of the specimens taken) respectively.

Table 5.6. Mean number of individuals, species and species diversity per trap for spiders taken from six traps at 13 north Pennine fell top sites during 1991. Simpson's D presented as reciprocal.

Site	Mean number of individuals	s.e. (±)	Mean number of species	s.e. (±)	Mean species diversity (1/D)	s.e. (±)
CF1	97	17.0	13	1.0	4.3	0.6
CF2	46	5.5	11	0.9	4.7	0.5
CF3	69	7.8	13	1.0	6.8	0.2
CF4	73	22.4	14	1.4	5.5	1.1
CF5	65	8.9	13	0.8	6.6	0.6
CF6	48	8.7	13	0.8	5.7	0.5
CF7	45	4.6	12	0.7	7.6	0.4
LDF1	88	10.5	14	1.0	6.0	0.3
LDF2	85	6.8	15	1.1	6.6	0.7
LDF3	122	9.6	12	0.6	2.6	0.2
GDF1	47	5.8	12	1.9	6.4	1.2
GDF2	34	7.3	8	1.5	3.7	0.4
GDF3	93	9.7	13	1.1	4.2	0.2

Table 5.7. Mean number of individuals, species and species diversity per trap for carabids taken from six traps at 13 north Pennine fell top sites during 1991. Simpson's D presented as reciprocal.

Site	Mean number of individuals	s.e. (±)	Mean number of species	s.e. (±)	Mean species diversity (1/D)	s.e. (±)
CF1	51	11.2	8	0.2	4.5	0.3
CF2	58	6.9	7	0.5	3.0	0.2
CF3	56	6.9	6	0.2	2.6	0.3
CF4	50	5.6	5	0.5	1.6	0.1
CF5	81	7.6	9	0.5	4.4	0.2
CF6	39	6.6	6	0.3	3.7	0.2
CF7	68	7.1	6	0.4	3.5	0.3
LDF1	56	6.9	8	0.3	3.5	0.2
LDF2	27	1.4	6	0.4	3.6	0.3
LDF3	46	2.9	6	0.7	3.1	0.3
GDF1	16	4.6	4	0.5	3.3	0.4
GDF2	6	2.1	3	0.8	2.5	0.5
GDF3	57	4.4	9	0.8	4.5	0.3

Figure 5.3. Mean number of individuals per trap (± s.e.) for spiders and carabids taken from six traps at 13 north Pennine fell tops during 1991.

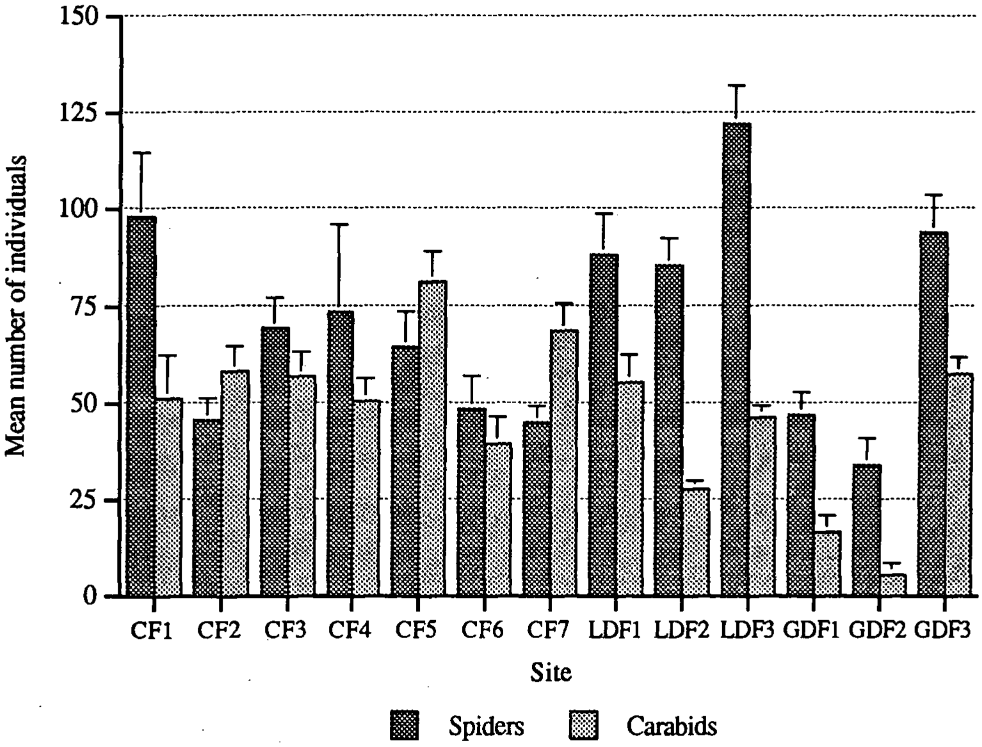


Figure 5.4. Mean number of species per trap (± s.e.) for spiders and carabids taken from six traps at 13 north Pennine fell tops during 1991.

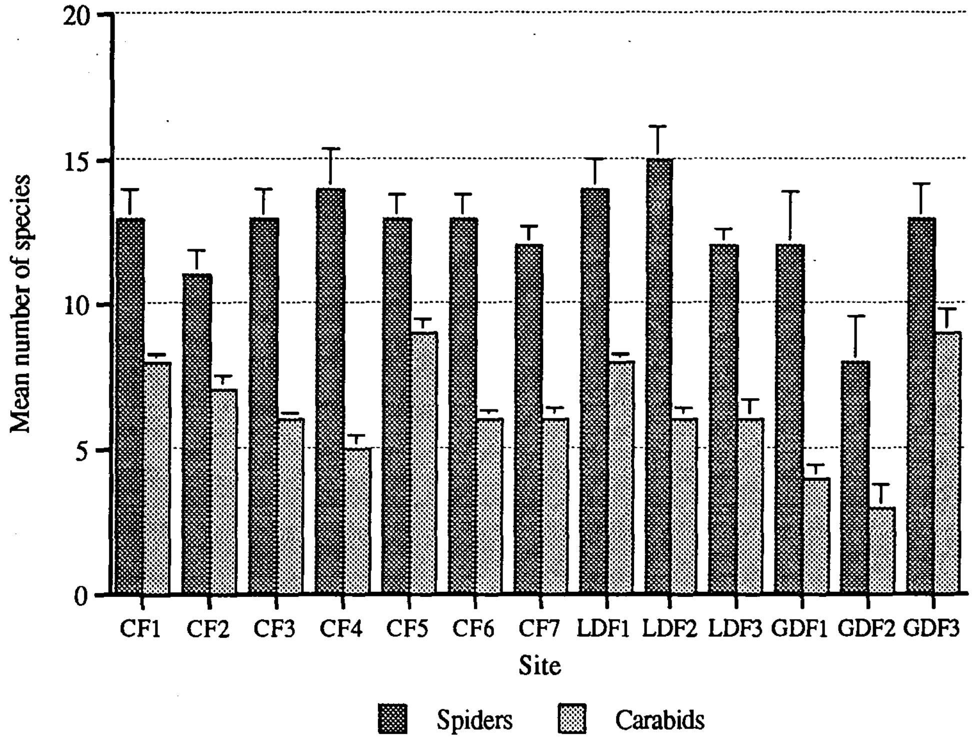
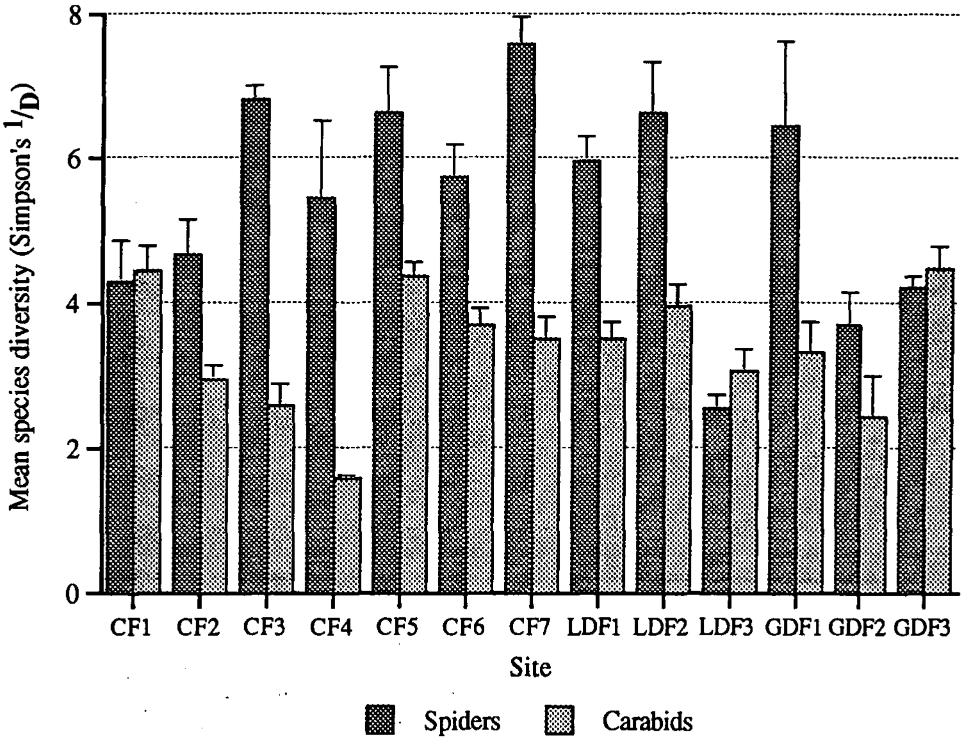


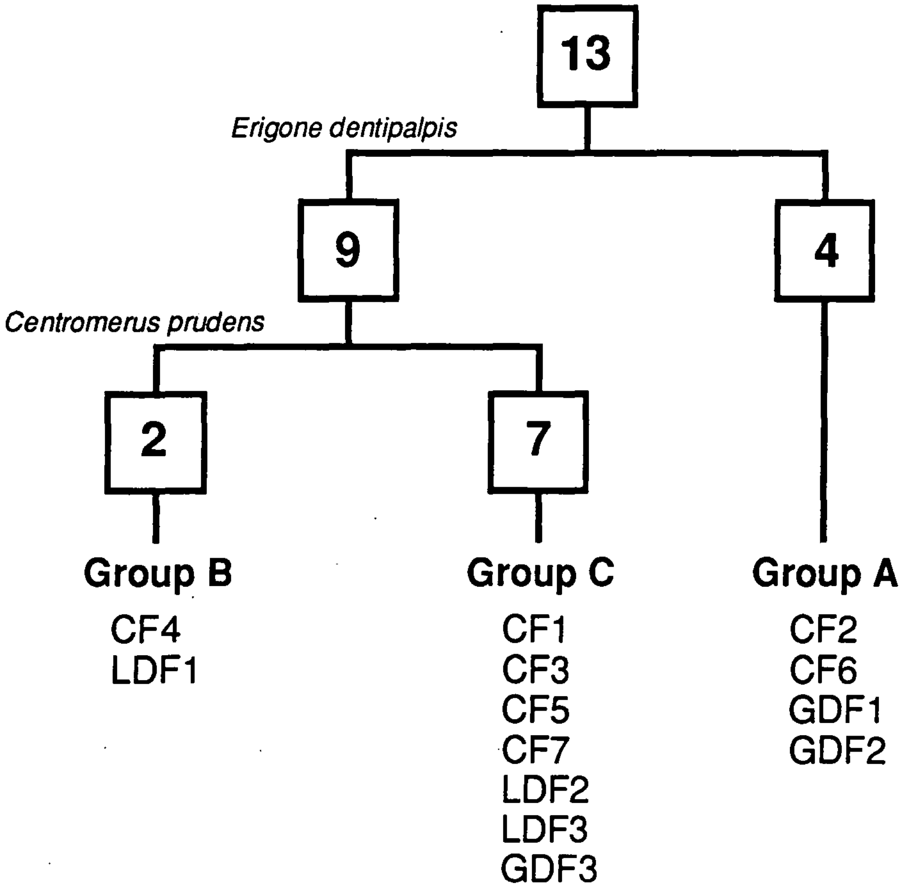
Figure 5.5. Mean species diversity per trap (± s.e.) for spiders and carabids taken from six traps at 13 north Pennine fell tops during 1991. Simpson's D presented as reciprocal.



5.4.2 The invertebrate communities

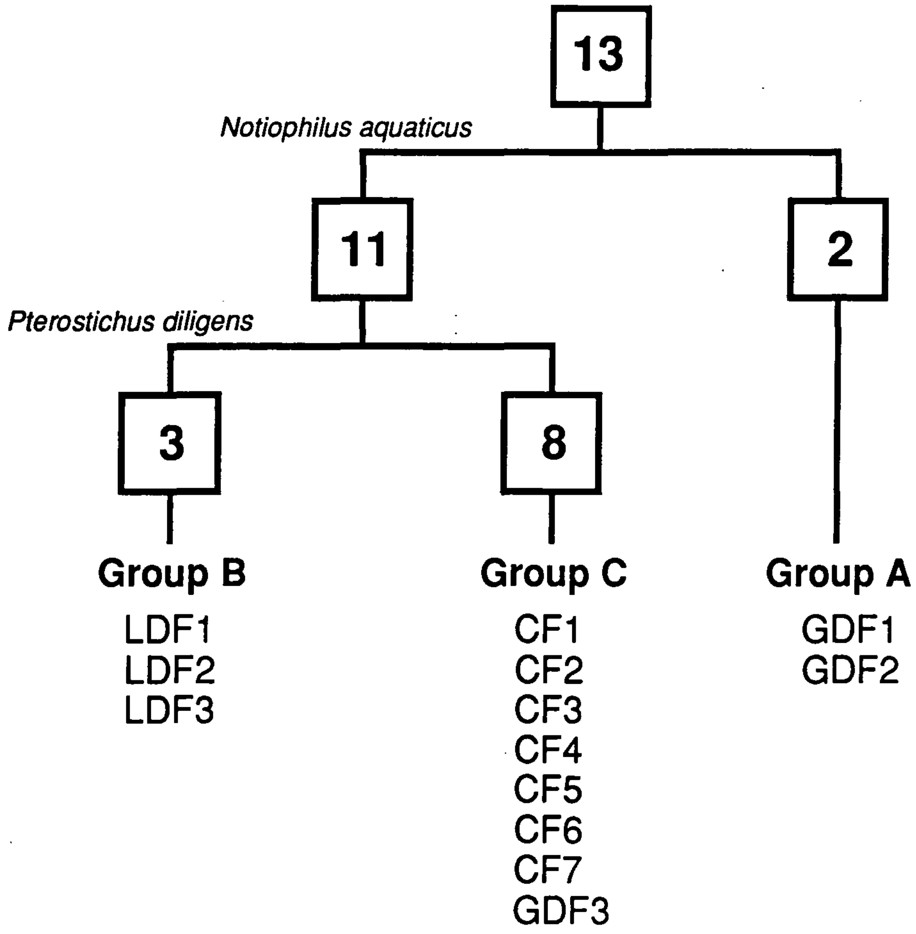
The patterns of classification and ordination of the fell top spiders and carabids are shown in Figures 5.6, 5.7, 5.8 and 5.9. From the original 13 sites, three groups of sites are identified based on their spider fauna using TWINSPAN. The first division of the sites (Figure 5.6) groups two peat sites (CF2 and GDF1) and two of the *Nardus* sites (CF6 and GDF2) together to form Group A. On the other side of the first division, a number of short grassland sites are grouped with one of the *Nardus* sites. This *Nardus* site (CF7) is highlighted as a borderline site, and has affinities with the sites included in Group A. The indicator species which proposed this split was the higher level of abundance of *Erigone dentipalpis* at the grass sites. This group is further divided into two groups consisting of sites CF4 and LDF1 (Group B) on one side, and on the other side CF1, CF3, CF4, CF7, LDF2, LDF3 AND GDF3 (Group C). The indicator species for this second split was *Centromerus prudens* which had a higher abundance at sites CF4 and LDF1 than at the Group C sites.

Figure 5.6. Dendrogram representing the major divisions and indicator species of a TWINSPAN classification of the 13 sites from the north Pennine fell tops, based on their spider fauna during 1991.



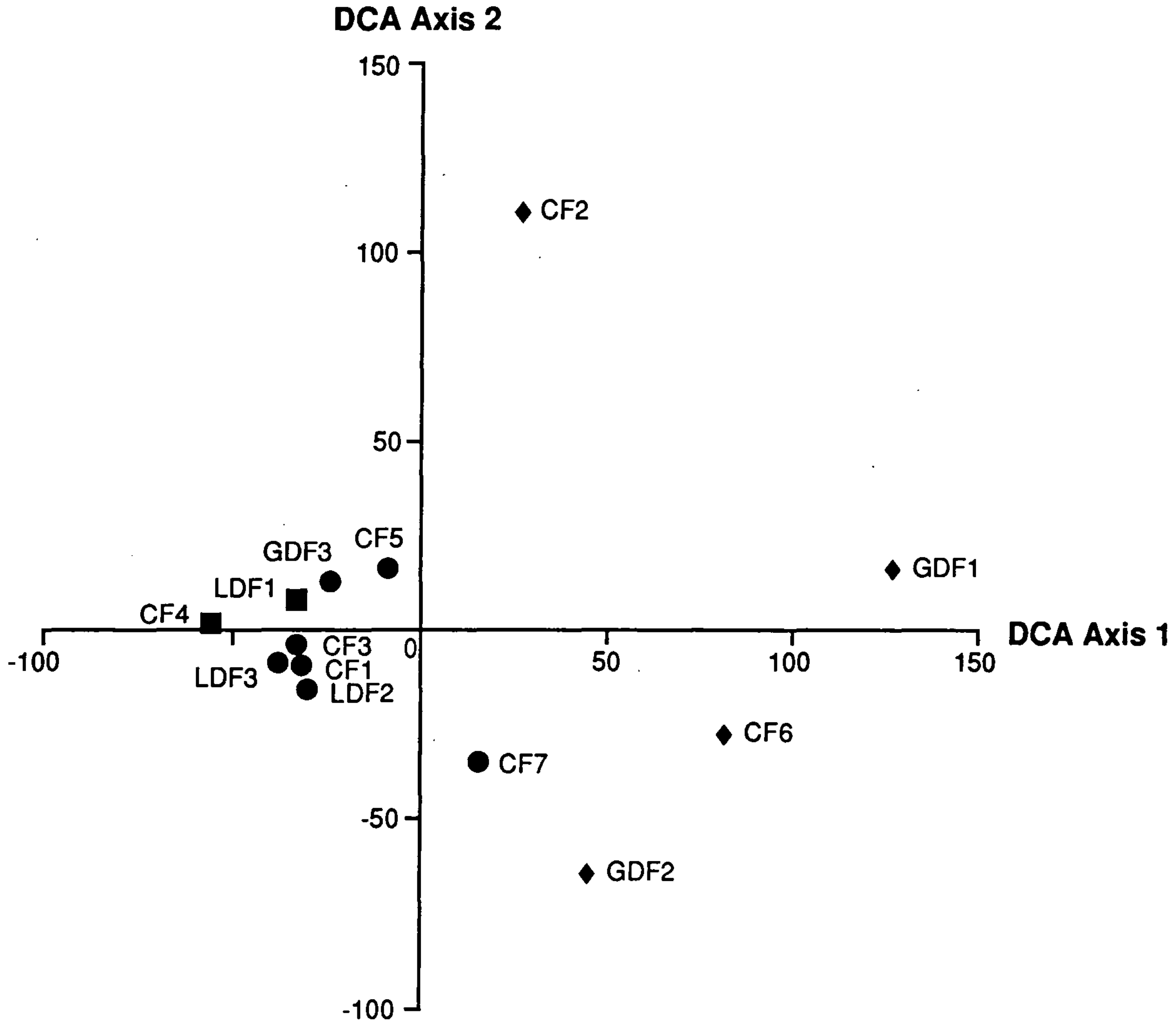
When the same procedure was used to classify the sites based on their carabid beetle fauna, three groups were also identified, but the sample composition of each group was different from that obtained using the spiders (Figure 5.7). The first division grouped two geographically close sites together, GDF1 and GDF2 (Group A) based on the absence of *Notiophilus aquaticus* . This species was commonly found at all the other sites. The remaining sites were split based on the abundance of *Pterostichus diligens*, which was more common at all the sites on Little Dun Fell (74% of the total catch from Little Dun Fell). Hence sites LDF1, LDF2 and LDF3 compose Group B. The remaining sites make up Group C (CF1, CF2, CF3, CF4, CF5, CF6, CF7 and GDF3).

Figure 5.7. Dendrogram representing the major divisions and indicator species of a TWINSPAN classification of the 13 sites from the north Pennine fell tops, based on their carabid fauna during 1991.



These groupings for both assemblages are also shown in ordination space using DCA. Figure 5.8 shows the distribution of the sites based on their spider fauna on Axes 1 and 2. The first division by TWINSPAN is clear on the ordination diagram, as the four sites with dense vegetation are well separated from the tightly clustered short grass sites. the *Nardus* site (CF7), which is included in Group C, is separated in ordination space from its associated sites, most likely due to the lower numbers (between 20% and 50% abundance of that of the *Festuca* grass sites) of *Erigone dentipalpis* in relation to the *Festuca* grass sites (this would have influenced site CF7's position as a borderline site in the TWINSPAN analysis). The second division by TWINSPAN is not obvious from Figure 5.8, but the Group B sites are separated from the Group C cluster on Axis 3 of the DCA space. These results suggest that there is a distinct assemblage of spiders associated with the short *Festuca* grassland of the fell tops with a small degree of internal variation, while the other sites which have dense

Figure 5.8. Ordination diagram of axis 1 against axis 2 using Detrended Correspondence Analysis of 13 north Pennine fell top sites based on their spider distribution during 1991. TWINSPAN groups are shown; Group A: diamonds, Group B: squares, Group C: circles. Eigenvalues: axis 1 - 0.21; axis 2 - 0.11.



vegetation are sufficiently different in composition from the short grass sites. There is also a high degree of variation within Group A.

Using cluster analysis, the same initial groupings were produced, following the same classification criteria as used by Butterfield and Coulson (1983). The results showed the *Festuca* sites having a high degree of similarity to each other (>60%), while the remaining sites were not similar to the *Festuca* group (<40%), and also had a low degree of similarity to each other than the grass sites (between 50% and 60%).

Figure 5.9 shows the distribution of the fell top sites based on their carabid fauna using DCA. As with the spiders, the TWINSPAN divisions are obvious on the ordination plot. Sites GDF1 and GDF2 (Group A) are well separated from the other sites along Axis 1, and sites LDF1, LDF2 and LDF3 (Group B) are separated from the Group C sites along Axis 2. Again, as with the spiders, similar results were obtained for the carabid beetles using the modified similarity index and cluster analysis.

Table 5.8 shows the distribution of the common species of spider (with an abundance of five or more specimens at one or more sites) in each group as produced by TWINSPAN. The results suggest that the main difference between the groups is not so much species distribution as the relative abundance of the species in each group. Most of the commonly occurring spiders are widespread and not restricted to specific fell top habitats. The three members of the *Erigone* genus (*E. dentipalpis, E. promiscua* and *E. atra*) were present at the sites in Group A, but were considerably more abundant in the sites in Groups B and C (ranging from between 2 times to approximately 100 times the abundance at Group A sites). Group B is separated by the common occurrence of *Silometopus elegans* and *Centromerus prudens.* Group C is a large group with several common species typical of short grassland, such as those species of *Erigone* and *Oedothorax* (Coulson and Butterfield 1986, Rushton and Eyre 1992). Group A has several common species, *Diplocephalus permixtus, Semljicola caliginosa, Lepthyphantes angulatus, Drepanotylus uncatus, Hilaira nubigena* and *Micrargus herbigradus.*

Setting aside the occurrences of less than five of these species, the above species from Group A are restricted to the sites with denser vegetation, within which there is still a degree of preference for habitat. Most of the species in Group A are associated with both the *Eriophorum* and *Nardus* sites, but not necessarily to every site within the group. *D. permixtus* occurs commonly at the two *Nardus* sites (CF6, CF7) and at the peaty site GDF1, but not at the other peat site CF2. *D. uncatus* is similar in that it occurs commonly at CF6, GDF1 and GDF2, but is scarce at the other dense vegetation sites CF2 and CF7. Almost all of the common species were from the family Linyphiidae, the only non-Linyphiidae included in Table 5.8 was a member of the Lycosidae, *Pardosa monticola,* found at sites CF3 and CF5, both *Carex-Racomitrium-Festuca* sites with low vegetation density. Only one species was common at all sites, *Hilaira frigida,* which occurred in 95% of the traps.

Figure 5.9. Ordination diagram of axis 1 against axis 2 using DCA of 13 north Pennine fell top sites based on their carabid beetle distribution during 1991. TWINSPAN groups are shown; Group A: diamonds, Group B: squares, Group C: circles. Eigenvalues: axis 1 - 0.17; axis 2 - 0.12.

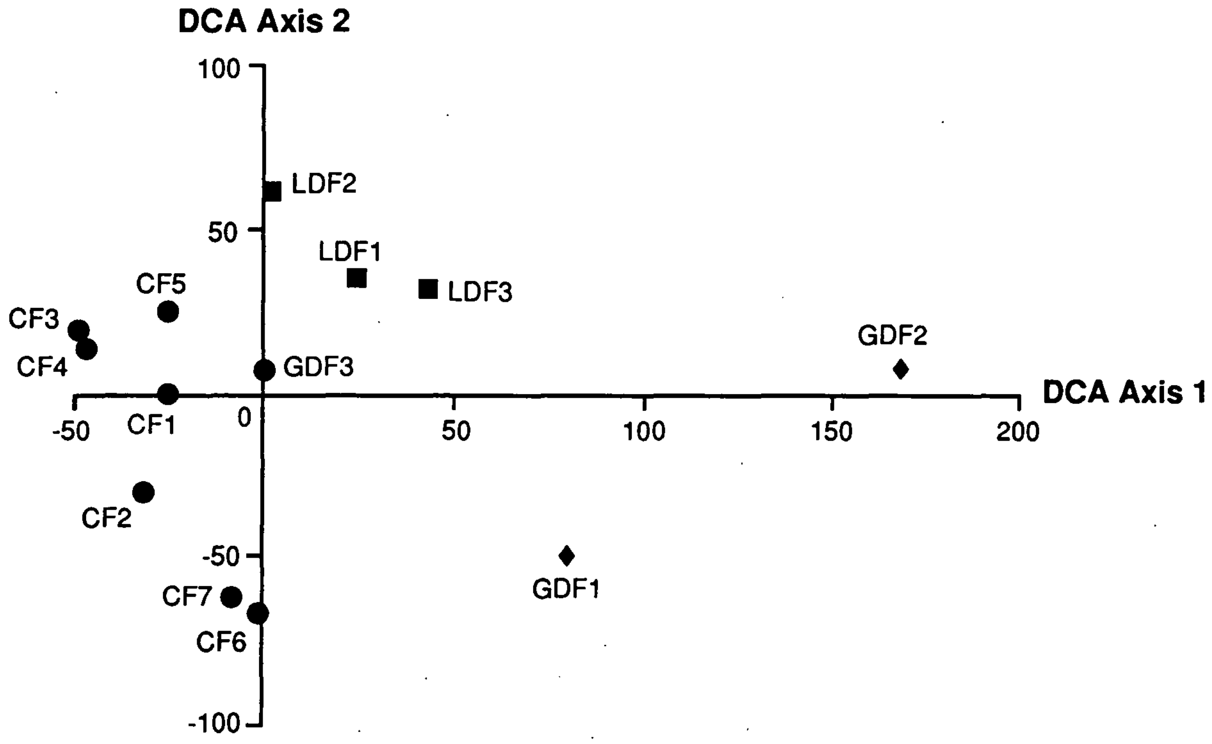


Table 5.9 shows the distribution of the common carabid beetle species (with an abundance of five or more at one or more sites) in each group as produced by TWINSPAN. The species mainly responsible for influencing the first division was *Notiophilus aquaticus*, which was absent from sites GDF1 and GDF2. Although TWINSPAN highlighted *Pterostichus diligens* as influencing the second division, the relative low abundances of *Nebria gyllenhali* and *Loricera pilicornis* at the sites where *P. diligens* occurred probably separated Group B from C also. Most other species were either widespread, such as *Carabus problematicus* and *Patrobus assimilis* (taken in 90% and 97% of the traps respectively), or infrequent, such as *Nebria salina* and *Miscodera arctica*. *P. assimilis* may have influenced the first division, as it had relatively low abundance, but not absent, at sites GDF1 and GDF2 (ranging from 3 - 10 times lower in abundance than at Groups B and C).

Table 5.8. Distribution of spider species with an abundance ≥ five specimens at any north Pennine site as indicated by TWINSPAN. Vertical lines represent position of major TWINSPAN divisions (• indicates value of less than 5).

Species	CF4	LDF1	CF1	LDF3	CF3	CF5	GDF3	LDF2	CF7	CF2	CF6	GDF2	GDF1
Oedothorax fuscus	•	•	•	•	7	8	•	5	•				
Meineta gulosa	•	•	•	•	•		•	6	•				
Oedothorax retusus	•	•	9	•	•	•	•	•	•		•		
Orenetides vaginatus	•	14	14	•	•	7	38	22	•	•	•		
Walckenaeria nudipalpis		•	8		•	•		•	•		•	•	•
Walckenaeria clavicornis	7	16	26	18	21	•	30	10	19	40	•	8	8
Walckenaeria cuspidata	•	•		•	•	57	5	•	10		14	15	
Erigone dentipalpis	42	118	77	82	75	60	67	133	26	6	5	9	•
Erigone promiscua	7	95	263	443	72	90	237	98	32	•	5	90	18
Erigone atra	18	56	59	89	56	55	29	81	31	•	12	29	•
Hilaira frigida	51	41	63	15	73	19	88	33	18	105	27	8	17
Centromerita bicolor	•	5	20	15	•	17	15	12	39	17	64	•	24
Centromerita concinna	14	20	18	27	28	33	13	16	•	35	•	•	•
Pardosa monticola		•	•		5	12	•	•		•			•
Savignya frontata	8	•	•	9	10	7	10	10	•		•	•	•
Silometopus elegans	118	116	6	•	32		•	51	36	•	28		•
Centromerus prudens	19	10		•	8	•	•	•	•	•	•		
Bathyphantes gracilis		•	•	•	5	•	7	•	•	•	•	•	22
Diplocephalus permixtus	•	•							34		73		27
Semljicola caliginosa			•	•	•		•	6			15	7	79
Lepthyphantes angulatus	•	•		•		•	•		•	28	•		6
Drepanotylus uncatus						•		•	•	•	10	19	19
Hilaira nubigena						•					7	•	36
Micrargus herbigradus										8			•

Table 5.9. Distribution of carabid species with an abundance ≥ five specimens at any north Pennine site as indicated by TWINSPAN. Vertical lines represent position of major TWINSPAN divisions (• indicates value of less than 5).

Species	LDF1	LDF2	LDF3	CF1	CF5	GDF3	CF2	CF3	CF4	CF6	CF7	GDF1	GDF2
Bembidion guttula												•	5
Pterostichus diligens	14	6	8	•	•	•				•		•	•
Leistus rufescens	6		8									8	
Calathus melanocephalus	•	•			20	•		•	•				
Notiophilus aquaticus	25	28	10	57	158	22	14	49	10	•	13		
Notiophilus germinyi	136	26	119	17	82	97	•	6	•	•	•	•	5
Trechus obtusus	•	5	•	26	7	12	23	13	•		•	•	
Patrobus assimilis	90	63	90	62	115	86	57	48	42	53	62	16	12
Nebria gyllenhali	7	•	14	103	36	67	188	205	248	65	105	•	•
Carabus problematicus	46	27	24	19	36	36	31	9	6	37	75	25	•
Loricera pilicornis	•		•	•	6	11	21	•		73	136	36	•
Notiophilus biguttatus	•	•		16	21	•	8	•	•	13	15	•	

5.4.3 Environmental factors influencing the invertebrate distribution

Using Canonical Correspondence Analysis (ter Braak 1988), it was possible to assess if the distribution of the invertebrate species was related to the environmental variables measured at each site. Only three environmental variables can be used sensibly in a model with only 13 sites (ter Braak pers. comm.) so intercorrelations of the variables were explored for multicollinearity. The different vegetation densities in each profile layer were not independent of each other, and the results (Table 5.10) showed that all three layers were highly correlated (all correlations, $p < 0.01$) indicating that if a site had dense vegetation in the 0-20mm layer, then it also had dense vegetation in the other two layers. All three layers were added to produce a Total Vegetation variable which was, as expected, very highly correlated with the three individual layers (all $r > 0.85$, $df = 11$, $p < 0.001$). Organic content and moisture content were removed as they were highly correlated with vegetation density. Soil pH was also removed due to low variance between sites and a correlation with Slope. This resulted in three variables for inclusion in the model; Soil depth, Slope and Total vegetation density.

Figure 5.10 shows the results of the ordination of the sites based on their spider fauna with respect to the three environmental variables for Axis 1 and 2. The eigenvalues for each axis, which give some indication of the amount of community variation explained by each axis, were 0.17, 0.06, 0.05 and 0.11, for axes 1 to 4 respectively. Only three constrained ordination axes were produced by CCA, as only three environmental variables were included in the model. A Monte Carlo significance test on the species distribution related to both Axis 1 and to all three axes combined was significant ($p < 0.01$) in both cases. Although the eigenvalues are low, they nevertheless indicate that the included variables explain a significant proportion of the variation. Table 5.11 shows the inter-set correlation coefficients (ter Braak 1988) between the variables and the spider species scores for each axis. Axis 1 accounts for 60% of the explained variance, and is defined by a combination of all three variables included in the model, as all three have significant correlation values with the species scores for axis 1. Of the three variables, vegetation density had the most influence on species distribution ($r = 0.89$, $df = 11$, $p < 0.001$), with all of the low density sites (*Festuca* grassland sites and GDF2) appearing on the negative side of Axis 1 (Figure 5.10), and those with high density on the positive side. Soil depth was also significant ($r = 0.70$, $df = 11$, $p < 0.01$) and caused some separation among the *Festuca* sites, a gradient forming from CF4, LDF1 and LDF2 to CF6, CF7 and GDF1. A similar gradient was produced for Slope ($r = 0.60$, $df = 11$, $p < 0.05$). The ordination diagram indicates that the principle axis is closely identifiable with that obtained by DCA and also shows similarities with the classification obtained by TWINSPAN. Axis 2 and 3 do not have any significant environmental variables

Table 5.10. Correlation coefficients between environmental variables for the North Pennine fell top sites ($n = 13$), * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	pH	Organic content	Moisture content	Soil depth	Slope	Vegetation 0-20mm	Vegetation 21-40mm	Vegetation >41mm
Organic content	-0.45							
Moisture content	0.15	0.70 **						
Soil depth	0.45	0.23	0.50					
Slope	0.53 *	0.01	0.08	0.40				
Vegetation 0-20mm	-0.30	0.58 *	0.39	0.07	0.23			
Vegetation 21-40mm	-0.01	0.63 *	0.57 *	0.54 *	0.53 *	0.76 **		
Vegetation >41mm	0.30	0.46	0.61 *	0.59 *	0.57 *	0.74 **	0.88 ***	
Total vegetation	0.16	0.55 *	0.61 *	0.50	0.51	0.86 ***	0.91 ***	0.97 ***

correlated with them, and only account for 22% and 18% of the explained variance respectively.

The presence of a fourth axis eigenvalue indicated variation in the community not explained by the three included variables, however it did not have a large eigenvalue, (0.11), and was not significant (ter Braak pers. comm.).

Table 5.11. Inter-set correlation coefficients (ter Braak 1988) between the environmental variables and the three CCA axes for spider species scores, obtained using CANOCO, from the north Pennines (n = 13).

Variable	Axis 1	Axis 2	Axis 3
Slope	0.60	-0.50	-0.48
Vegetation density	0.89	0.25	-0.11
Soil depth	0.70	-0.36	0.48

Figure 5.10. Ordination diagram of axis 1 against axis 2 using Canonical Correspondence Analysis of 13 north Pennine fell top sites based on their spider distribution during 1991. Arrows indicate the direction and strengths of the significant environmental variables. TWINSPAN groups are shown; Group A: diamonds, Group B: squares, Group C: circles. Eigenvalues: axis 1 - 0.17; axis 2 - 0.06.

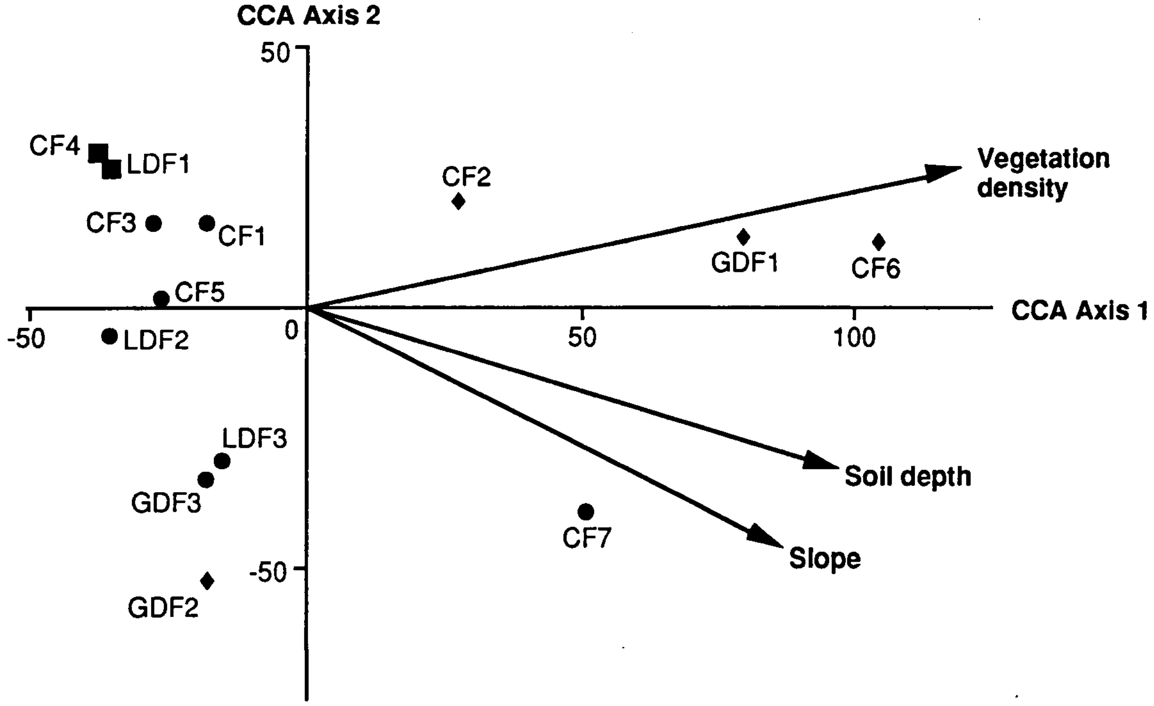
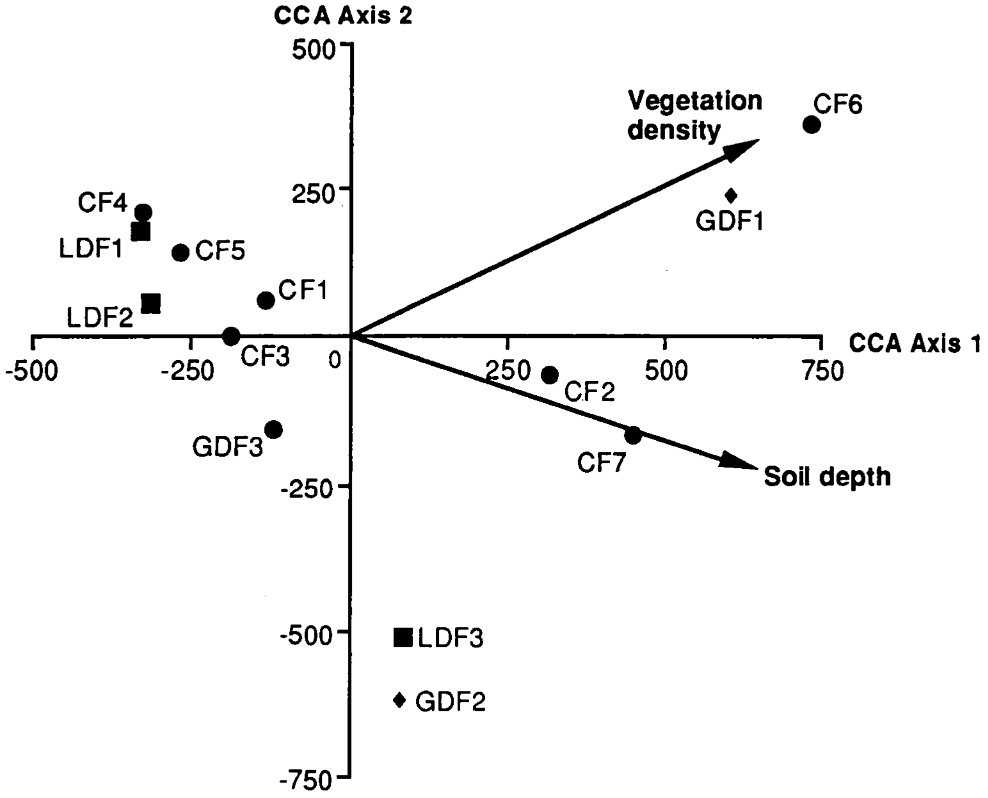


Figure 5.11 shows the distribution of sites with respect to the environmental variables along axes 1 and 2, based on their carabid fauna using CCA. The eigenvalues for each axis were 0.11, 0.06, 0.04 and 0.15, for axes 1 to 4 respectively. The same three environmental variables (total vegetation density, soil depth and slope) were used in the model, and this resulted in only three constrained axes being produced by the analysis. The distribution of carabid species along Axis 1 was significant (Monte Carlo test, $p < 0.02$), but the test for all three constrained axes was not significant. All eigenvalues are however low, and the fourth axis value is larger than axes 1, 2 or 3, suggesting that there is variation in the community which accounts for more variation in the species distribution than any of the environmental variable included in the model. The sample distribution using CCA (Figure 5.11) bears little similarity with the DCA ordination of Figure 5.9, which suggests that though the samples and species are constrained to the variables included, this is not a realistic distribution. Table 5.12 shows the inter-set correlation coefficients between the environmental variables and the species scores for each axis. Axis 1 was significantly correlated with Vegetation Density ($r = 0.81$, $df = 11$, $p < 0.001$) and Soil Depth ($r = 0.85$, $df = 11$, $p < 0.001$). Axis 2 was not significantly correlated with any variables, and Axis 3 was significantly correlated with Slope ($r = -0.69$, $df = 11$, $p < 0.01$). The Monte Carlo test result for Axis 1 indicates that this was a significant distribution, although the test for all three axes combined indicated that the distribution of the species was not significantly correlated with the variables. This suggests that while both Vegetation Density and Soil Depth influence the distribution of the north Pennine carabid species, it is much less than the variation in the community, the major influence presumable from a variable which was not measured. The eigenvalues in this model support this explanation.

Table 5.12. Inter-set correlation coefficients (ter Braak 1988) between the environmental variables and the three CCA axes for carabid species scores, obtained using CANOCO, from the north Pennines (n = 13). Slope included based on significance with axis 3.

Variable	Axis 1	Axis 2	Axis 3
Slope	0.53	-0.02	-0.69
Vegetation density	0.81	0.35	-0.05
Soil depth	0.85	-0.28	0.15

Figure 5.11. Ordination diagram of axis 1 against axis 2 using CCA of 13 north Pennine fell top sites based on their carabid beetle distribution during 1991. Arrows indicate the direction and strengths of the significant environmental variables. TWINSPAN groups are shown; Group A: diamonds, Group B: squares, Group C: circles. Eigenvalues: axis 1 - 0.11; axis 2 - 0.06.



5.5 Discussion

5.5.1 The spider assemblages

Coulson and Butterfield (1986) identified eight upland spider communities from northern England, two associated with upland grasslands on mineral soils and six on peat soils. They suggested that the main differences between their communities depended on the "plant architecture", identified by the combination of several species, most readily seen in the commonly occurring species. In this study, three additional spider assemblages (communities *sensu* Coulson and Butterfield), have been found on the fell tops on the northern Pennines.

1. A high altitude grassland assemblage, separated from those of Coulson and Butterfield by the increased dominance of the *Erigone* species, and the relative absence of the *Oedothorax* species, both genera commonly associated with grassland areas.

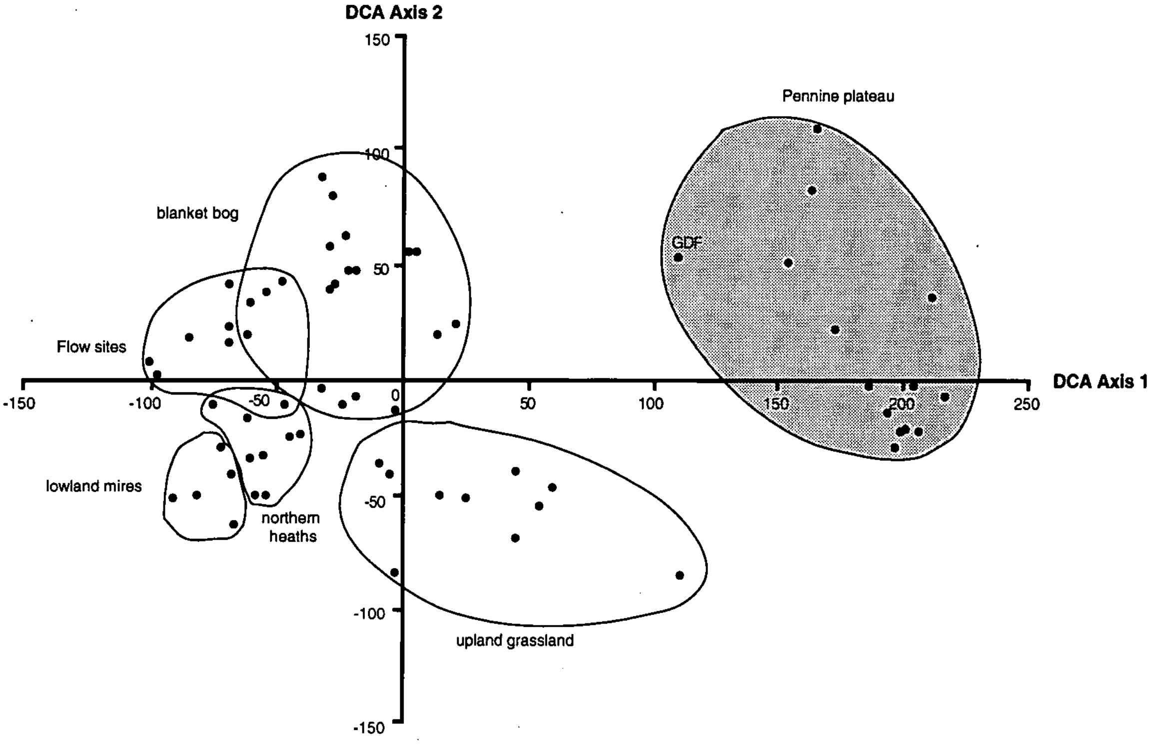
2. A high altitude grassland assemblage, similar to above but with increased proportion of *Centromerus prudens* and *Silometopus elegans*. These species were not found together in numbers at any sites examined by Coulson and Butterfield.

3. A dense vegetation assemblage, consisting of a combination of species not abundant in the traps of Coulson and Butterfield, presumably due to the increased altitude on the plateaux areas. The dominant spider fauna of these dense vegetation habitats varied, making it probable that there were other factors (not measured) contributing to the variation between the sites. Characteristic species included *Semljicola caliginosa*, *Hilaira nubigena*, *Diplocephalus permixtus*, *Drepanotylus uncatus* and *Lepthyphantes angulatus*. *Semljicola caliginosa* and *Hilaira nubigena* are both indicative of sub-montane wetlands and upland bogs in the north of England and Scotland (Ratcliffe 1977) and are considered notable species (**Nb** and **Na** respectively; Merrett 1990). The remainder have more widespread but local distributions throughout Britain (Locket and Millidge 1953, Roberts 1985).

To highlight the separation of the summit study sites from those of other peat and upland grassland areas, DCA was performed to compare the present sites with those of Coulson and Butterfield (1986), and with those from a survey of peatland areas in the Scottish Flows (Coulson *et al.* 1995). The results of Axis 1 against Axis 2 are shown in Figure 5.12. They show clear variation amongst the peat and grassland sites and also a clear separation of the Pennine fell top sites from all the other sites, and Axis 1 was closely correlated with altitude ($r = 0.87$, $df = 62$, $p < 0.001$).

and Butterfield did sample one site on the plateau of Great Dun Fell at 825m, and that site was closer in ordination space to the present fell top sites than any other of the sites examined, based on its spider fauna. Indeed, in their initial classification, this site was an ungrouped site, unattached to any of the eight communities they described.

Figure 5.12. Ordination diagram of axis 1 and axis 2 using DCA of 64 sites from the north Pennines (England), and the Flows (Sutherland, Scotland), based on their spider fauna trapped in pitfall traps. Data taken from this survey, Coulson and Butterfield (1986) and Coulson *et al.* (1995). Pennine plateau site sampled by Coulson and Butterfield labelled GDF. Eigenvalues: axis 1 - 0.43; axis 2 - 0.16.



Vegetation structure is considered to be one of the most important features controlling spider distribution (Cherrett 1964, Coulson and Butterfield 1986), along with prey distribution (Otto and Svensson 1982), which is probably influenced by the vegetation (Cherrett 1964). In the present study, much of the systematic variation among spider assemblages reflected in the results is attributable to an increase in vegetation density throughout all levels of the profile. Sites CF2, CF6, CF7 and GDF1 had much denser vegetation at all levels and these sites were the only habitats studied in which the vegetation extended above 40mm. Management is also considered to be an important factor determining the structure of spider communities in both lowland and upland grasslands (Rushton and Eyre 1992), and indeed in most cases vegetation structure is directly related to management through grazing. The slope and soil depth also contributed to the sub-montane spider distribution, presumably influencing microclimate characteristics.

Affinities of the spider species with other upland areas

Most of the spider species found on the north Pennine fell tops are characteristic of high ground in Scotland and northern England, and the Pennine communities show affinities with those of the montane and sub-montane plateaux of the Cairngorms in eastern Scotland. The similarity between these areas was assessed using data from the Pennine plateaux and data from a pitfall trap survey on three montane plateaux areas in the Grampian region, Scotland during 1989; Cairn Gorm (1248m, NJ 301803), Glas Maol (1070m, NO 307776) and Drumochter (916m, NN 267779) summits (I. S. Downie, unpublished). Of the 56 species recorded in the Pennine summits, 28 were also found in the Cairngorms (of 50 species found during 1989). Percentage similarity values between the Pennine summits and the Grampian summit sites ranged from 37% to 52%. However, the number of species restricted to high altitude is greater in the Cairngorms. The proportion of species categorised as being typical of montane and sub-montane (following Ratcliffe 1977) taken in the north Pennines is 4% and 13% respectively. Of the 64 species taken from the summits in the Grampian Region (between 1987 and 1989 by Scottish Natural Heritage, unpublished data), the proportions are higher; 14% of the species are montane and 14% are sub-montane. Table 5.13 indicates the similarities between the three Pennine summits and the three Grampian summits based on the presence/absence of the spider species trapped in pitfalls. The presence of these species in the north of England is also indicated using presence/absence data from Coulson and Butterfield (1986). Four montane species were commonly trapped in the Cairngorm survey, yet absent from the north Pennine plateaux; *Tricca alpigena* is restricted to the Cairngorm massif; *Erigone tirolensis* was abundant on Glas Maol, but has also been found on Ben Hope (Merrett 1971); *Rhaebothorax peatulus* is restricted to Glas Maol and *Meioneta nigripes* is restricted to *Juncus trifidus* habitats on Cairn Gorm. Few species which occurred commonly in the north Pennines were scarce or absent from the Cairngorms, but these included *Walckenaeria cuspidata*, *Diplocephalus permixtus*, *Semljicola caliginosa*, *Drepanotylus uncatus* and *Hilaira nubigena*. Most of the variation between the two areas is represented by species with small numbers of specimens.

Both the north Pennine summits and the Grampian plateau areas have a similar spider family composition, with Linyphiidae forming over 80% of the species found. The relative proportions of high altitude species suggests that the influence of both widespread species and lower altitude species from bordering areas has a much greater impact on the species composition on the north Pennines. The Cairngorm massif is set within a much larger area of upland habitat and possesses a larger reservoir of typical montane species.

5.5.2 The carabid assemblages

Three carabid assemblages were also identified using multivariate methods. As with the spiders, they are different from the carabid beetle communities identified by Butterfield and Coulson (1983).

1. An upland grassland assemblage with high numbers of *Pterostichus diligens* and *Notiophilus aquaticus* in the catch. *Pterostichus diligens* only occurred in high numbers at the three sites on Little Dun Fell. This assemblage is also characterised by a relative decrease in the numbers of *Nebria gyllenhali.*

2. An assemblage from a variety of vegetation types, all of which possessed relatively high numbers of *Notiophilus aquaticus* as above, and also high numbers of *Nebria gyllenhali* in the catch. Only one or two specimens of *Pterostichus diligens* occurred in this assemblage.

3. An assemblage characterised by the complete absence of *Notiophilus aquaticus* and a reduced abundance of *Nebria gyllenhali,* but the presence of some of the more widespread species, such as *Patrobus assimilis.*

The carabid assemblages are less clearly defined than those of the summit spiders, but there are some similarities with the communities identified by Butterfield and Coulson. The main difference in the carabids of the present summit assemblages from the majority of those of Butterfield and Coulson is in the increase of higher altitude or open grassland species, such as *Nebria gyllenhali* and *Notiophilus aquaticus* respectively. However, three of their mineral grassland and three high altitude sites are more similar to the summit sites than most. These sites are still different, based on the absence of *Carabus violaceus* and *Pterostichus madidus* (only one specimen taken, site LDF2) and the increased abundance of *Notiophilus germinyi* at the summit plateaux sites. They characterised a fell top grassland community by the presence of *Nebria gyllenhali, Notiophilus germinyi* and *Patrobus assimilis* (from the summits of Great and Little Dun Fell). In this study, both *N. gyllenhali* and *P. assimilis* were widespread, only *N. germinyi* is clearly associated with the grassland habitats. Butterfield and Coulson also proposed a high altitude peat community, including *Pterostichus diligens*, *Patrobus assimilis*, *Loricera pilicornis*, *Notiophilus aquaticus* and *Calathus melanocephalus*. In this study, only *L. pilicornis* is clearly associated with the peat soils, the rest are either widespread, few in numbers or more associated with grassland assemblages, such as *P. diligens*. Butterfield and Coulson grouped both L. *pilicornis* and *P. diligens* as being characteristic of wet peat and wet grassland habitats, yet they clearly prefer different habitats in the present study.

Figure 5.13 shows an ordination diagram using DCA comparing the present sites, those of Coulson and Butterfield (1986), and those from a survey of peatland areas in the Scottish Flows (Coulson *et al.* 1995). In ordination space, the north Pennine plateaux sites are separated along Axis 1, which is strongly correlated with altitude ($r = 0.83$, $df = 62$, $p < 0.001$), suggesting that the carabid species composition of the present study sites have an increased higher altitude component. Similar results are shown for an identical analysis using staphylinid beetles indicating that the staphylinid species of the north Pennines have a higher altitude component (Figure 5.14. Correlation with altitude, $r = 0.90$, $df = 62$, $p < 0.001$). As with the spiders, the carabid and staphylinid composition of the single summit site sampled by Butterfield and Coulson is sufficiently similar in species content and abundance to be placed within the groupings of the present study sites on the ordination diagrams.

Butterfield and Coulson (1983) concluded that upland carabid distribution is more dependent on factors such as soil moisture and temperature, and that vegetation structure only accounts for a small part of the variation. Thingstad (1987) also concluded that there is not always a correlation between the vegetation types and the carabid beetle communities of alpine and sub-alpine habitats in Norway, as in these habitats, the local topography, climatic and edaphic conditions give rise to particular types of vegetation. The individual carabid species respond in different ways to the same abiotic environmental conditions, giving the different carabid assemblages. These communities will therefore, in some way, be correlated with the same abiotic factors as the vegetation. Some characteristic carabid associations were obtained by ordination methods, and relationships between species and vegetation types are present. *Loricera pilicornis* is closely related to the dense vegetation sites of CF2, CF6, CF7 and GDF1. *Notiophilus germinyi*, although widespread, is the opposite, associated with the less dense vegetation of the *Festuca* grasslands at CF5, LDF1, LDF2, LDF3 and GDF3. The findings of Butterfield and Coulson (1983) and Thingstad (1987) regarding vegetation density having only a small influence on the carabid distribution is mirrored in this study, as the results of the CCA suggest that vegetation density and soil depth contributed to the distribution of some species, but the results indicate that this was not a major component of the spatial distribution.

Festuca and other grasses, they are subject to both rapid flooding and desiccation. The organic content of these grasslands may also be influenced by their thickness, with plant root systems and bedrock in close proximity to each other. The high proportion of stone at the soil surface of most sites will also influence the carabid distribution as scope for refuges, the only sites without a high stone volume (at least in close proximity) were sites GDF1 and GDF2, and this may be one of the factors which separated these sites in the initial classification based on their species content.

Figure 5.13. Ordination diagram of axis 1 and axis 2 using DCA of 64 sites from the north Pennines (England), and the Flows (Sutherland, Scotland), based on their carabid fauna trapped in pitfall traps. Data taken from this survey, Butterfield and Coulson (1983) and Coulson *et al.* (1995). Pennine plateau site sampled by Butterfield and Coulson labelled GDF. Eigenvalues: axis 1 - 0.38; axis 2 - 0.29.

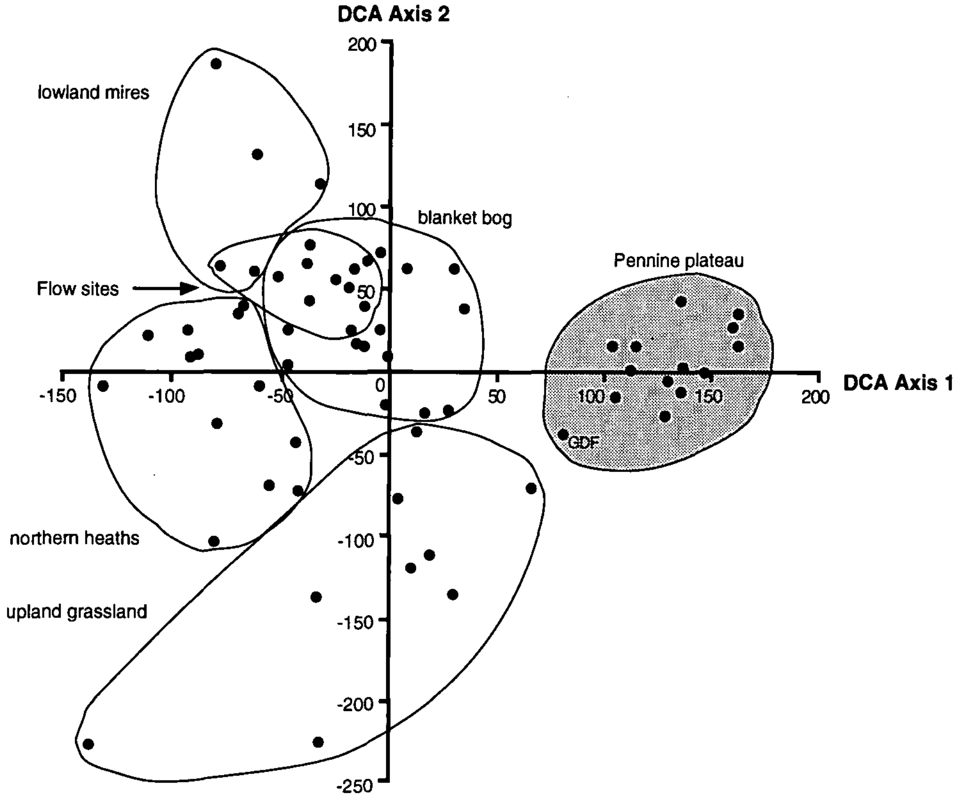
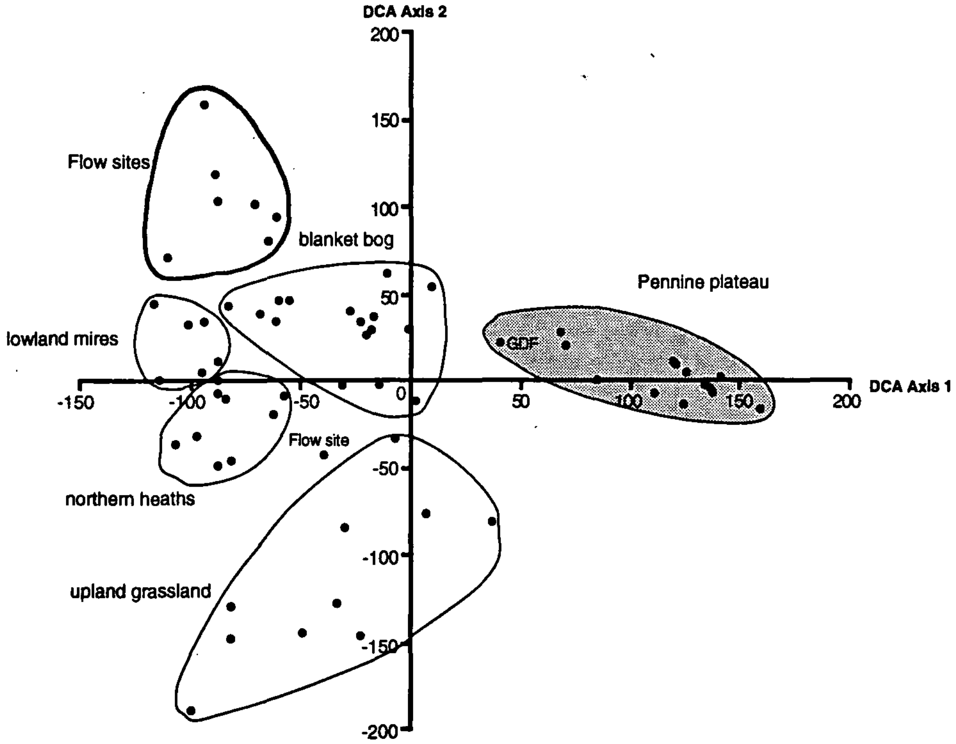


Figure 5.14. Ordination diagram of axis 1 and axis 2 using DCA of 64 sites from the north Pennines (England), and the Flows (Sutherland, Scotland), based on their staphylinid fauna trapped in pitfall traps. Data taken from this survey and Coulson *et al.* (1995). Pennine plateau site sampled by Coulson *et al.* labelled GDF. Eigenvalues: axis 1 - 0.44; axis 2 - 0.24.



5.5.3 The influence of altitude

Coulson and Butterfield (1986) found that with increasing altitude, the number of non-linyphiid spider species decreases while the number of linyphiid species remains relatively constant, resulting in the proportion of linyphiid species in the catch increasing with altitude. Cherrett (1964) recorded 73% linyphiid species (from a total of 71 species trapped) from Moor House NNR, and Goodier (1970) showed a progressive increase in the proportion of linyphiids from 41% to 67% over an altitudinal transect from 308m to 875m on Snowdon, North Wales. Although Goodier's study reached a higher altitude, the area was much further south, possibly with a warmer climate, making this a useful comparison relevant to Cherrett and Coulson and Butterfield. Another useful comparison arises from the spider species studied by Duffey (1962) from a lowland limestone grassland, where the linyphiid proportion only composed 41%. In the present study, 88% of the spider species trapped were linyphiids, showing a definite altitudinal trend.

The high altitude environment also plays an important role in the alteration of the ecology of individual species of invertebrate. Species restricted to specific habitats at montane altitudes (*Hilaira frigida* on open moorland; Ratcliffe 1977) occur in a greater variety of habitats at slightly lower altitudes. Species from specific habitats at low altitudes can become more generalist at higher altitudes (*Patrobus assimilis*) and species from a wide range of habitats at lower altitudes (*Loricera pilicornis*; Houston 1970, 1971), either become more restricted at the higher altitude or alter their habitats completely (*Carabus problematicus*, a forest species at lower levels; Thiele 1977).

Cherrett (1964) described seven common species of lycosid spider caught from Moor House NNR, of which four were common; *Pardosa palustris*, *Pardosa pullata*, *Alopecosa pulverulenta* and *Pirata piraticus*. Both *P. pullata* and *P. piraticus* showed affinities with *Eriophorum vaginatum* habitats and *A. pulverulenta* appeared to prefer alluvial grassland. Of these, only three were recorded from the fell top sites, *P. pullata*, *A. pulverulenta* and *P.* piraticus, and they were not common or specific to any habitat type. The only other lycosid to occur on the summits was *Pardosa monticola*, again not abundantly.

When compared to the lower altitudes, the entire fell top habitat is a much wetter environment (possessing lesser internal environmental variation), as precipitation and number of cloud cover days increase with altitude. Greenslade (1968), in a comparison of the Carabidae of Argyll with a less atlantic climate in S.E. England, showed that in the higher altitudes, the lowland fauna was impoverished, especially in the absence of many diurnal species of open habitat. Among the remaining species there were corresponding shifts in habitat from woodland towards more open situations. Greenslade suggested these restrictions and modifications in ecology (physical and behavioural) were caused by the mountain climate, where the complex of low temperature and high humidity may be limiting for most carabids.

5.5.4 The north Pennine plateaux

The Pennine summit plateaux included in this survey are internationally important areas for both their peatland and upland grassland habitats (Ratcliffe 1977). They are one of the largest areas of high plateaux in Britain south of Scotland, and possess vegetation types unique in northern England. The invertebrate communities of these areas form distinct assemblages not found elsewhere in Britain, and possess some notable and important species. There are similarities in spider and carabid species present with other mountainous areas in Britain, as well as with some of the larger islands of Scotland (Ashmole 1979), but it appears that it is the combinations of abundant species which differentiate the north Pennine areas from other similar habitat types in Britain. Comparison with spider species from three alpine habitats in southern Norway (Hauge and Refseth 1979) shows that the Pennine summits have fewer species present, and only a few are common to both areas (32%). The Cairngorms are more similar to the alpine sites in south Norway (45%), but also have fewer species. The carabids of the summit areas show similar trends, with a much more impoverished species list and low similarity when compared to alpine and sub-alpine sites in north Norway (Thingstad 1987). The increased oceanicity, isolation and differing vegetation account for the differences of the British upland spider and carabid fauna compared to Arctic Europe (Coulson and Butterfield 1986).

As one of the major upland areas in Britain, the north Pennine plateaux is highly susceptible to recreational damage and disturbance, and little is known about the adverse effects on the invertebrate communities. Duffey (1975) showed that on sub-montane grasslands, invertebrates responded to levels of human trampling that had little effect on the plant communities. One of the major disturbances in the north Pennines is from extensive sheep grazing and its influence on the vegetation. Much of the summit areas are overgrazed, following the indications of Thompson *et al.* (1987), with a high proportion of grasses among the mosses. However, there are patches of *Eriophorum* and *Nardus* still persisting, and these areas contain the spider assemblage most dissimilar to those of surrounding lowland areas. It may be that the distinct spider communities of the summit vegetation types occur as a direct result of the type of human disturbance described above, or that the summits are outliers of the main montane areas in Scotland, with influences from the surrounding lowland areas.

5.5.5 Concluding remarks

This chapter has shown that the different habitats associated with the sub-montane plateaux acted as true isolates for many of the spider species found, while the carabid species appeared much more widespread. Although there is a wealth of information examining the variation in invertebrate species of isolated habitats, there have been few studies which investigate the influence of the heterogeneity of the local environment, and the interactions of the invertebrates across the boundaries between them. The next chapter introduces and examines this influence.

Table 5.13. Comparison of the spider fauna from three North Pennine summits during 1991, three Grampian summits during 1987-1989 and from 42 upland sites in northern England during 1976-1977 (Coulson & Butterfield 1986), based on presence/absence data from pitfall trap sampling.

	North Pennines			Grampians			North England Survey
	Cross Fell	Little Dun Fell	Great Dun Fell	Cairn Gorm	Drumo-chter	Glas Maol	
Haplodrassus signifer (C.L. Koch, 1839)				+			+
Clubiona trivialis C.L. Koch, 1841					+		+
Clubiona diversa O.P.-Cambridge, 1862	+						+
Agroeca proxima (O.P.-Cambridge, 1871)				+			+
Xysticus cristatus (Clerck, 1757)	+	+	+	+	+		+
Xysticus sabulosus (Hahn, 1832)	+			+			
Pardosa monticola (Clerck, 1757)	+	+	+		+		
Pardosa palustris (Linnaeus, 1758)				+	+	+	+
Pardosa pullata (Clerck, 1757)	+	+	+	+		+	+
Pardosa amentata (Clerk, 1757)					+		+
Alopecosa pulverulenta (Clerck, 1757)	+	+	+	+	+	+	+
Pirata piraticus (Clerck, 1757)	+						+
Tricca alpigena (Doleschall, 1852)				+			
Antistea elegans (Blackwall, 1841)	+						+
Robertus lividus (Blackwall, 1836)			+	+	+		+
Ceratinella brevipes (Westring, 1851)	+	+	+	+	+	+	+
Walckenaeria nudipalpis (Westring, 1851)	+	+	+		+		+
Walckenaeria antica (Wider, 1834)	+	+					+
Walckenaeria clavicornis (Emerton, 1882)	+	+	+	+	+	+	+
Walckenaeria cuspidata (Blackwall, 1833)	+	+	+	+	+		+
Walckenaeria capito (Westring, 1861)	+						
Walckenaeria acuminata Blackwall, 1833		+					+

cont.

	Cross Fell	Little Dun Fell	Great Dun Fell	Cairn Gorm	Drumo-chter	Glas Maol	North England
Dicymbium nigrum (Blackwall, 1834)						+	
Dicymbium n.f. *brevisetosum* Locket, 1962	+	+	+				+
Dicymbium tibiale (Blackwall, 1836)		+	+				+
Hypomma bituberculatum (Wider, 1834)	+			+	+	+	+
Gonatium rubens (Blackwall, 1833)			+				+
Pocadicnemis pumila (Blackwall, 1841)					+		+
Oedothorax gibbosus (Blackwall, 1841)				+		+	+
Oedothorax fuscus (Blackwall, 1834)	+	+	+			+	+
Oedothorax agrestis (Blackwall, 1853)		+					
Oedothorax retusus (Westring, 1851)	+	+	+	+	+	+	+
Pelecopsis mengei (Simon, 1884)	+	+	+				+
Pelecopsis parallela (Wider, 1834)				+			+
Silometopus elegans (O.P.-Cambridge, 1872)	+	+	+	+	+	+	+
Tiso vagans (Blackwall, 1834)	+	+	+				+
Tiso aestivus (L. Koch, 1872)				+	+		
Monocephalus fuscipes (Blackwall, 1836)	+					+	+
Monocephalus castaneipes (Simon, 1884)		+					+
Lophomma punctatum (Blackwall, 1841)			+				+
Gongylidiellum vivum (O.P.-Cambridge,1875)						+	+
Micrargus herbigradus (Blackwall, 1854)	+		+				+
Erigonella hiemalis (Blackwall, 1841)	+			+			+
Savignya frontata (Blackwall, 1833)	+	+	+	+	+	+	+
Diplocephalus permixtus (O.P.-Cambridge,1871)	+	+	+				+
Araeoncus crassiceps (Westring, 1861)	+	+	+				
Scotinotylus evansi (O.P.-Cambridge, 1894)				+	+		+
Typhochrestus digitatus (O.P.-Cambridge,1872)		+	+				+
Diplocentria bidentata (Emerton, 1882)				+			+

cont.

	Cross Fell	Little Dun Fell	Great Dun Fell	Cairn Gorm	Drumo-chter	Glas Maol	North England
Erigone dentipalpis (Wider, 1834)	+	+	+	+	+	+	+
Erigone promiscua (O.P.-Cambridge, 1872)	+	+	+		+	+	+
Erigone atra (Blackwall, 1841)	+	+	+	+	+	+	+
Erigone tirolensis L.Koch, 1872				+		+	
Erigone psychrophila Thorell, 1871				+			
Rhaebothorax morulus (O.P.-Cambridge,1873)	+	+		+	+	+	+
Rhaebothorax paetulus (O.P.-Cambridge,1875)						+	
Latithorax faustus (O.P.-Cambridge, 1900)					+		+
Semljicola caliginosa (Flaconer, 1910)	+	+	+				+
Leptorhoptrum robustum (Westring, 1851)			+				+
Drepanotylus uncatus (O.P.-Cambridge,1873)	+	+	+				+
Leptothrix hardyi (Blackwall, 1850)	+						+
Hilaira frigida (Thorell, 1872)	+	+	+	+	+	+	+
Hilaira nubigena Hull, 1911	+		+				+
Halorates holmgreni (Thorell, 1871)				+	+	+	
Jacksonella falconeri (Jackson, 1908)				+			
Porrhomma pallidum Jackson, 1913	+	+					+
Porrhomma campbelli F.O.P.-Cambridge,1894						+	+
Porrhomma montanum Jackson, 1913						+	+
Agyneta subtilis (O.P.-Cambridge, 1863)				+		+	+
Agyneta decora (O.P.-Cambridge, 1870)						+	+
Agyneta conigera (O.P.-Cambridge, 1863)	+			+			+
Agyneta ramosa Jackson, 1912				+		-	
Meioneta rurestris (C.L. Koch, 1836)					+		+
Meioneta gulosa (L. Koch, 1869)	+	+	+	+	+	+	+
Meioneta nigripes (Simon, 1884)				+	+	+	
Centromerus prudens (O.P.-Cambridge, 1873)	+	+	+	+	+		+

cont.

	Cross Fell	Little Dun Fell	Great Dun Fell	Cairn Gorm	Drumo-chter	Glas Maol	North England
Centromerus arcanus (O.P.-Cambridge, 1873)				+	+		+
Centromerita bicolor (Blackwall, 1833)	+	+	+	+	+	+	+
Centromerita concinna (Thorell, 1875)	+	+	+	+	+	+	+
Oreonetides vaginatus (Thorell, 1872)	+	+	+	+	+	+	+
Macrargus carpenteri (O.P.-Cambridge, 1894)				+	+		+
Bathyphantes gracilis (Blackwall, 1841)	+	+	+				+
Bolyphantes luteolus (Blackwall, 1833)					+		+
Lepthyphantes zimmermanni Bertkau, 1890				+	+	+	+
Lepthyphantes mengei Kulczynski, 1887	+	+		+	+	+	+
Lepthyphantes tenebricola (Wider, 1834)				+			
Lepthyphantes ericaeus (Blackwall, 1853)					+	+	+
Lepthyphantes angulatus (O.P.-Cambridge,1881)	+	+	+	+	+	+	+
Lepthyphantes antroniensis Schenkel, 1933					+	+	
Allomengea scopigera (Grube, 1859)			+				+

6.1 Introduction

Ecotones are generally considered to be transition zones, most common in the area of contact between two different community types. Odum (1971) described an ecotone as a transitional phase between two or more diverse ecological communities, which may have considerable linear extent, but which is narrower than the adjoining community areas themselves. More recently, di Castri and Hansen (1992) defined the ecotone as a "zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales, and by the strength of the interactions between adjacent ecological systems." They may be of varying width, primarily determined by the size of adjacent habitats and also by the degree of difference between the habitat types (Yahner 1988). In nature, spatial patterns may be abrupt or gradual, although it is sometimes preferable to refer to gradual changes as ecoclines (di Castri and Hansen 1992). However, the ecotones may be identified at any scale, from centimetres, such as the gradient between two distinct vegetation types, to kilometres, as in the differences between global climate zones. Within a terrestrial system, the change in animal species composition across the ecotone is rarely abrupt, and there is usually some interchange between the habitats resulting from dispersal behaviour. Sharp boundaries are best observed where two adjacent habitat types show strong differences (Terrel-Nield 1986, Bauer 1989).

Most studies on the influence of surrounding habitats succeed in describing little more than the relationship between perimeter and area (Malcolm 1994), concentrating on the diversity and species richness of habitat fragments to ascertain the influence (Webb and Hopkins 1984, Niemelä *et al.* 1988, Usher *et al.* 1993). Few studies have examined the extent of influence of these surrounding habitats at the interface, especially on the invertebrate populations. The simplest scenario is to imagine a strip of edge modified habitat parallel to the interface (Levenson 1981), and a slightly more realistic version assumes that the magnitude of the edge influence within the strip declines with increasing distance from the interface (Malcolm 1994). The distance of influence from the interface may also be variable between different groups of invertebrate, as well as between species.

Many years ago, Cameron (1917) studied the insects of the meadow, pasture and mixed deciduous forest, observing the differences in the fauna of these habitats and their border zones, and concluded that some species preferred the borders and that mixing of species from the habitats occurred at the boundary. Pollard (1968) studied the distribution of Carabidae along a transect crossing a woodland glade, and found that certain species were trapped more often at the glade edges. Heublein

(1983) found that there was a peak in both numbers of individuals and species of spider in pitfall traps close to the interface of a forest - meadow ecotone, and this was due primarily to the coexistence of both forest and meadow species than to the existence of species preferring the forest edge. Terrel-Nield (1986) used pitfall traps to determine invertebrate species diversity and to demonstrate the effect of the field-woodland interface, and found that separate communities could be found in both field and woodland, demonstrated by the sudden increases in diversity across the boundary. Bauer (1989) studied carabid and staphylinid communities of isolated limestone outcrops on blanket peat in the north Pennines. Marked variation in faunal composition between habitats was noted, and a transect across a limestone grassland-blanket peat interface indicated an intermingling of limestone and peat species at the boundary. The degree of interchange was found to be dependent on species-area relationships. Duelli *et al.* (1990) examined the edge permeability of several invertebrate groups between habitat patches of semi-natural and agricultural land, and almost all groups showed population exchanges over a 300m transect sampling several different habitat types and their associated borders. Surface-dwelling invertebrate species tended to show gradual transitions in abundance over the habitat boundaries. Rusek (1992) examined the distribution and dynamics of soil organisms across three different ecotones; a grassland-forest interface, a grassland with a moisture gradient and a microecotone inside a spruce forest, representing meso-, macro- and microecotones respectively. In most cases, the soil organisms increased in density, biomass and diversity in the transitional zones. Recently, Bedford and Usher (1994) examined the distribution of spiders and carabids across deciduous woodland - arable field ecotones, and found that at the edge both groups had an elevated species richness. This increase however was composed of a mixture of both woodland and field preferring species, invading from the distinct species assemblages found in either habitat. However, the edge effect found did not extend beyond approximately 5m from the interface.

The boundary between grassland and tree plantation is usually well defined through modern agricultural and forestry policies, providing both structural and species differences over a short distance. Often a fence or other artificial barrier enclosing grazing stock prevents the encroachment of one habitat into the other, making a sharp transition. However, a degree of interchange of organisms usually occurs, and the ecotonal flora and fauna contain many species (both generalists and specialists) typical of the two adjacent communities as well as species restricted to the ecotone itself. This often results in an increase in both number of species present, and the densities of some species, compared with the neighbouring communities; a characteristic termed the edge effect (Terrel-Nield, 1986). The pasture - plantation interface is a linear feature, which provides the simplest ecotone situation to study any invertebrate distribution influenced specifically by the edge, haphazard or variable edges provide complications in producing several directions of influence in close proximity to the edge.

The boundary between two types of upland grassland is a more subtle gradient compared to the grass to tree transition, based on the increased similarity between the two habitat types. Nevertheless, the potential for species to use the ecotone as a preferred habitat, as either a specialist (restricted to the ecotone) or a generalist (ability to utilise both habitats and ecotone) is possible. This upland ecotone study is dealt with in Chapter 7.

In this chapter, the numbers of surface-active invertebrates trapped along a transect across an ecotone with a pasture-plantation interface were studied using pitfall trapping methods. Spatial distributions of spider and carabid beetle species were analysed to investigate the influence of the interface and to assess the degree of variation between habitat types at the species level.

The initial sampling of the pasture-plantation interface will indicate the presence of any interactions between the two different habitats and any variation in community structure across the interface. The exclosure on Little Dun Fell (Chapter 7) will provide a comparison of the intensity of influence caused by a boundary between a predominately *Festuca - Deschampsia* grassland interface and that of the pasture-plantation interface, where the edge effect has already been investigated. The upland grassland ecotone allows investigation of levels of interaction between habitat types previously studied and where the interface gradient is less extreme than that of the pasture-plantation.

6.2 Sampling sites

The three pasture - plantation replicate sites were located at Bedburn, Hamsterley (site A, 230m altitude, National grid reference NZ 090320), Standalone Farm, Brandon (site B, 200m, NZ 195408) and Dicken House Farm, East Hedleyhope (site C, 250m, NZ 158397). All sites were in west Durham (Figure 2.1), and consisted of a grass field used for sheep grazing, adjacent to a coniferous plantation. The dominant tree species in each plantation was Lodge-pole Pine (*Pinus contorta* Douglas), with the occasional Sitka Spruce (*Picea sitchensis* (Bong.)) occurring at site B, and some Silver Birch (*Betula pendula* Roth) and Sycamore (*Acer pseudoplantanus* L.) at site C. All stands are approximately 35 to 40 years old.

The sites were selected where the boundary was maintained by a fence, which allowed free movement of surface-active invertebrates between the habitat types and gave a defined structural boundary which prevented sheep from entering and disturbing the woodland habitat. The fence also approximated the edge of the tree canopy. The interface between a pasture and coniferous plantation was selected as it produced the sharpest edge or boundary between the tussocks of grass and the minimal vegetation (litter layer composed of pine needles) beneath a dense woodland canopy. All three sites were similar to the "new to young" edges described in Ranney *et al.* (1981) where there is little or no under-storey development at the interface. Plate 3 shows a typical pasture - plantation interface area (site A; Bedburn, Hamsterley).

6.3 Methods

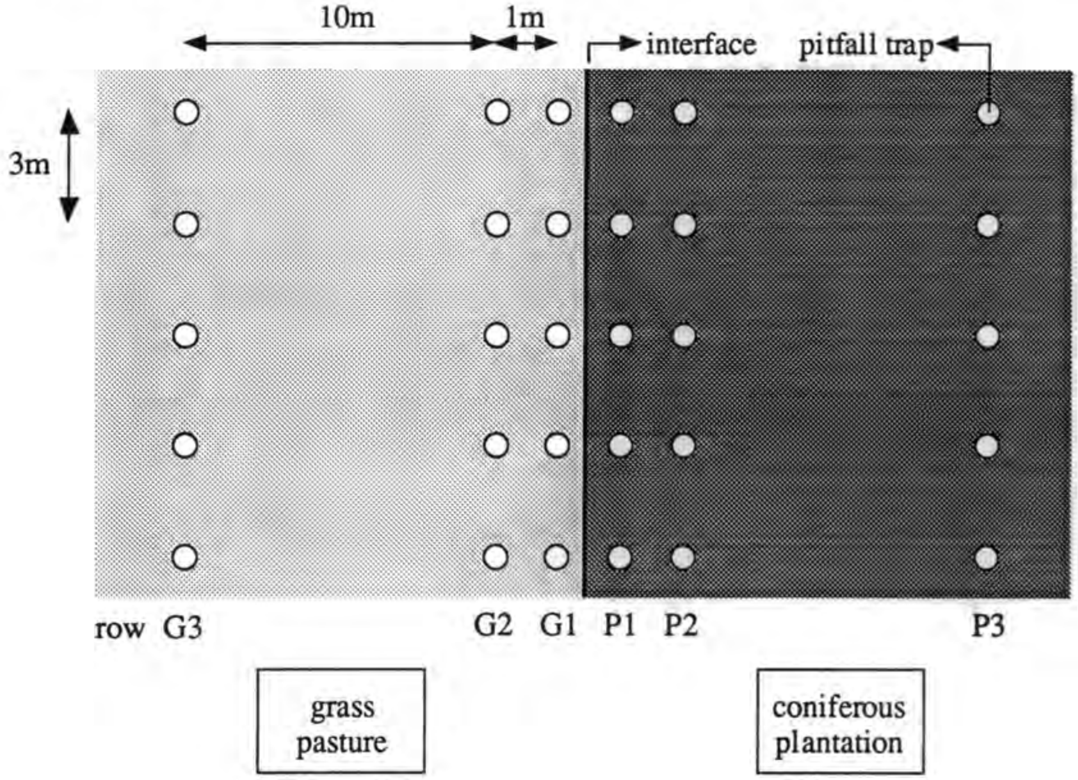
6.3.1 Pitfall traps across the habitat interface

At each habitat interface sampling area, 30 traps were operated, 15 in each habitat on either side of the interface. In order to sample both habitat and ecotone fauna and to ensure a sufficient number of replicates, the traps were arranged in six rows of five traps in a straight line, with 3m between the traps in each row, all rows positioned parallel to the interface. Row G3 was placed 11m from the interface into grass pasture habitat, row G2 placed 1m from the interface and row G1 placed just inside the grass pasture habitat at the boundary. Rows P1, P2 and P3 were placed in corresponding positions inside the plantation habitat, see Figure 6.1 for details. The traps were emptied every two weeks, from 6 April to 23 June, and from 14 August to 31 October 1992 at each site, which gave two sampling periods, consisting of approximately 80 days in each. The traps were not operated between these periods.

This sampling regime was also used to sample the invertebrates across an upland grassland interface at the sheep exclosure on Little Dun Fell. This upland grassland ecotone is dealt with in Chapter 7.

Plate 3. Pasture - plantation interface (site A: Hamsterley).

Figure 6.1. Plan of the grass pasture - coniferous plantation interface showing sampling grid arrangement.



6.3.2 Community parameters

For each site, the numbers of individuals, species richness and species diversity of the spider and carabid beetle communities were determined. Counts were log transformed for all statistical analyses to normalise the data. Species diversity was measured using the inverse of Simpson's Index (see section 4.1). One of the drawbacks with community indices (e.g. species diversity) is that similar values can be obtained with mutually exclusive sets of taxa. These values do not indicate how similar the taxonomic compositions of communities are along the transect. Similarity measurements between rows were calculated using a modified form of the Sørensen Index (see sections 4.2 and 5.3.3). The modified form incorporates a measure of abundance by using "pseudospecies" to represent common species (> 29 specimens) at each row position, using the criteria followed in Butterfield and Coulson (1983). Presence/absence similarity between rows using the Sørensen Index was also used for comparison.

6.3.3 Categorisation methods

Spider and carabid beetle species were categorised according to their habitat preferences, by testing for significant differences in abundance between row positions. The aim of this classification was to define species to specific areas of the ecotone. Several statistical models are available to test for significant differences between the row positions.

The χ^2 one-sample test can show whether a significant difference exists between an observed number of spiders or carabids at each row position, with an expected number based on the null hypothesis of an equal distribution between rows. However, it should be noted that when the degrees of freedom are greater than one, χ^2 tests are insensitive to the effects of order, (where differences occur) and thus when a hypothesis takes order into account, χ^2 may not be the most suitable test (Siegel, 1956).

The Student's t-test may be used to test between two sets of data. In order to compare each row position with the others, several individual t-tests must be performed, leading to the possibility of type I statistical errors. The best possible differentiation allowed by t-test methods would be the comparison of pasture and plantation traps. This denies the detail needed to show gradual changes of each species across the interface, and also does not allow classification of potential ecotone species.

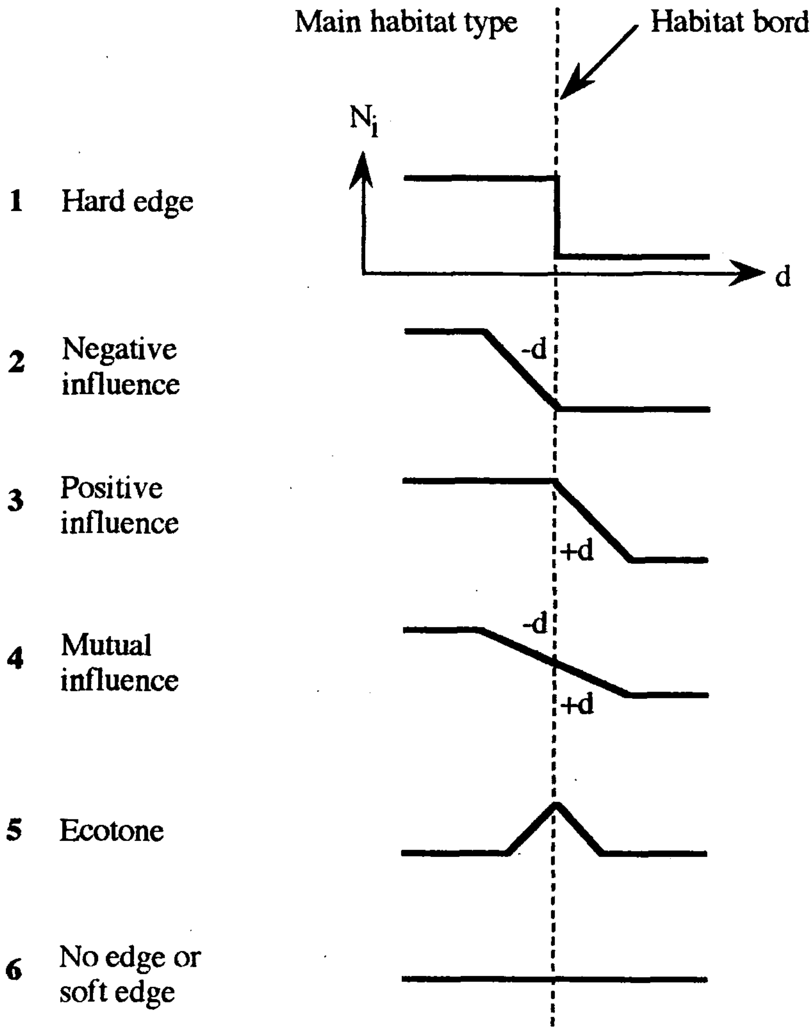
Analysis of variance, like the χ^2 test, gives a single probability of a significant difference occurring along the transect. However, the acceptance of a significant result does not imply that all the values are different from one another, and also we know neither how many differences there are, nor where differences are located amongst the rows. Again, it might be tempting to make a series of pair-wise comparisons of the populations using the t-test method above, but this approach produces statistical problems. The chance of rejecting a true hypothesis is, say, 5% on each test, and when several tests are made the chance of rejecting at least one true hypothesis becomes considerably larger than 5%. Multiple comparison methods used in conjunction with analysis of variance, overcome this problem (Zolman 1993). There are several different multiple comparison methods available, and as yet there is no agreement as to the 'best' procedure to use routinely (Snedecor and Cochran 1967 Zar 1974). One of the more commonly used is the Duncan's Multiple Range Test (Steel and Torrie 1960, Sokal and Rohlf 1981) which is more powerful than other popular tests such as the Student-Newman-Keuls test, the Tukey test and the Scheffe' test (Zolman 1993). Duncan's test was used as it will test differences among all possible pairs of rows regardless of the number of rows involved, and still maintain the prescribed level of significance, where the t-test will not. It is described as a variation of a t-test (Klockers and Sax, 1986).

Analysis of variance (ANOVA) was used to test for significant differences in abundance among the six rows, and differences among row means were tested using Duncan's multiple range test (at the $p < 0.05$ level of significance). Two levels of species abundance were used for categorising the species. Species with fewer than five individuals were not considered as they were of too low abundance, either rare or not susceptible to pitfall trapping. Species with an abundance of over 30 individuals at any one site were categorised using the ANOVA model, as this provided a potential of at least five individuals at each row position (the minimum number required to establish a significant difference using the χ^2 test). Although species with between 5 and 30 individuals were not included in the ANOVA model, any species which showed consistent distribution at all three sites (i.e. all specimens trapped at a similar area in the transect) were also categorised according to the habitat in which they were sampled.

Using these methods, the spider and carabid species were assigned to six categories of border transition based on Duelli *et al.* (1990), who used the degree of overlap between habitats. Figure 6.2 outlines these categories. Species defined as 'Hard edge' (category 1) showed no measurable evidence of population exchange between the pasture and plantation habitats. Category 2 species usually did not leave their preferred habitat and show a decrease in numbers towards the interface. The contrary is true for Category 3 species, which thrive in their preferred habitat and invade the adjacent areas. Some species show both these trends and form Category 4 species. Category 5 species have the highest abundance at the edge, and Category 6 show no significant variation across the whole transect.

The above classification method relies on the differences in the abundance of species taken across the transect. However, as mentioned in section 3.1, pitfall traps captures are a function of both the density of species and also the behaviour and activity during the sampling period, so they can only be used to compare abundances of species under certain conditions (Maelfait and de Keer 1990). Maelfait and Baert (1975) showed that pitfall trap captures of a species taken at different places but during the same period are a reflection of the relative abundances at these places, provided the habitats are not too different in vegetation structure. Using this principle it was possible to classify the species. If any given species showed variation in abundance between two row positions where the vegetation was the same (i.e. rows G3 and G2 or row P2 and P3), then it is expected that the influence of differences in vegetation structure on activity and trap efficiency are negligible.

Figure 6.2. The six categories used for grouping species of spider and carabid based on their distribution across the transect using pitfall trapping (following Duelli *et al.* 1990). The main habitat on the left may be pasture or plantation. N_i is the number of individuals; d is the distance of negative (-d) or positive (+d) faunal influence.



6.4 Results

6.4.1 Seasonal variation at the pasture - plantation sites

This section presents the seasonal variation in the numbers of individuals of spider and carabid collected using pitfall traps between April and October 1992 at three sites representing pasture-plantation interfaces near Durham City (Table 6.1). Individual species of both spider and carabid beetle are dealt with later.

The variation in numbers of spiders trapped between April and October 1992 is shown in Figure 6.3. All three sites showed at least three peaks in the patterns of abundance. Site A had a large maximum occurring in late May, and two smaller peaks, one during the break in sampling and the other in early October. Sites B and C showed the same three peaks, but their main maximums were estimated to occur between sampling periods, during early July. The carabids (Figure 6.4) illustrate a different abundance pattern to the spiders. The highest densities of carabids at site A occurred mid-season, and sites B and C had maximums in late September. Immediately after each peak, the numbers reduced rapidly to very low numbers of individuals. Although there is variation in numbers taken between sites for both spiders and carabids, similar trends in abundance were found at all three sites over the sampling period for both groups.

Table 6.1. Total numbers of spiders and carabid beetles trapped in 30 pitfall traps at each site during each sampling period between April and October 1992. Traps initiated 6 April 1992.

		Spiders			Carabids	
Pick-up date	Site A	Site B	Site C	Site A	Site B	Site C
22/4/92	706	241	448	210	381	531
7/5/92	1089	482	682	238	323	448
22/5/92	1264	463	675	382	375	557
9/6/92	857	301	420	465	322	583
23/6/92	628	682	1163	391	487	384
31/8/92	792	677	435	514	651	585
15/9/92	529	264	285	463	641	525
30/9/92	440	259	228	366	665	652
16/10/92	623	391	442	193	484	265
31/10/92	445	261	441	47	121	65

Figure 6.3. Seasonal variation in pitfall trap catches of spiders during 1992 from three pasture - plantation sites.

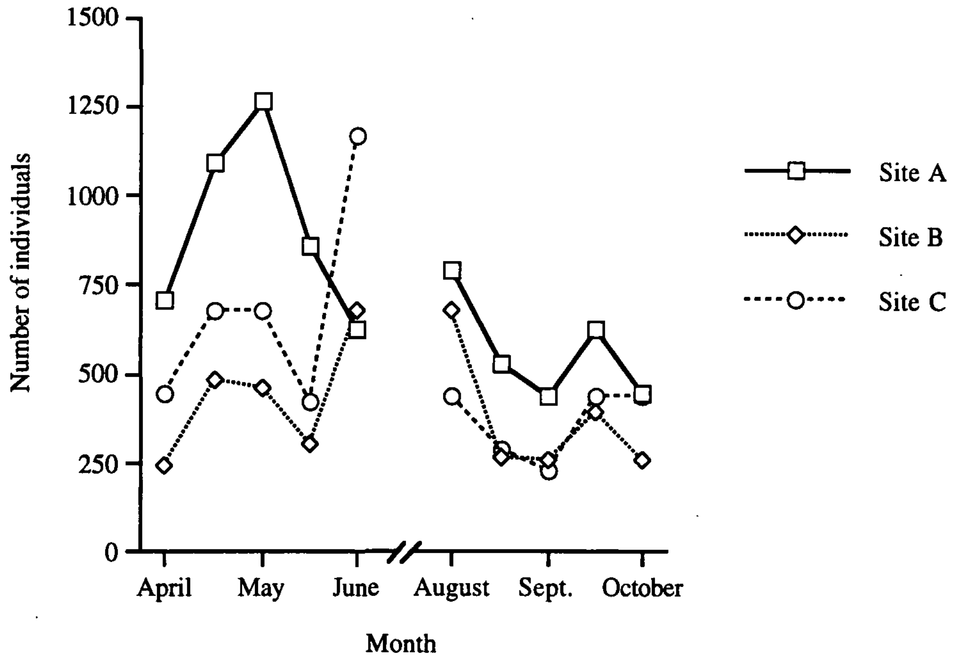
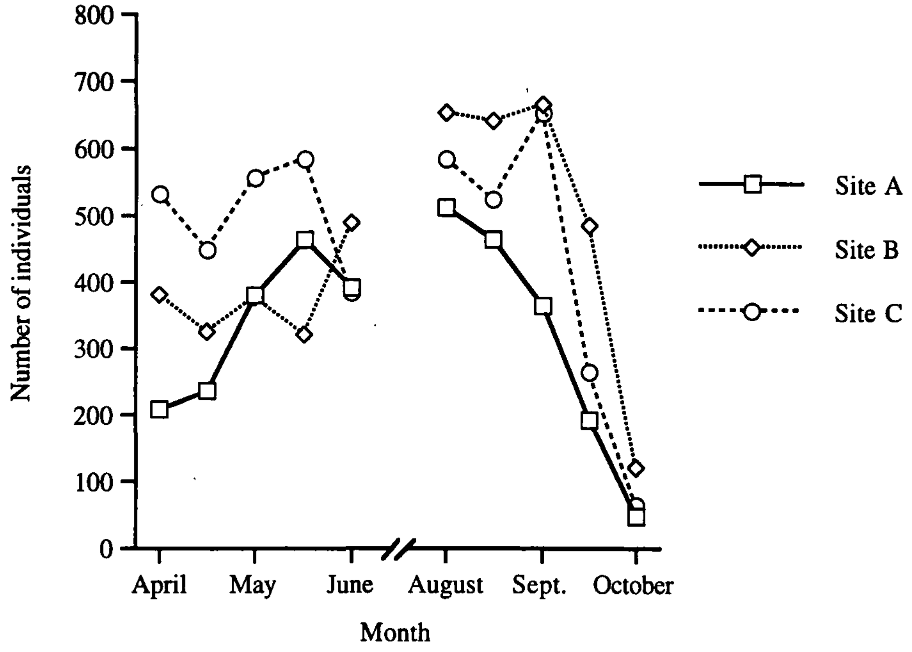


Figure 6.4. Seasonal variation in pitfall catches of carabids during 1992 from three pasture-plantation sites.



6.4.2 Abundance and diversity across the ecotone

A total of 14 143 individual adult spiders belonging to 127 species (representing 13 families) and 11 859 individuals of carabid beetle belonging to 46 species were taken in pitfall traps at all three sites during 1992. A total of 1844 immature specimens of spider were also taken which were not identified. The majority of the spider species belonged to the Linyphiidae (71%). Table 6.2 shows the distribution of the spider families and the numbers of species and individuals of each family, expressed as a percentage of the whole catch. The number of species in each family recorded is closely correlated with the number of individuals captured in that family from all sites combined ($r = 0.98$, $df = 11$, $p < 0.001$). However, only two of the major families trapped (> 1% of the total number of adults (N_T)), Lycosidae and Linyphiidae, are represented by more than five species. Of the other families, each is dominated by one or two species. Only one species of Amaurobiidae was trapped, *Amaurobius fenestralis*. *Drassodes cupreus* and *Haplodrassus signifer* were the most abundant Gnaphosidae, and *Coelotes atropos* and *Cryphoeca silvicola* contributed 99.8% of the Agelenidae caught, with only two individuals of *Textrix denticulata* trapped. Within the Tetragnathidae, *Pachygnatha degeeri* formed 98.5% of the total catch, only three other species were recorded.

Table 6.2. Number of mature individuals and species of each spider family trapped at all three sites during 1992. S_T and N_T represent the total number of species and individual adults caught respectively.

Family	S	% of S_T	N	% of N_T
Amaurobiidae	1	1	440	3.11
Segestriidae	1	1	2	.01
Gnaphosidae	5	4	288	2.03
Clubionidae	4	3	11	.08
Zoridae	1	1	2	.01
Thomisidae	2	2	63	.44
Salticidae	2	2	2	.01
Lycosidae	8	6	1672	11.81
Agelenidae	3	2	988	6.98
Mimetidae	1	1	16	.11
Theridiidae	4	3	97	.68
Tetragnathidae	4	3	1758	12.41
Linyphiidae	91	71	8823	62.30
	S_T 127		N_T 14162	

Three species of carabid beetle contributed over 10% of the total at all three sites; *Nebria brevicollis*, *Calathus fuscipes* and *Calathus melanocephalus*. Also abundant were *Pterostichus madidus* (13% of the catch at site A) and *Calathus micropterous* (12% of the catch at site C). The total numbers of individuals of each species of spider and carabid are given for each site in Appendices 2a - c (spiders) and 2d - f (carabids).

An initial analysis of the spider and carabid beetle distributions at each site displayed similar trends in both numbers of species and individuals trapped, and also in species composition at each of the sites. All three sites showed high similarity values using the Sørensen Index and presence/absence values (spiders: 77% - 85%, carabids: 78% - 88% similarity). All three sites were subsequently combined by row position giving a total of 15 replicate pitfall traps at each row across the transect.

The three rows on each side of the interface were grouped to examine the differences between the pasture and the plantation community types; this gave a total of 45 traps for each habitat type. The mean number of individuals (Table 6.3) of both spiders and carabids trapped in the pasture was more than double the numbers taken in the plantation (spiders: $t = 7.2$, carabids: $t = 10.0$; both cases: $df = 88$, $p < 0.001$), possibly caused by the variation in surface vegetation structure. The mean number of spider species trapped in the pasture was not significantly larger than the number of species trapped in the plantation ($t = 0.4$, $df = 88$, ns), though the mean number of carabid species taken in the pasture was significantly greater than in the plantation ($t = 7.6$, $df = 88$, $p < 0.001$).

Table 6.3. Mean number of individuals and species of spider and carabid per trap taken in 45 pitfall traps in adjacent pasture and plantation habitats for all three sites combined during 1992. Significance tested with Student's t-test using log transformed values; *** = $p < 0.001$, ns = not significant.

		Pasture mean	s.e.	Plantation mean	s.e.	Significance of difference
Spiders	Individuals	210	15	104	5	t = 7.2 ***
	Species	27	2	25	1	t = 0.4 ns
Carabids	Individuals	191	12	72	7	t = 10.0 ***
	Species	16	0.4	11	0.4	t = 7.6 ***

The source of variation across the transect becomes clearer when the catch totals are examined by row. Tables 6.4 and 6.5 show the mean numbers of individuals, numbers of species and the species diversity of spiders and carabids respectively along the transect from row G3 (pasture) to row P3 (plantation) from a total of 15 traps per row (Figure 6.5).

Significant differences in mean numbers of spider were found between rows using ANOVA ($F_{5,84} = 17.1$, $p < 0.001$). The largest number of individuals of spider were trapped at row G3 (248 ± 22) and decreased progressively to the smallest at row P3 (86 ± 6). Row G3 trapped significantly more individuals than rows G1, P1, P2 and P3; row G2 trapped significantly more than all plantation rows, and rows G1 and P1 trapped significantly more than rows P2 and P3 (Table 6.6).

There was also significant variation in numbers of individuals of carabid beetles ($F_{5,84} = 36.2$, $p < 0.001$) along the transect with the largest numbers taken from row G1 (242 ± 28) at the interface and the lowest at row P3 (51 ± 10) in the plantation. Row G1 trapped significantly more individuals than rows G3 and G2. All pasture rows trapped significantly greater numbers than were taken from the plantation rows, and significantly more carabids were taken at row P1 than were taken at rows P2 and P3 (Table 6.6). The peak at row G1 was primarily caused by the increase in numbers of *Nebria brevicollis* and *Calathus fuscipes* at site B (Appendix 2e).

Table 6.4. Mean number of individuals, species and species diversity of spiders per trap taken from 15 traps at each row position from all three sites combined during 1992. Diversity presented as reciprocal of Simpson's D. Significant differences in means across rows tested with one-way analysis of variance (ANOVA) using log transformed values; *** = $p < 0.001$.

Row	Mean number of individuals	s.e.	Mean number of species	s.e.	Mean species diversity (1/D)	s.e.
G3	248	22	19	1.3	3.4	0.2
G2	218	34	26	1.6	5.1	0.3
G1	165	18	36	3.0	11.6	1.0
P1	135	9	32	1.6	9.4	0.8
P2	90	6	24	1.5	7.2	0.6
P3	86	6	20	1.3	5.3	0.3
ANOVA	F = 17.1 ***		F = 12.3 ***		F = 30.7 ***	

Figure 6.5. Mean number of individuals of spider and carabid per trap at each row position. Means derived from five pitfall traps at each site combined during 1992 (± s.e., n = 15). Only positive errors are shown for both spiders and carabids. Position of the interface indicated.

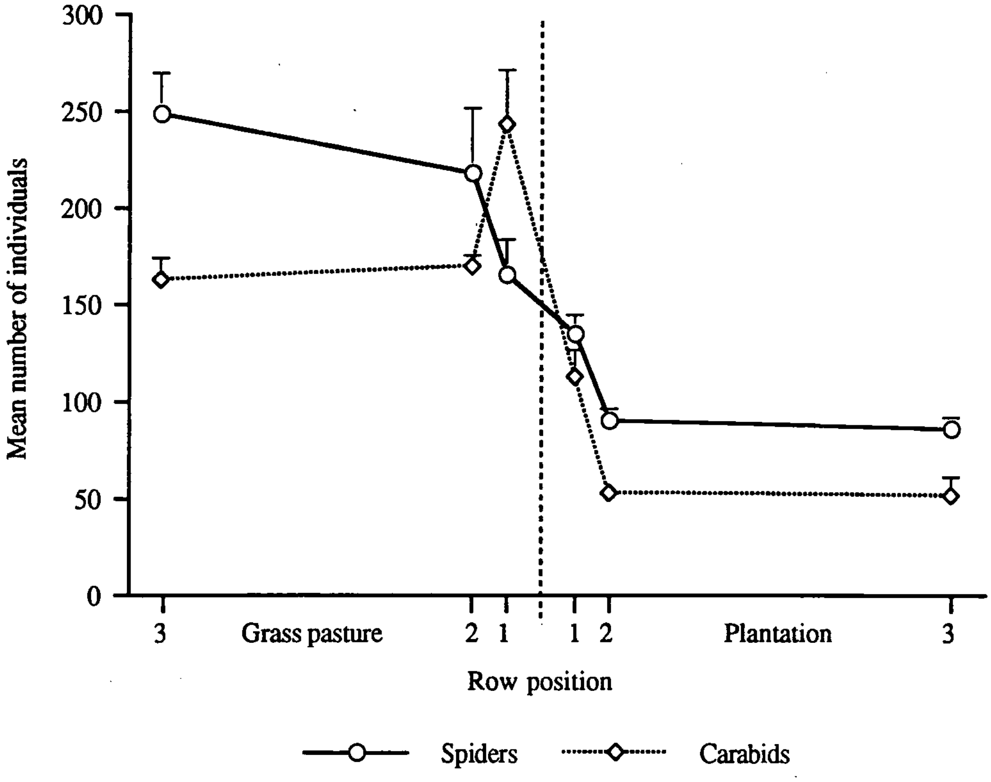


Table 6.5. Mean number of individuals, species and species diversity of carabids per trap taken from 15 traps at each row position from all three sites combined during 1992. Diversity presented as reciprocal of Simpson's D. Significant differences in means across rows tested with ANOVA using log transformed values; ** = $p < 0.01$, *** = $p < 0.001$.

Row	Mean number of individuals	s.e.	Mean number of species	s.e.	Mean species diversity (1/D)	s.e.
G3	162	12	15	0.8	4.0	0.3
G2	169	6	17	0.5	5.3	0.4
G1	243	28	16	0.8	4.5	0.4
P1	113	14	14	0.9	4.8	0.3
P2	53	5	11	0.6	6.0	0.4
P3	51	10	9	0.3	5.0	0.4
ANOVA	F = 36.2 ***		F = 19.4 ***		F = 3.6 **	

Although the number of individuals of spider was larger in the pasture compared to the plantation, a function of difference in habitat type, the number of species of spider was highest at the interface, a function of the interface itself (Figure 6.6). Highest species richness (36 ± 3) was found at row G1, and the lowest (19 ± 1) at row G3 ($F_{5,84} = 12.3$, $p < 0.001$). Rows G1 and P1 had a significantly greater mean number of spider species than all other rows; row G2 had significantly more species than rows G3 and P3, and row P2 was greater than row G3 (Table 6.6).

Unlike the spiders, the mean number of species of carabid beetle was significantly greater in the pasture ($F_{5,84} = 19.4$, $p < 0.001$), than in the plantation and there was no major increase in species richness at the interface, indicating the interface had less influence on the carabids than the spider distribution (Figure 6.6). There were no significant differences between any of the pasture rows in terms of numbers of species, though the numbers reduced progressively from the interface into the plantation. Rows G2 and G1 were significantly greater than all the plantation rows and row G3 was significantly greater than rows P2 and P3. Row P2 was also significantly greater than row P3 (Table 6.6).

Figure 6.6. Mean species richness of spiders and carabids per trap at each row position. Means derived from five pitfall traps at each site combined during 1992 (± s.e., n = 15). Position of the interface indicated.

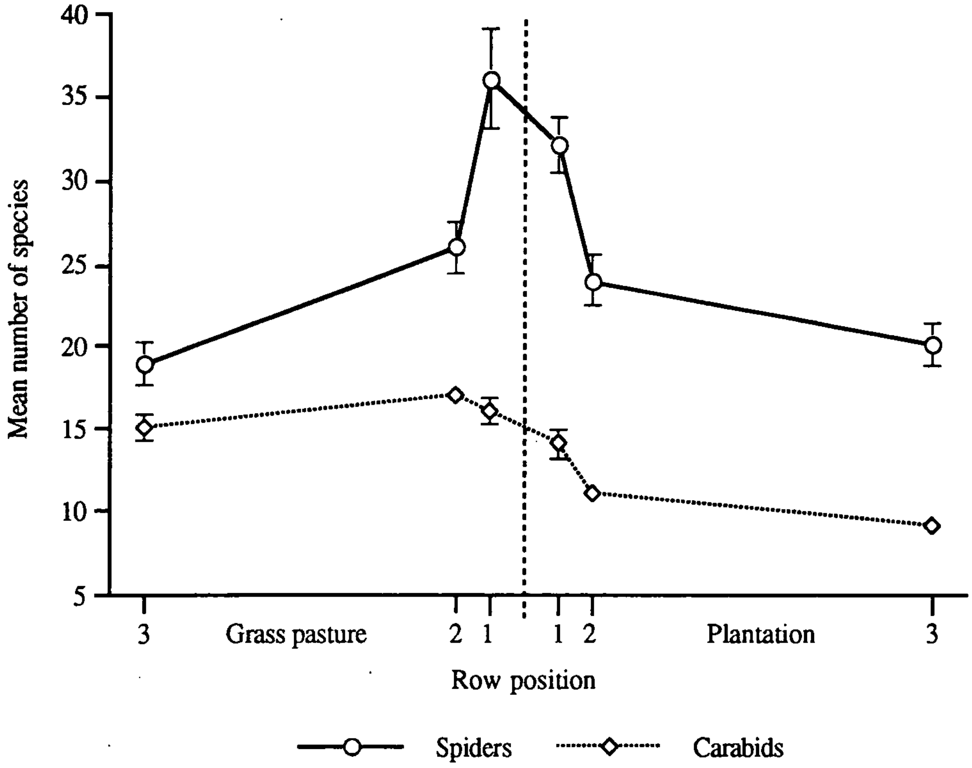
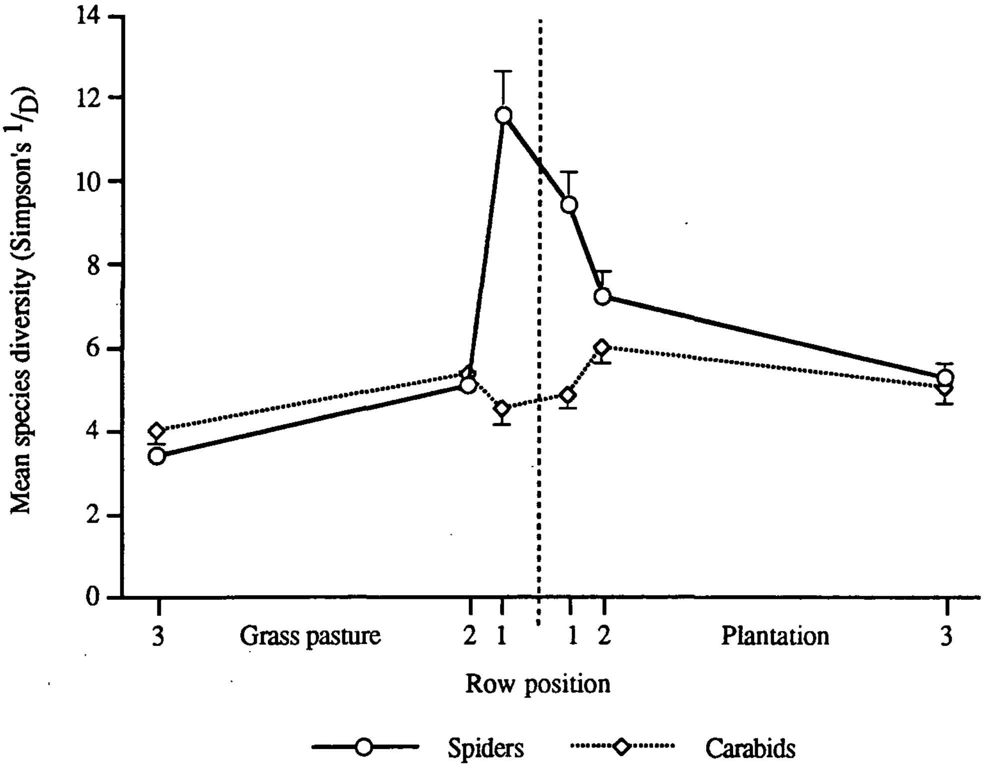


Figure 6.7. Mean species diversity of spiders and carabids per trap at each row position. Means derived from five pitfall traps at each site combined during 1992 (± s.e., n = 15). Positive errors shown for spiders; negative errors for carabids. Position of the interface indicated.



The mean spider species diversity (Table 6.4) follows a similar pattern to the species richness at each row position (Figure 6.7). The highest diversity was found at the two interface rows, G1 (11.6 ± 1.0) and P1 (9.4 ± 0.8), and decreased away from the interface ($F_{5,84}$ = 30.7, $p < 0.001$). The diversity at rows G3 (3.4 ± 0.2) and P3 (5.3 ± 0.3) was less than half of the diversity at the interface. Rows G1 and P1 had significantly higher diversity than all other rows; row P2 was significantly more diverse than rows G3 and G2, and rows G2 and P3 were significantly more diverse than row G3 (Table 6.6). Catches that were characterised by low diversity tended to be dominated by one or a few species. For example, at row G3, *Pachygnatha degeeri*, *Oedothorax fuscus* and *Erigone dentipalpis* contributed 78% of all spiders sampled, from a total catch of 57 species. In contrast, row G1 had the highest diversity and the three most abundant spiders, *Pardosa pullata*, *Coelotes atropos* and *P. degeeri* only contributed 25% of the total number of individuals, from a total of 100 species. The results show that spiders have a significantly more diverse community composition at the interface between the two habitats, which poses the question of what is the cause of this increase in species and diversity. There are two possible explanations;

a. The increase in diversity and species richness of spiders is caused by a large proportion of species specific to the interface, which do not occur away from the interface, or

b. The increase in diversity and richness is caused by the overlap of species from each habitat type, with few species specific to the interface.

The solution is found by analysing the distribution of each species of spider, defining potential habitat preferences and the degree of spread across the pitfall transect at each site.

The mean species diversity of the carabid beetles along the transect showed different results from the carabid species richness (Figures 6.6 and 6.7), unlike the spiders, with a decrease at the interface compared to the two outer interface rows (G2 and P2). Significant variation along the transect did occur ($F_{5,84} = 3.6$, $p < 0.01$), the lowest diversity occurring at row G3 (4.0 ± 0.3), and the highest at row P2 (6.0 ± 0.4). Carabid diversity was generally lower than the spiders, a result of lower numbers of species contributing to the index measurement. Row P2 was significantly more diverse than rows G3 and G1, and row G2 was significantly more diverse than row G3 (Table 6.6)

The patterns of abundance, richness and diversity discussed above are all based on the cumulative catch from the entire sampling period. These values give no insight into the temporal fluctuations in abundance of specific species, and indeed, not all species occur during the same season. There could, hypothetically, be a faster turnover of some species in certain parts of the transect compared to species in other parts, with the possibility of a higher measurement of richness in the pooled final results, but no real variation in the measurements during any two week trapping period. However similar results for all three measurements were found when the two-week sampling periods were analysed individually, indicating similar trends to those obtained for the whole season, for both spiders and carabids.

Figure 6.8 shows dendrograms constructed using Cluster Analysis with the average linkage method based on the similarity (Sørensen's Index) of the mean spider composition of each row. Two analyses were performed using; a) presence/absence values, and b) pseudospecies values. The cluster using presence/absence values shows that all rows were grouped above a 60% similarity level. The cluster using pseudospecies abundance shows less similarity between rows. Two groups were formed below 50% similarity, separating rows G2 and G3 from the others. The other rows were further split at the 52% similarity level into ecotone (rows G1 and P1) and plantation rows (P2 and P3). The mean percentage similarity between all rows was 72% (± 2 s.e.) using presence/absence, and 44% (± 6) when pseudospecies abundance was used.

The results suggest that the spider species content was generally similar over the transect across the interface, but that the community structure, i.e. numbers of individuals of the more abundant species varied across the transect, indicating that some species have preferences for a particular habitat and overlapped into the adjacent habitat. The separation using pseudospecies of rows G1 and P1 at the 52% similarity level from the other rows suggests that specialist ecotone spider species are also present.

Figure 6.8. Rows clustered according to the similarity of their spider fauna. Data based on catches from five pitfall traps at each site combined during 1991. Clustering strategies: a) presence/absence values; b) pseudospecies abundance.

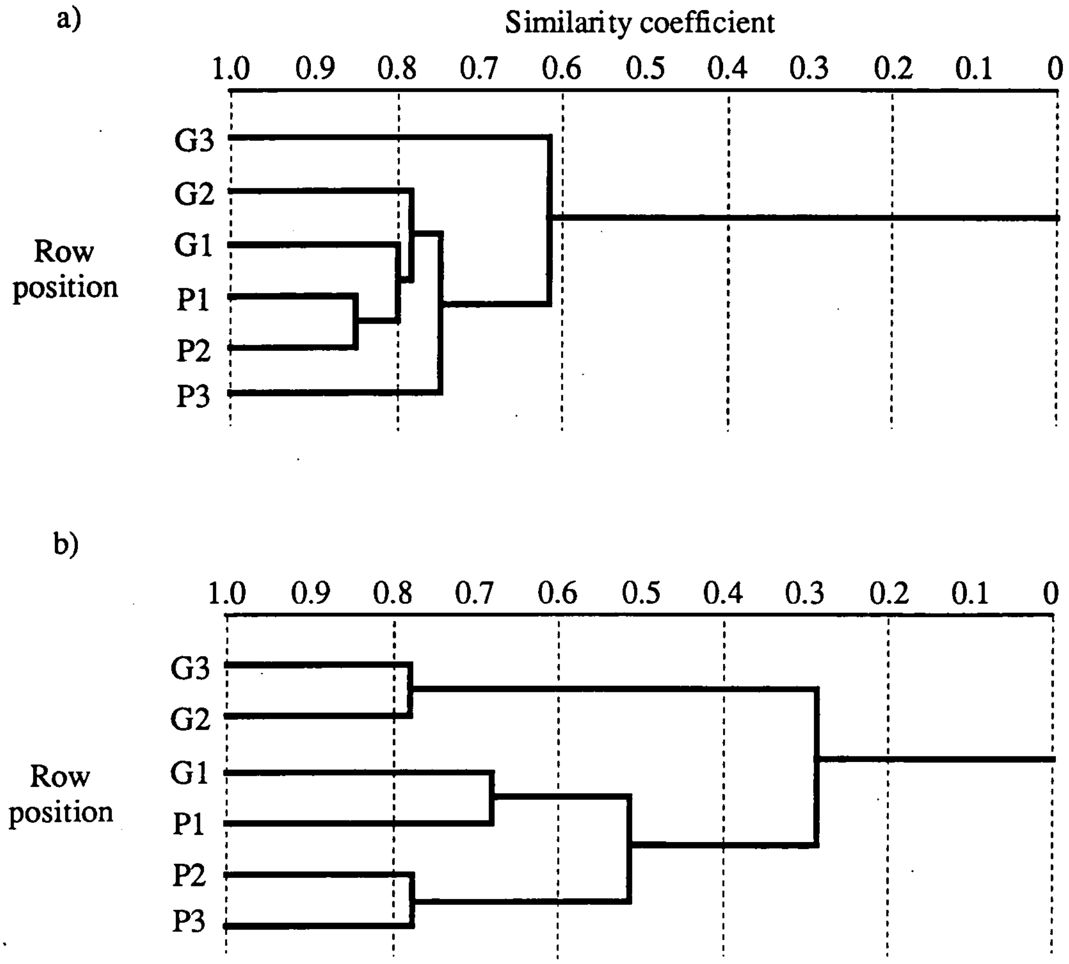
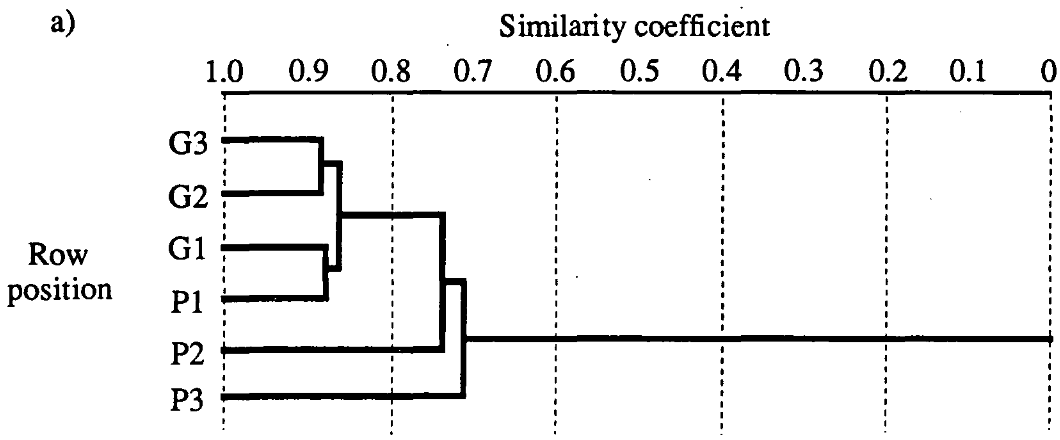


Figure 6.9 shows the same cluster procedure and criteria applied to the carabid beetles. The carabid assemblages across the transect show much greater similarity than was found between the spider assemblages. Using presence/absence values (Figure 6.9a), all row positions were grouped above the 71% similarity level, suggesting little variation between rows in terms of species composition. The modified form decreased the similarity between rows (Figure 6.9b), though the percentage similarity was still high (all rows grouped at 57%), suggesting that there was also little variation between the carabid assemblages in terms of the structure and abundance of the species. The mean percentage similarity between all rows was 78% (± 2) using presence/absence, and 66% (± 4) when pseudospecies abundance was used. The divisions indicated in Figure 6.9 (a and b) suggest that there is closer similarity in species within the pasture sites than in the plantation, and that more species of low abundance unique to the plantation were found in rows P1, P2 and P3.

Figure 6.9. Rows clustered according to the similarity of their carabid fauna. Data based on catches from five pitfall traps at each site combined during 1992. Clustering strategies: a) presence/absence values; b) pseudospecies abundance.



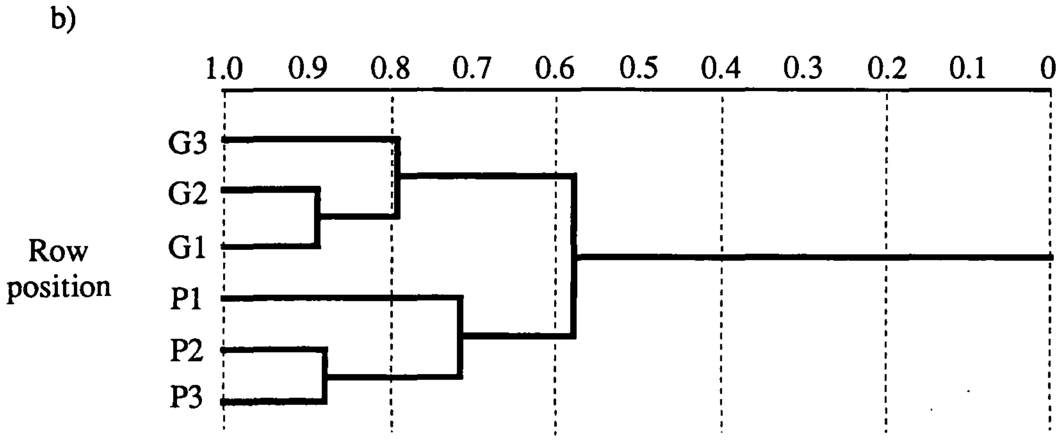


Table 6.6. Duncan's multiple range test for the multiple comparison of row means for significant differences in the number of individuals, species and species diversity of spiders and carabids. Means derived from five pitfall traps at each site combined during 1992. * = $p < 0.05$, ** = $p < 0.01$.

Number of individuals

Row	G3	G2	G1	P1	P2	P3	
G3	▨		*	**	**	**	
G2		▨	*	**	**	**	
G1	**		▨	**	**	**	Carabids
P1	**	*		▨	**	**	
P2	**	**	**	**	▨		
P3	**	**	**	**		▨	
			Spiders				

Number of species

Row	G3	G2	G1	P1	P2	P3	
G3	▨				**	**	
G2	**	▨		**	**	**	
G1	**	**	▨	**	**	**	Carabids
P1	**	*		▨	*	**	
P2	*		**	**	▨	*	
P3		*	**	**		▨	
			Spiders				

Species diversity

Row	G3	G2	G1	P1	P2	P3	
G3	▨	*			**		
G2	**	▨					
G1	**	**	▨		*		Carabids
P1	**	**		▨			
P2	**	*	**	*	▨		
P3	**		**	**	*	▨	
			Spiders				

6.4.3 Categorisation of the spider and carabid species

The spider and carabid species were categorised as preferring pasture, ecotone or plantation habitats by their mean abundance at each row position based on the Duelli *et al.* (1990) classification (Figure 6.2). The inclusion of all six row positions allowed a greater possible degree of categorisation, with gradual changes and overlaps into adjacent habitats becoming more noticeable. ANOVA and Duncan's multiple range test showed significant differences in means between rows for each species. Totals of 50 species of spider and 23 carabid species were categorised, which accounted for over 94% and 98% of all individuals of spider and carabid trapped respectively. The remaining species were not numerous enough to be categorised.

The distribution of *Oedothorax fuscus*, a linyphiid spider with a clear preference for the pasture, is taken as an example of the procedure used in the categorisation of each species. Significant differences in numbers of individuals of *O. fuscus* between rows were obtained ($F_{5,84} = 154.9$, $p < 0.001$). Duncan's test indicated significant differences between row position means. Figure 6.10 shows clearly that *O. fuscus* has a preference for the pasture (86% of the total number trapped at row G3), and it also shows a negative interface influence in the row positions approaching the interface (13% and 3% of the total catch at rows G2 and G1 respectively). Only 0.2% of the total catch of *O. fuscus* was taken in the plantation rows. *Oedothorax fuscus* was significantly more abundant at row G3 than row G2 (Table 6.7), which also had a significantly higher abundance than row G1. Row G1 had a significantly higher abundance than any plantation row. No individuals were taken at row P3. Thus *O. fuscus* was classed as a category 2 pasture species.

Table 6.7. Duncan's multiple range test for the multiple comparison of row means for significant differences in the number of individuals of *Oedothorax fuscus*. Means derived from five pitfall traps at each site combined during 1992. * = $p < 0.05$, ** = $p < 0.01$.

Row	G3	G2	G1	P1	P2
G3					
G2	**				
G1	**	**			
P1	**	**	**		
P2	**	**	**		
P3	**	**	**		

Figure 6.10. Distribution of *Oedothorax fuscus* per trap along the transect. Means derived from five pitfall traps at each site combined during 1992 (± s.e., n = 15). Position of the interface indicated.

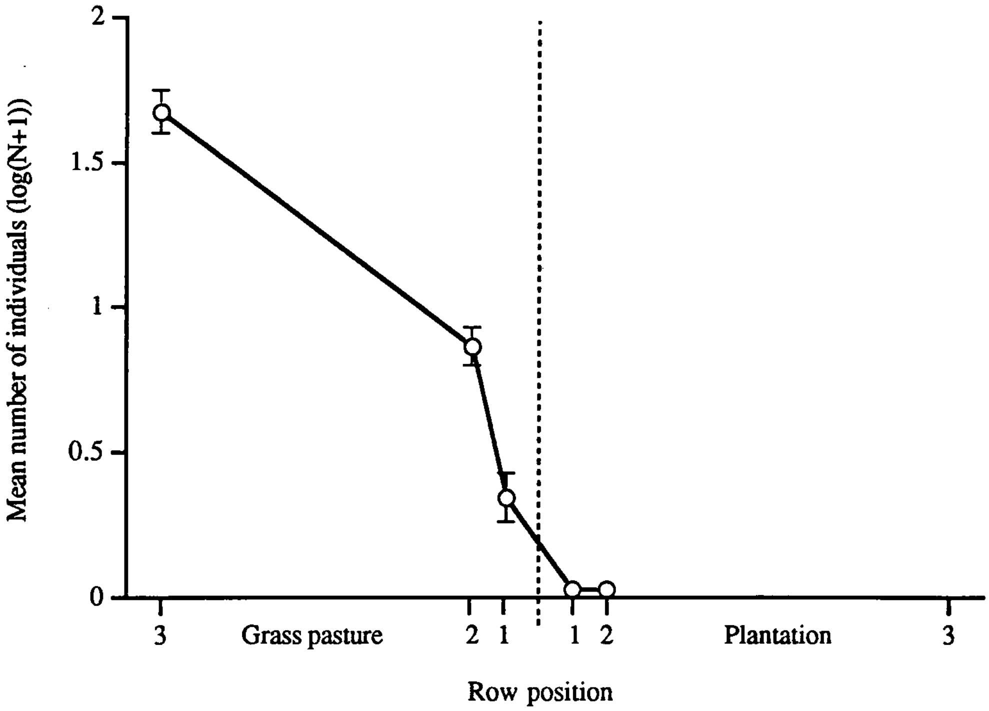


Table 6.8 shows the classification applied to the 50 species of spider which could be categorised indicating their preference for pasture, ecotone, woodland or widespread. The majority of species categorised as either pasture or plantation were species which overlapped across the interface (categories 3 and 4). These overlapping species (58% of the pasture species and 75% of the plantation species), along with the species classed as ecotone (category 5), contribute to the increase in species richness at the interface. Only 13 of the 50 classified species were categorised as having an ecotone preference, and only two species were classed as widespread.

Table 6.9 shows the 23 carabid species which were categorised and their preferences. The majority of species were classed as pasture species (70% of the species), and most of those species were category 3 or 4 (69% of the pasture species) which overlapped across the interface. Four species were considered as having a preference for the ecotone row positions, and only three species were classed as preferring the plantation (all category 3 species). No species were considered as being widespread.

Table 6.8. Categorisation of spider species based on Duelli *et al.* (1990). Category 1 species are hard edge; category 2 species show negative influence towards non-preferred habitat; category 3 species show positive influence; category 4 species show mutual influence; category 5 species show an ecotone preference and category 6 species are widespread.

	Preferred habitat			
Species	Pasture	Ecotone	Plantation	Widespread
Amaurobius fenestralis		5		
Drassodes cupreus		5		
Haplodrassus signifer		5		
Micaria pulicaria		5		
Agroeca proxima		5		
Xysticus cristatus	4			
Pardosa palustris	2			
Pardosa pullata	4			
Pardosa amentata	3			
Pardosa nigriceps	2			
Alopecosa pulverulenta	4			
Trochosa terricola	4			
Coleotes atropos			4	
Cryphoeca silvicola			3	
Robertus lividus			3	
Pachygnatha degeeri	3			
Ceratinella brevipes		5		
Walckenaeria cucullata			1	
Walckenaeria acuminata				6
Dicymbium n. f. *brevisetosum*	3			
Gonatium rubens		5		
Oedothorax fuscus	2			
Oedothorax retusus	2			
Cnephalocotes obscurus		5		
Tiso vagans	3			
Tapinocyba pallens			4	
Monocephalus fuscipes			3	
Savignya frontata	3			
Milleriana inerrans	2			
Erigone dentipalpis	2			
Erigone atra	2			
Agyneta conigera		5		
Meioneta rurestris	3			
Centromerus prudens		5		
Centromerita bicolor	1			
Sintula cornigera		5		
Saaristoa abnormis			3	
Bathyphantes gracilis	3			
Diplostyla concolor		5		
Drapetisca socialis			2	

cont.

		Preferred habitat		
Species	Pasture	Ecotone	Plantation	Widespread
Tapinopa longidens			3	
Labulla thoracica			3	
Bolyphantes alticeps		5		
Lepthyphantes minutus			3	
Lepthyphantes alacris			2	
Lepthyphantes tenuis				6
Lepthyphantes zimmermanni			4	
Lepthyphantes ericaeus			3	
Lepthyphantes pallidus			4	
Helophora insignis			2	
Totals	19	13	16	2

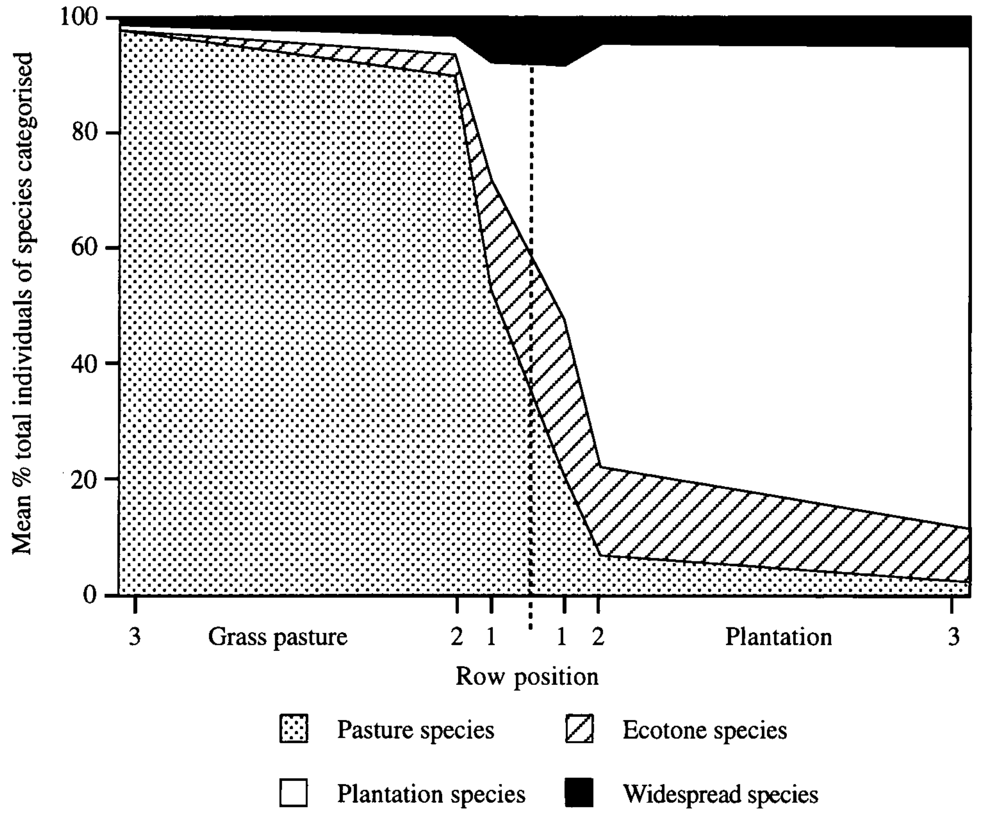
Table 6.9. Categorisation of carabid species based on Duelli *et al.* (1990). Categories as for Table 6.8. Note absence of widespread species.

		Preferred habitat	
Species	Pasture	Ecotone	Plantation
Carabus problematicus			3
Leistus ferrugineus		5	
Nebria brevicollis	3		
Notiophilus biguttatus		5	
Loricera pilicornis	3		
Clivina fossor	3		
Trechus quadristriatus	3		
Bembidion lampros	3		
Bembidion aeneum	2		
Bembidion guttula	2		
Pterostichus diligens		5	
Pterostichus madidus	3		
Pterostichus melanarius	3		
Pterostichus strenuus	3		
Calathus fuscipes	3		
Calathus melanocephalus		5	
Calathus micropterous			3
Calathus piceus			3
Agonum muelleri	2		
Amara aenea	4		
Amara communis	1		
Amara familiaris	4		
Amara lunicollis	2		
Totals	16	4	3

Almost all the species categorised using their abundance across the ecotone were done so with confidence knowing the drawbacks of the pitfall trap method. Only species which were category 1 or 6 might be susceptible to error in the analysis due to trapping efficiency. These species (4 spider and 1 carabid species) showed either a complete absence in their non-preferred habitat (cat. 1) or were trapped in equal numbers at all row positions (cat. 6). Where there is well defined variation in the vegetation structure of the two habitats with such clear cut values of abundance, it is expected that the pitfalls would under-estimate the catch in one of the habitats compared to the other. Category 1 species might still be present in the both habitats, but they could prove to be exceptional at avoiding the traps. Likewise, the distribution of the category 6 species could be biased to one habitat, but could be more efficiently caught in one, prejudicing the results. However, with this in mind, if they did have a preference for one habitat in real life, then it would be expected that there would be a gradual decrease in abundance away from that habitat.

The proportionate abundances of the categorised spider species combined from all three sites are shown in Figure 6.11. The proportion of individuals characteristic of each main habitat decreased towards the interface while the number of species and individuals from the other habitat increased. The mean proportion of individuals of pasture species declined from 97% at row G3 to only 2% at row P3. Conversely, the mean proportion of plantation species decreased from 83% at row P3 to less than 1% at row G3. These results suggest that there is a definite invasion or overlap of species of spider into the adjacent habitat across the interface. However the proportions of individuals of each species in the other habitat type across the interface was exceptionally low, suggesting that very few spiders from each species penetrate the interface. The mean proportion of widespread species was low, always less than 9% of the total categorised, and there was little variation and no significant difference in the numbers of individuals between the pasture and the plantation ($t = 0.59$, $df = 14$, ns), although their abundance did peak at the interface. The mean proportion of ecotone species was also low, never comprising the majority of the species at any row including the interface. The mean maxima of individuals of ecotone species (Figure 6.13) occurred at row P1 (27% of individuals categorised) where plantation species were in the majority (44%) and row G1 (19%) where pasture species were the majority (53%). These results suggest that the increase in spider species richness at the boundary is caused by both the presence of species with a preference for the interface, and also by the overlap of pasture or plantation preference species. However, the community patterns across the interface indicate that pasture or plantation species contribute little to the community content in the adjacent habitats (< 30% in both). The species with an ecotone preference contribute little to the spider community structure at the interface as, even at their peak, they contribute fewer individuals than the combined pasture and plantation specimens.

Figure 6.11. Mean percentage spider composition (number of individuals) per trap along the transect for categorised species. Means derived from five pitfall traps at each site combined during 1992 (n = 15). Position of the interface indicated.



The distribution of carabid species showed similar trends to those of the spiders although there were differences in the proportions of individuals along the transect (Figure 6.12). Both pasture and plantation species showed a decrease towards the interface while the number of species and individuals from the other habitat increased. However, the proportions of pasture individuals which crossed the interface into the plantation followed different patterns to those of the spiders. The mean proportion of individuals of pasture species was 90% at row G3 and declined to 33% at row P3 in the plantation (as opposed to 97% to 2% for spiders). The mean proportion of plantation species decreased from 51% at row P3 to less than 1% at row G3. These results suggest that an overlap of species of carabid into the adjacent habitat does occur, and that the degree of overlap is much larger than present in the spiders. The overlap of plantation species into the pasture is similar to the overlap found in plantation spiders, though this was presumably due to the reduced number of species which occur in the plantation (Table 6.5). The fact that pasture species still account for 33% of the individuals 11m into the plantation, and the low numbers of category 2 species (25% of the pasture species), suggests that the interface is having a lesser influence on the carabid species than was found in the spiders, possibly a result of their greater mobility. The mean proportion of ecotone species was always lower than the pasture component at any row position, never comprising the majority of the individuals at any row including the interface. The mean maxima of individuals of carabid ecotone species (Figure 6.13) occurred at row P1 (33%), similar to the spiders, but the pasture species were still in a majority (51%).

Figure 6.12. Mean percentage carabid composition (number of individuals) per trap along the transect for categorised species. Means derived from five pitfall traps at each site combined during 1992 (n = 15). Position of the interface indicated.

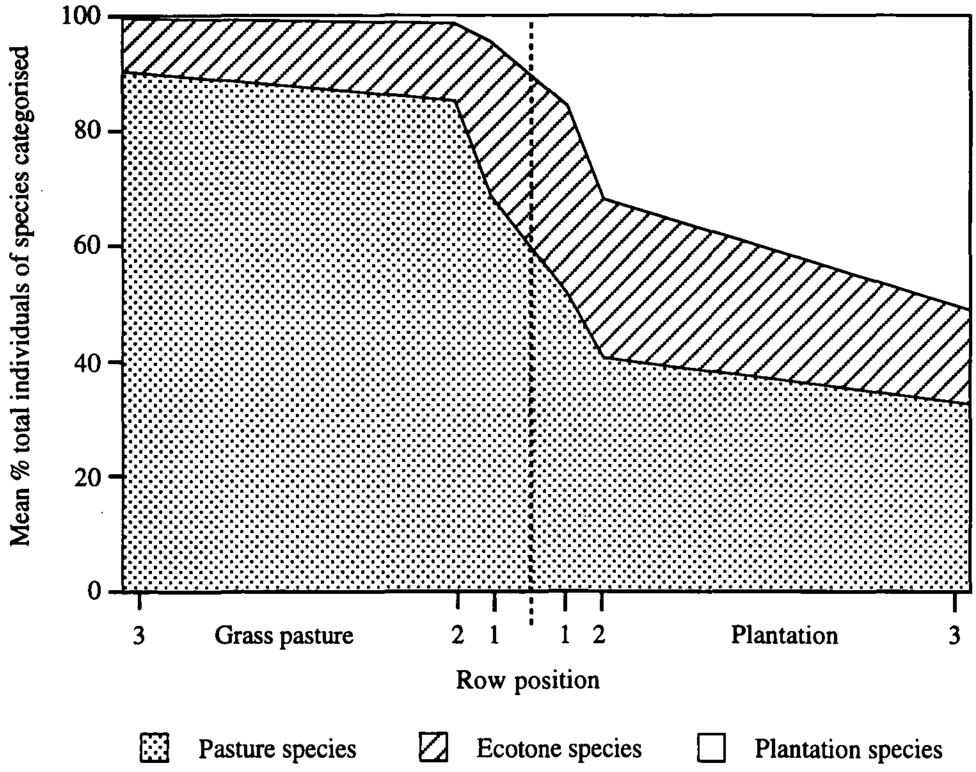
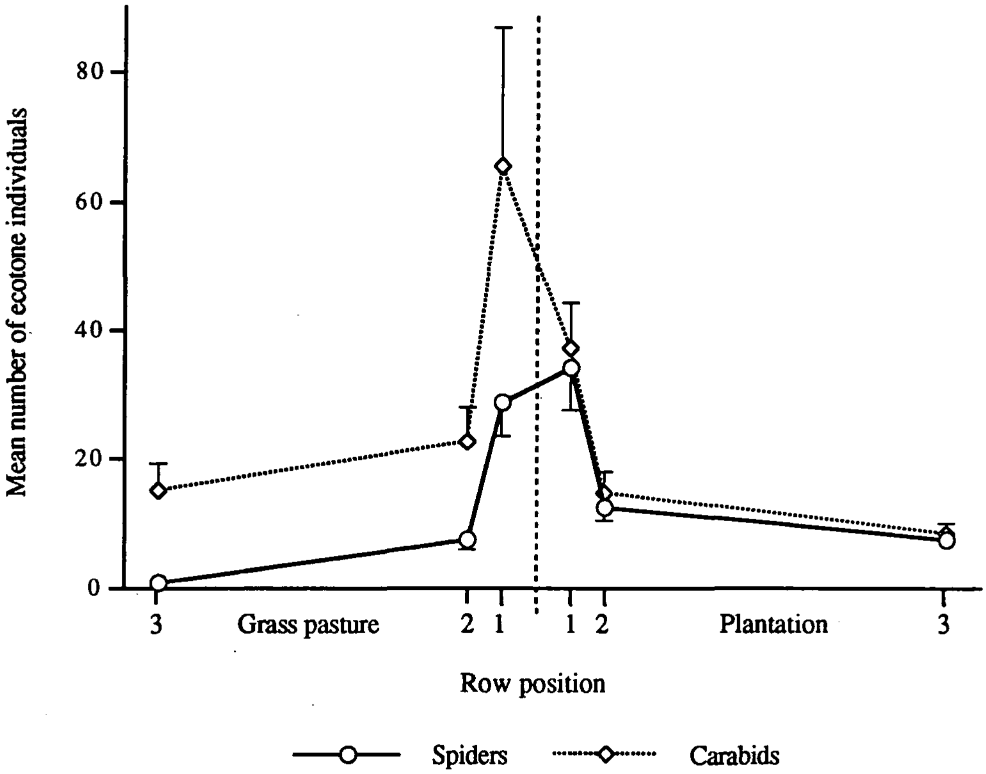
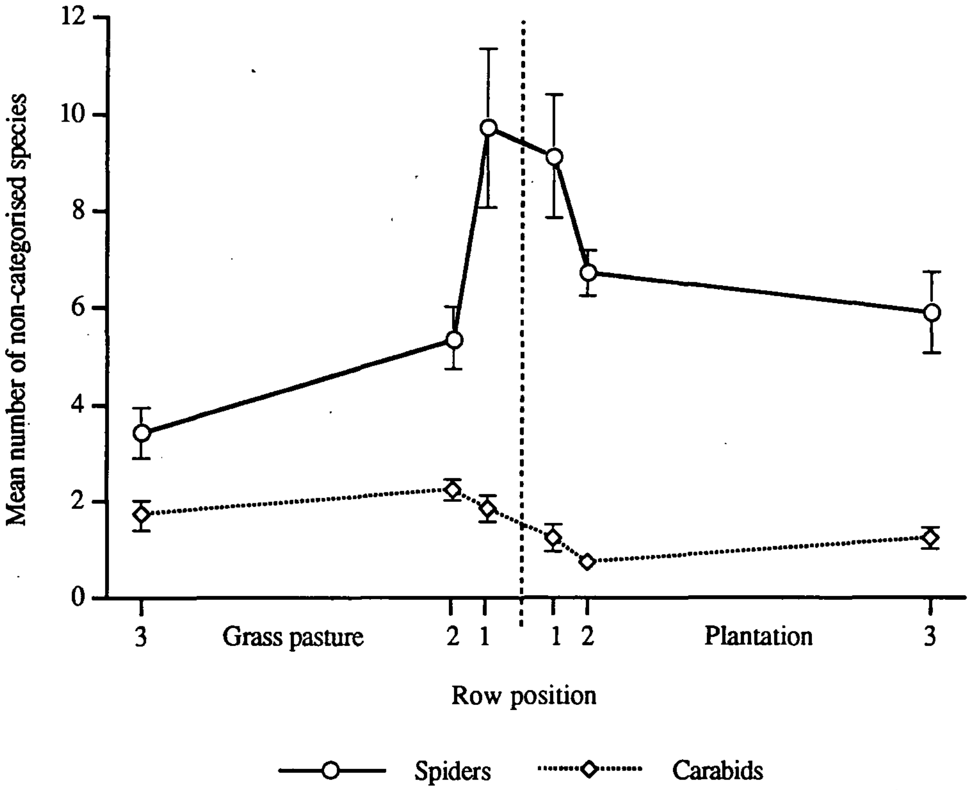


Figure 6.13. Mean number of individuals of ecotone species of spider and carabid per trap at each row position. Means derived from five pitfall traps at each site combined during 1992 (± s.e., n = 15). Negative errors shown for spiders; positive errors for carabids. Position of the interface indicated.



Although the categorised species from both groups accounted for almost the entire number of individuals in the pasture - plantation transect, the remaining species also contributed to the increase in species richness at the boundary. Figure 6.14 shows the mean number of non-categorised species trapped at each row position for both spiders and carabids. The maximum number of non-categorised spider species were recorded at rows G1 and P1 ($F_{5,84} = 6.7$, $p < 0.001$), which is where total species richness was also greatest. The number of non-categorised carabid species also followed the same trend as the total mean carabid species richness, with highest numbers found at row G2 ($F_{5,84} = 4.3$, $p < 0.01$). In both groups the ratio of non-categorised:categorised species was higher at row P3 than at other rows indicating that there is a greater number of species in the plantation which have low abundance.

Figure 6.14. Mean number of species of spider and carabid not categorised per trap at each row position. Means derived from five pitfall traps at each site combined during 1992 (± s.e., n = 15). Position of the interface indicated.



6.5 Discussion

This study examined surface dwelling spiders and carabids of the classical grassland-forest ecotone, one of the most frequently studied boundaries between habitats (Pollard 1968, Terrel-Nield 1986, Rusek 1992). Most studies on habitat fragmentation and the edge effect on invertebrate communities have shown that abundance, richness and diversity usually increase towards the edge of habitats (Heublein 1983, Helle and Muona 1985, Duelli *et al.* 1990, Dennis and Fry 1992). However in this study, spider abundance as indicated by numbers trapped was much higher in the pasture, with a progressive decrease towards and continuing past the interface penetrating 11m into the plantation (row G3 trapped 188% more individuals than row P3). Similar results were found by Maelfait and Keer (1990), who found that the mean number of spiders taken in pitfall traps within a grazed pasture was 47% higher than at its border zone. The numbers of individuals of carabids trapped showed a similar trend found by other authors, with a peak occurring at the interface, although in general more individuals were found in the pasture as a whole. The pasture habitat had short vegetation compared to the interface and plantation, and the smaller number of structural niches resulted in species of both groups with a pasture preference in this study being caught more readily by pitfall traps, such as the *Erigone* spp. (Maelfait and de Keer 1990), the *Oedothorax* spp. (de Keer and Maelfait 1987) and *Nebria brevicollis* (Greenslade 1964b). The microclimate characteristics within the pasture, such as increased solar radiation, also influenced the activity of some species, for example the Lycosidae are very active under warm, sunny conditions (Vlijm and Kessler-Geschiere 1967).

There was a 72% increase in spider species richness at the interface rows compared to the two main habitats and spider species diversity increased by 141% at the interface compared to either the pasture or plantation. This high diversity at the interface was produced by both the increase in number of species and the influence of pasture and plantation species overlapping the interface. These pasture/plantation species became proportionately smaller in their abundance approaching and beyond the interface, providing a more even distribution among the species. Maelfait and de Keer (1990) also found a comparable increase in species richness at the border of a grazed pasture compared to deeper within the pasture (77% increase). This increase in species richness and diversity at the interface is consistent with other studies on spiders (Heublein 1983, Terrel-Nield 1986, Dennis and Fry 1992, Bedford and Usher 1994) and other invertebrate taxa (Pollard 1968, Rusek 1992), although the percentage increases at the interface found by these authors could not be estimated. The lower diversity in the pasture and plantation habitats (rows G3 and P3 respectively) was due to both the high abundance of a few species compared to the other species trapped, as well as fewer species in total.

Carabid species richness and diversity showed different trends to the spiders, with no major peaks at the interface rows. Highest species richness was found in the pasture, and there was a progressive decrease across and into the plantation. There was a 45% increase in species richness in the three pasture rows compared to the plantation rows. Similar results were found by Niemelä and Halme (1992) where highest species richness and diversity was recorded in fields and pastures and lowest in forests on islands in south-west Finland. Bedford and Usher (1994) did find highest carabid species richness at the interface between arable fields and woodlands, although they still recorded higher species richness in the fields compared to the plantation. Carabid species diversity increased towards the interface between habitats, and the highest species diversity was found in the two outer interface rows. However, there was an uncharacteristic drop in diversity at the two inner interface rows. This was probably due to the relative super-abundance of some common species, such as *Nebria brevicollis, Calathus fuscipes* (both pasture species) and *Calathus melanocephalus* (an ecotone species).

6.5.1 Community content across the ecotone

The larger part of the spider community (69% of individuals and 70% of species categorised) at the interface rows (G1 and P1) was formed by the overlap of both pasture and plantation species encroaching across the interface through dispersal or foraging processes. Species with a particular preference for the interface were present but contributed less to the interface community content than the other species categories (23% of the individuals and 25% of the species categorised at rows G1 and P1 were category 5). The carabid community showed similar trends to the spiders, but there was a definite bias of more pasture species compared to species of other habitats. At the interface rows the ecotone component comprised only 30% of the individuals and only 26% of the species categorised, and at all rows except row P3 the pasture species were the major part of the catch. The reduced number of plantation carabid species partially accounts for the absence of an increase in species richness at the interface, as they did not contribute a large proportion of the catch across the transect.

Cluster analysis using pseudospecies abundance indicated that different pasture and plantation assemblages of both spiders and carabids were present; the similarity of community content between rows G3 and P3 was only 6% for spiders and 35% for carabids. The spider community content at the interface rows was more similar to the plantation habitats (52%) than to the pasture (29%), suggesting that pasture species were more influenced by the alteration in habitat type across the transect and less likely to cross the interface than forest species are. The carabid community content at the interface rows showed a stronger allegiance to the main habitats, row G1 was more similar to the other pasture rows and row P1 was more similar to the other plantation rows. Only two species (both spider), *Walckenaeria acuminata* Blackwall and *Lepthyphantes tenuis* (Blackwall), were widespread within the area sampled with similar abundance on both sides of the interface. Similar results were found by Bedford and Usher (1994), where both the arable fields and deciduous woodlands supported distinct species assemblages which mixed for only a few metres on either side of the boundary, and only a few species were considered widespread.

6.5.2 The influence of the interface

The concepts of habitat islands, edge to size ratio and habitat similarity are important considerations in a study such as this. It appears that structural similarity between habitats is important in controlling the degree of interchange of invertebrate animals across the interface (and hence edge permeability; Stamps *et al.* 1987). When the difference is marked, the level of interchange is minimal, and when adjacent habitats are more similar, the distance of invading invertebrate species crossing the interface will be greater (Terrel-Nield 1986, Bauer 1989). Duelli *et al.* (1990) found that invertebrate population exchanges over field borders was a common event. However, they found their highest levels of edge permeability to be between crop fields, habitats which were more structurally similar to each other than the pasture-plantation boundary studied here.

The level of permeability between the two habitats in this study seemed initially high with most species trapped on both sides of the interface (74% of the spider species and all carabid species categorised), the fence providing no obstruction to the movement of species. However, the exceptionally reduced numbers of spiders trapped in their non-preferential habitat indicated that few species utilised that habitat or ventured from it beyond the outer interface areas (rows G2 and P2). Indeed, Bedford and Usher (1994) found that the species influence of the arable field did not extend more than 5m into the woodland. Lower numbers of carabids with a pasture preference were trapped in the plantation, but that proportion was still large (33% of the total at P3). The plantation carabid species were considerably less abundant across the interface.

Edge to size ratio is also important, smaller areas of habitat have a larger edge to interior ratio and are likely to show a greater influence from surrounding habitats, as well as containing fewer resident species (Usher *et al.* 1993). Mader (1984) estimated the proportion of invading field species of carabid beetle would exceed that of resident species in 2-5 ha woodland isolates, and suggested that in patches of woodland smaller than 0.5 ha the entire area would be influenced by the edges, though presumably this would also be influenced by the adjacent vegetation types. Mader also suggested that the minimum area of forest required to contain a higher proportion of characteristic forest species of wandering spider was possibly some 10 ha.

The degree of interchange of spider species in this study suggests that the 10 ha described by Mader (1984) above is unrealistically large. The majority of spider species trapped in pitfalls are actively mobile species (at least in the breeding season), although as shown, few were trapped beyond the outer interface rows in their non-preferred habitats. Even highly mobile spiders, such as the Lycosidae and Tetragnathidae (predominately pasture species) were rarely trapped in their non-preferred habitat (< 0.5% of the total Lycosidae and Tetragnathidae catch occurred at row P3). In this study, both of the main habitat types were deemed large enough to provide a reservoir of species representative of that habitat. However, Mader's conclusions concerning carabids seem to be valid in this study, the degree of invasion by pasture species across the boundary was greater than the transect distance in this study, and although this transect measured a linear feature with influence in one direction only, extrapolating the point within the plantation where pasture or ecotone carabid species have no influence seems similar to the distances indicated during his study.

Although there are large differences in environmental factors between typical pasture and plantation habitats, such as direct sunlight, humidity (Heublein 1983) and CO_2 flux (Golley *et al.* 1992), it appears that forest edges also generate microclimate gradients which result in a physical environment that differs from both open fields and the forest interior (Ranney *et al.* 1981). Plants are primarily influenced by variations in solar radiation and wind exposure which affect transpiration rates. This study has shown that the edge effect is influencing the distribution of certain surface dwelling spiders and carabids, shown by species possessing an ecotone preference and by the variation in species abundance between rows in homogenous habitats (as in category 2 species).

Many studies have commented on habitat structure as being the primary factor controlling spider distribution (Cherrett 1964, Coulson and Butterfield 1986, Wise 1993, Downie *et al.* 1995), and also influencing the carabid distribution (Thiele 1977). However, close to the interface the vegetation structure appears less important than other factors which the ecotone presents, such as changes in microclimate or possible competitive effects, highlighted by the category 2 species. These species, such as *Oedothorax fuscus*, showed marked decreases in their abundance in habitats close to the interface (rows G2 and G1) which had similar structural characteristics to row G3, their preferred habitat, the pasture.

This study has shown an edge effect influence on the spiders and carabids across a sharp boundary between two structurally different habitats. However evidence suggests that this minimal edge habitat does not support assemblages quantitatively distinct from the adjacent habitats as the interface species composition is more similar than dissimilar to the main habitats. Also, the number of species and proportion of individuals which were classed as ecotone are much lower at the interface than the proportion represented by the main habitats. The question of how wide an interface area would have to be for the invertebrate content to be accepted as a quantitatively distinct assemblage, and therefore whether that area would be termed an interface or a separate habitat type, is a subject for possible future study. On the other hand, the influences of variation in the edge permeability between two habitats is also an important issue, assuming that the penetrability of the invertebrates described above is low, then how would invertebrates react across an interface between two more similar habitats. This subject is the basis for the next chapter, which will also allow inferences to be made on the stability of different invertebrate assemblages in a relatively heterogeneous environment, the Cross Fell and Dun Fell summits.

Chapter 7. The boundary effect at an upland plateau site

7.1 Introduction

As previously described, the creation of habitat edges strongly affects the environment close to the interface. Some species increase in abundance close to the edge, others decrease, and some are unique to the ecotone area. Chapter 6 concluded that there is a measurable edge effect in both spider and carabid beetle species between extremely contrasting habitat types; that the intensity of influence of the interface is variable between species; and that the primary causal factors are the differences in physical parameters between habitats, but not necessarily the vegetation structure close to the edge. The aim of this chapter is to investigate and compare the intensity of the interface influence existing between two habitats which are structurally more similar to each other than those sampled in the previous chapter. The numbers of individuals and species of both spiders and carabid beetles across an upland grassland ecotone on a sub-montane plateau in the north Pennines, northern England, were sampled by pitfall trapping using similar methods to further test the edge effect theory.

This area of sub-montane plateau was previously sampled in detail during 1991 (chapter 5), when pitfall traps were used to examine the spider and carabid beetle species present in the dominant vegetation types. However no attention was given to the interface with other habitats in close proximity. This chapter will discuss the influence of the mosaic of different habitat types on the spider and carabid species composition of the dominant vegetation areas on the sub-montane plateaux. Here, the interfaces are less extreme and the habitat types more alike than the grassland - forest border situation where edge effects within the invertebrate assemblages are clearly apparent (chapter 6). Therefore this chapter complements the findings of both chapters 5 and 6.

In 1955, the Nature Conservancy Council established several exclosures on the Moor House National Nature Reserve, the initial purpose of which was to examine the long-term effects of excluding sheep grazing on the vegetation. However, opportunistic work by Hayward and Whittaker (1979) also allowed a quantitative examination of the invertebrate fauna of the exclosure on Knock Fell (747m). They found that the considerable changes in the structure of the grasslands where grazing had ceased (found by Welch and Rawes 1964) was benefiting the invertebrate fauna. After 24 years of exclosure, the numbers of individuals of invertebrates increased 3-4 fold compared to the grazed grasslands, and diversity increased slightly within the exclosure (Rawes 1981). Similar results were found on chalk grasslands by Morris (1968), where 3.7 times as many invertebrates were extracted from ungrazed grassland exclosure compared to grazed areas using soil turves. However, little attention has been paid to the distribution of these invertebrates across the interfaces between grazed and ungrazed areas, which is an important aspect when comparing the two habitats.

7.2 Study area

The upland grassland interface was located on an area of sub-montane plateau on Little Dun Fell in the north Pennines (NY 704332). Section 5.2 gives a detailed description of this area, its climate and its general botanical content. In 1955, a 40m by 40m exclosure was erected on the summit plateau (see Figure 5.2) to examine the long-term effects on the vegetation content and structure of excluding grazing sheep from an otherwise heavily grazed area (Welch and Rawes 1964, Rawes 1981).

The development of the vegetation within the exclosure has been well documented since its establishment. Since exclosure, the species poor *Festuca* dominant grassland, typical of a large proportion of the summit of Little Dun Fell, (Welch and Rawes 1964, Eddy *et al.* 1969, Downie *et al.* 1995) has become dominated by the more succulent grasses, for example *Deschampsia flexuosa*, based on observations recorded at 8 years (Welch and Rawes 1964), 24 years (Rawes 1981) and 38 years (this study). After 24 years, *Carex bigelowii* had increased to cover large areas and *Festuca ovina*, earlier suppressed by *Deschampsia flexuosa*, showed signs of recovery. Changes in the structure of the vegetation inside the exclosure compared to outside are considerable, both the structural density and sward height have increased. Figure 7.1 shows the mean number of contacts per pin through the vegetation profile (a measure of the density) and Table 7.1 shows the mean sward height based on 20 samples at each row position (row O3 was located 11m from the interface outside the exclosure; row O2 was located 1m from the interface and O1 placed just outside the exclosure; rows I1, I2 and I3 were located in corresponding positions inside the exclosure; see Figure 6.1 for details). Significantly more vegetation contacts per pin were recorded from the rows inside the exclosure ($F_{5,114}$ = 33.3, $P < 0.001$) compared to the grazed areas outside. There was no significant variation in density of the vegetation between the rows outside the exclosure, or between the rows inside (Fig. 7.1). This increase in vegetation density was independent of the increase in sward height ($F_{5,114}$ = 104.1, $P < 0.001$ for contacts in the 0 - 30mm profile only at each row position, with a 180% increase in the number of contacts recorded in the exclosure rows).

The change in vegetation structure across the ecotone is pronounced at the interface. However the habitats are essentially more similar in structure and micro-climate characteristics to each other than the extreme variation between grass pastures and coniferous plantations. Both the vegetation outside and inside the exclosure recorded by Welch and Rawes (1964) and Rawes (1981) show close similarities with the *Carex bigelowii* - *Racomitrium lanuginosum* moss heath of the NVC (U10: Rodwell 1992), although the vegetation outside is the grazed *Galium saxatile* sub-community (U10a; 88% similarity) while the vegetation inside is the more typical type (U10b; 90%). Hereafter the vegetation types will simply be called *Festuca* grassland for the rows outside the exclosure, and *Deschampsia* grassland for the rows inside, which relate to the dominant species present. In the previous ecotone situation, the variation between habitats not only consisted of differences in structure, but also in temperature, solar radiation and other climatic variable associated with forests (Ranney *et al.* 1981). These differences are not as pronounced between the upland grasslands areas.

As in the ecotone sampled in Chapter 6, the boundary between the two habitat types in the study was maintained by a fence, which allowed free movement of wandering invertebrates across the interface in both directions.

Figure 7.1. The mean number of vegetation contacts per pin (± s.e., n = 20) at each row position across the transect at Little Dun Fell. Samples taken July 1993. Rows O3 to O1 are outside the exclosure, I1 to I3 inside, arrow indicates position of interface. Significant differences between rows indicated using Duncan's Multiple Range test; *** = $p < 0.001$.

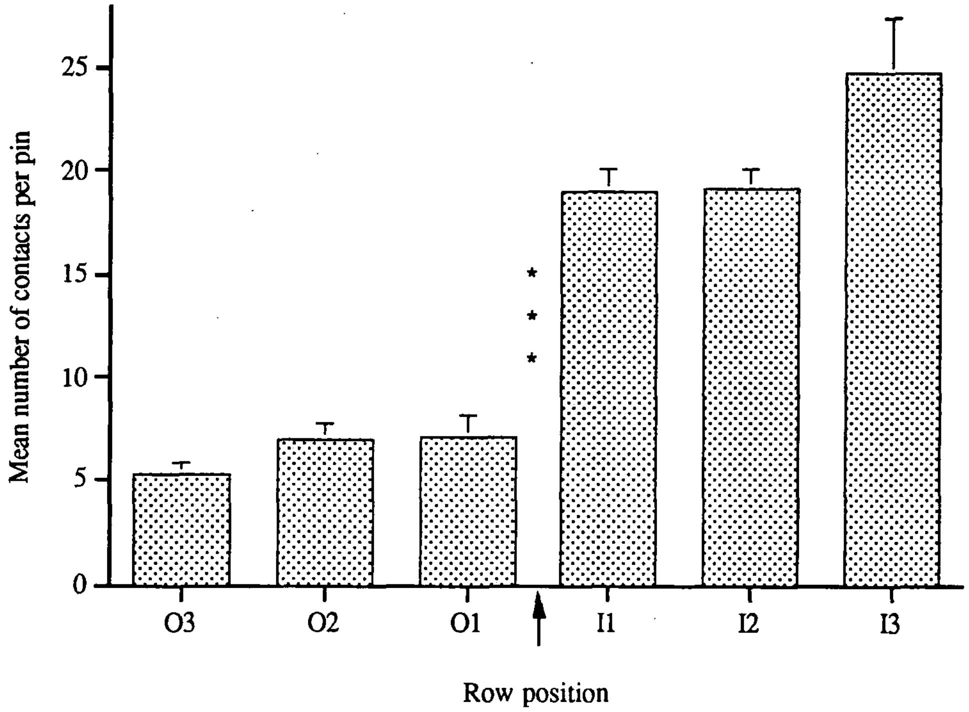


Table 7.1. The mean sward height (in mm) at each row position across the transect at Little Dun Fell (n = 20). Samples taken July 1993. Rows O3 to O1 are outside the exclosure, I1 to I3 inside.

	O3	O2	O1	I1	I2	I3
Mean	25	27	26	95	105	164
s.e.	1.2	1.5	1.5	4.6	4.1	14.1

7.3 Methods

The pitfall trap sampling grid across the interface outlined in section 6.3.1 (Figure 6.1) was the same as that applied to the ecotone situation on Little Dun Fell during 1993. The transect sampled from row O3 in the *Festuca* grassland outside the exclosure to row I3 in the *Deschampsia* grassland inside the exclosure. Samples were taken twice every month from 1 May 1993 to 1 September 1993, and then monthly until 31 October 1993. Methods identical to those outlined in section 6.3.2 and 6.3.3 were used to both examine the community parameters and to categorise the species found.

7.4 Results

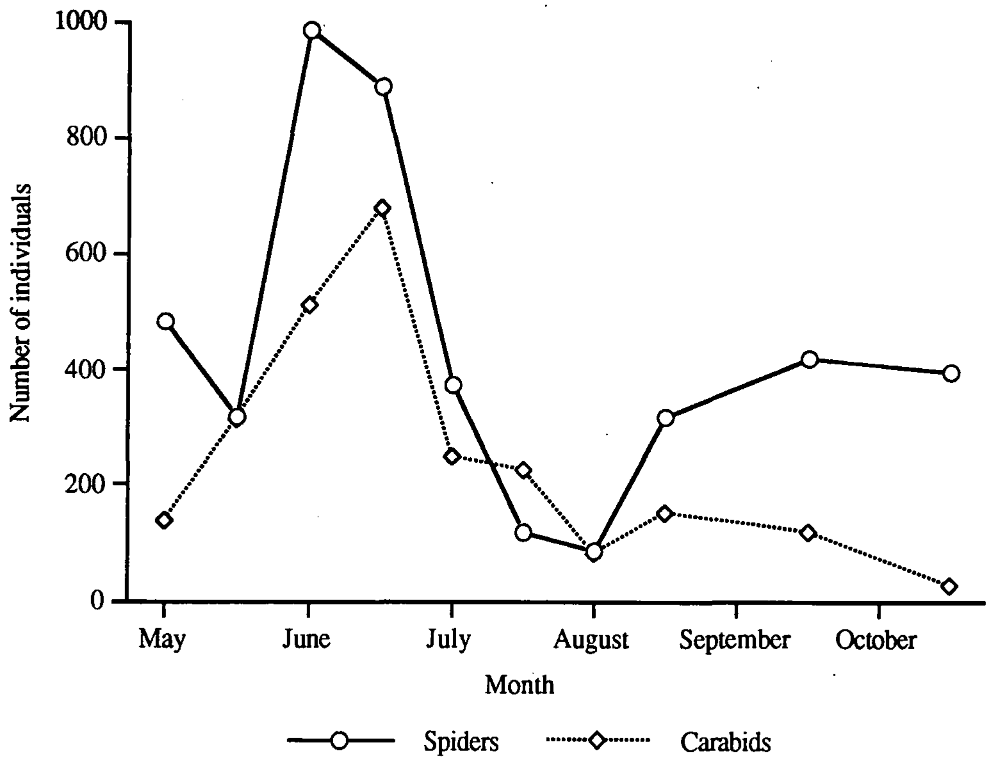
7.4.1 Seasonal variation at the upland ecotone

The seasonal variation in numbers of spiders and carabids between May and October 1993 at the exclosure site transect on Little Dun Fell is shown in Table 7.2 and Figure 7.2. Both groups showed a maximum in total numbers trapped (from 30 traps) in June, then the numbers decreased during July and August. A second peak during late August and September was recorded for spiders, though no complimentary peak was found in the carabids.

Table 7.2. Total numbers of spiders and carabids trapped in 30 pitfall traps at each site during each sampling period between May and October 1993. Trapping was initiated on 1 May 1993. The last two sampling periods were collected after trapping duration of one month.

Pick-up date	Spiders	Carabids
17/5/93	483	135
1/6/93	319	314
15/6/93	984	512
1/7/93	887	677
17/7/93	374	249
1/7/93	119	225
17/8/93	87	82
1/9/93	318	152
30/9/93	418	118
31/10/93	394	26

Figure 7.2. Seasonal variation in 30 pitfall trap catches of spiders and carabids during 1993 on Little Dun Fell.



7.4.2 Abundance and diversity across the ecotone

A total of 3972 individual adult spiders belonging to 56 species (representing 5 families) and 2426 individuals of carabid beetle belonging to 18 species were taken in pitfall traps at the Little Dun Fell site during 1993. A total of 387 immature specimens of spider were also taken which were not identified. As has been previously found (both Chapter 5 and 6) the majority of spider species taken in the pitfall traps from upland areas during this study belonged to the Linyphiidae (88% of the species recorded and 99% of the specimens trapped). Four species of Lycosidae were taken (7% of the species), and the remainder of the catch was made up of single specimens of species from three families; Gnaphosidae, Clubionidae and Thomisidae. The carabid beetle catch was dominated by three species which accounted for 90% of the total catch from 1993; *Patrobus assimilis* (74% of the catch), *Carabus problematicus* (11%) and *Notiophilus germinyi* (5%). The total numbers of individuals of each species of spider and carabid are given in Appendices 3a and 3b respectively.

Both invertebrate groups showed similar trends in the numbers of individuals trapped with more specimens taken from inside the exclosure than taken from the three outside rows (Table 7.3). Although the mean numbers of spiders was not significantly greater in the exclosure (19% increase), the mean numbers of carabids trapped increased by 69% compared to outside ($t = 4.8$, $df = 28$, $p < 0.001$). There were no significant differences in the numbers of species from either group taken from both sides of the interface.

Table 7.3. Mean number of individuals and species of spider and carabid per trap taken in 15 pitfall traps in adjacent *Festuca* grassland (outside exclosure) and *Deshampsia* grassland (inside) habitats during 1993. Significance tested with Student's t-test using log transformed values; *** = $p < 0.001$, ns = not significant.

		Outside		Inside		Significance	
		mean	s.e.	mean	s.e.	of difference	
Spiders	Individuals	121	10	144	14	t = 1.3	ns
	Species	16.8	0.83	17.5	0.39	t = 0.9	ns
Carabids	Individuals	61	5	103	8	t = 4.8	***
	Species	7.0	0.31	6.1	0.41	t = 1.9	ns

Tables 7.4 and 7.5 show the mean numbers of individuals, numbers of species and the species diversity of spiders and carabids respectively trapped along the transect from row O3 (*Festuca* grassland) to row I3 (*Deschampsia* grassland) from a total of five traps per row.

No significant differences in the mean number of individuals of spiders trapped across the transect were found. However, there was significant variation in the mean number of carabid individuals, with a maxima in the exclosure at row I1 ($F_{5,24} = 7.2$, $p < 0.001$). Row I1 trapped significantly more individuals than rows O3, O2, O1 and I3. Row I2 also trapped significantly more individuals than rows O3 and O2 (Table 7.6).

There were no significant differences in the numbers of species of either group trapped across the transect (Tables 7.4 and 7.5).

Significant variation in the species diversity across the transect was found for both spiders ($F_{5,24} = 6.2$, $p < 0.001$) and carabids ($F_{5,24} = 3.6$, $p < 0.05$). Both groups showed maximum diversity at row O2 outside the exclosure. The spider species trapped were significantly more diverse at row O2 compared to rows O3, I1, I2 and I3. Row O1 was also more diverse than the three exclosure rows. The carabid species trapped at row O2 were significantly more diverse than rows O1, I1 and I2, and row O1 was significantly more diverse than rows I1 and I2 (Table 7.6).

Table 7.4. Mean number of individuals, species and species diversity of spiders per trap taken from 5 traps at each row position from Little Dun Fell over 1993. Diversity presented as reciprocal of Simpson's D. Significant differences in means across rows tested with one-way analysis of variance (ANOVA); *** = p < 0.001, ns = not significant.

Row	Mean number of individuals	s.e.	Mean number of species	s.e.	Mean species diversity (1/D)	s.e.
O3	126	16	15.6	1.36	5.3	0.21
O2	92	5	17.2	1.83	7.3	0.66
O1	144	20	17.6	1.21	6.5	0.63
I1	123	9	18.2	0.58	4.6	0.20
I2	158	26	17.8	0.58	4.7	0.52
I3	152	32	16.4	0.68	4.6	0.41
ANOVA	F = 1.4 ns		F = 0.7 ns		F = 6.2 ***	

Figure 7.3. Mean number of individuals of spider and carabid per trap at each row position on Little Dun Fell (± s.e., n = 5). Positive errors shown for spiders; negative errors for carabids. Position of interface indicated.

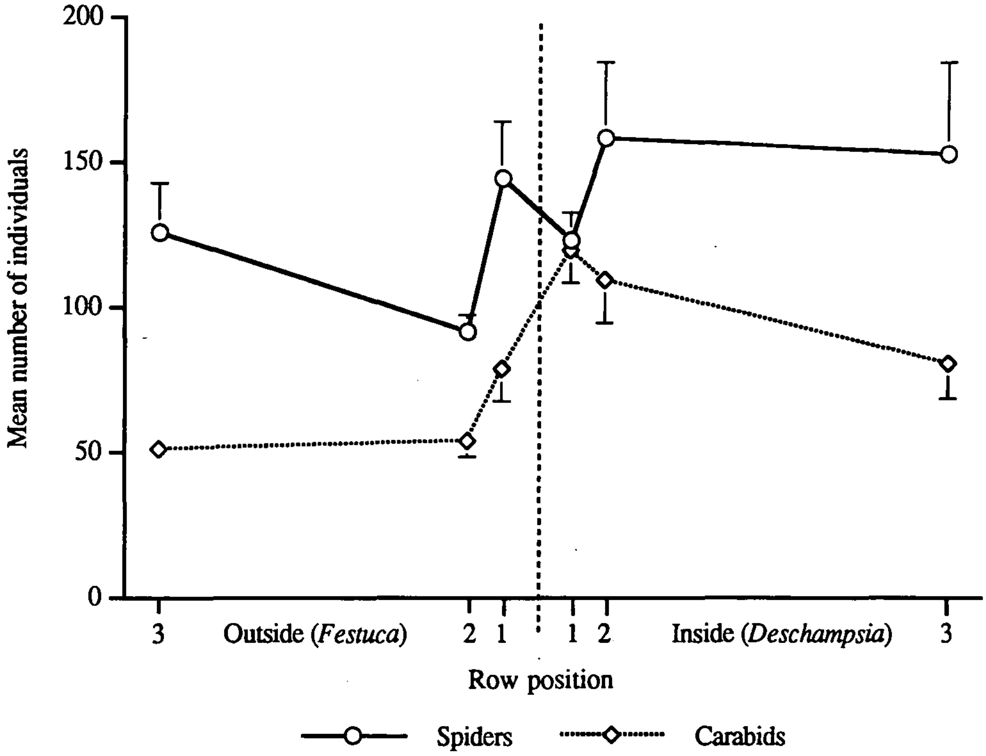


Table 7.5. Mean number of individuals, species and species diversity of carabids per trap taken from 5 traps at each row position from Little Dun Fell over 1993. Diversity presented as reciprocal of Simpson's D. Significant differences in means across rows tested with one-way analysis of variance (ANOVA); * = $p < 0.05$, *** = $p < 0.001$, ns = not significant.

Row	Mean number of individuals	s.e.	Mean number of species	s.e.	Mean species diversity (1/D)	s.e.
O3	51	2	6.8	0.58	2.1	0.23
O2	53	5	6.8	0.58	2.2	0.15
O1	78	11	7.4	0.51	1.8	0.18
I1	119	11	6.8	0.97	1.5	0.07
I2	109	15	6.4	0.40	1.6	0.08
I3	80	12	5.2	0.58	2.0	0.12
ANOVA	F = 7.2 ***		F = 1.4 ns		F = 3.6 *	

Figure 7.4. Mean species richness of spider and carabid per trap at each row position on Little Dun Fell (± s.e., n = 5). Position of interface indicated.

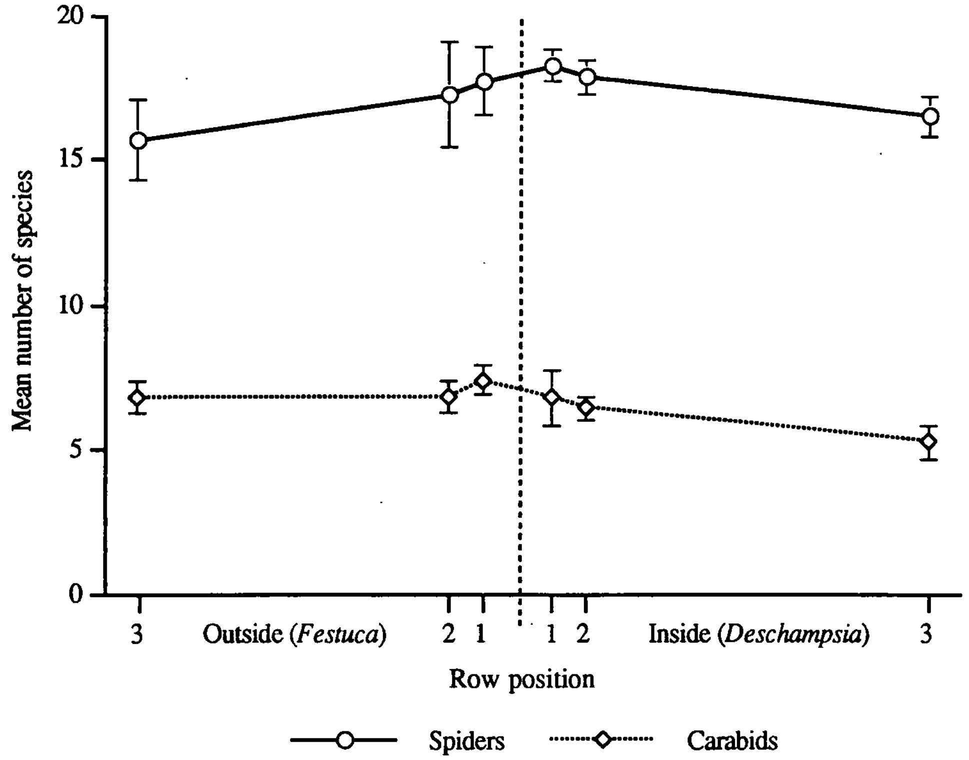


Figure 7.5. Mean species diversity of spider and carabid per trap at each row position on Little Dun Fell (± s.e., n = 5). Position of interface indicated.

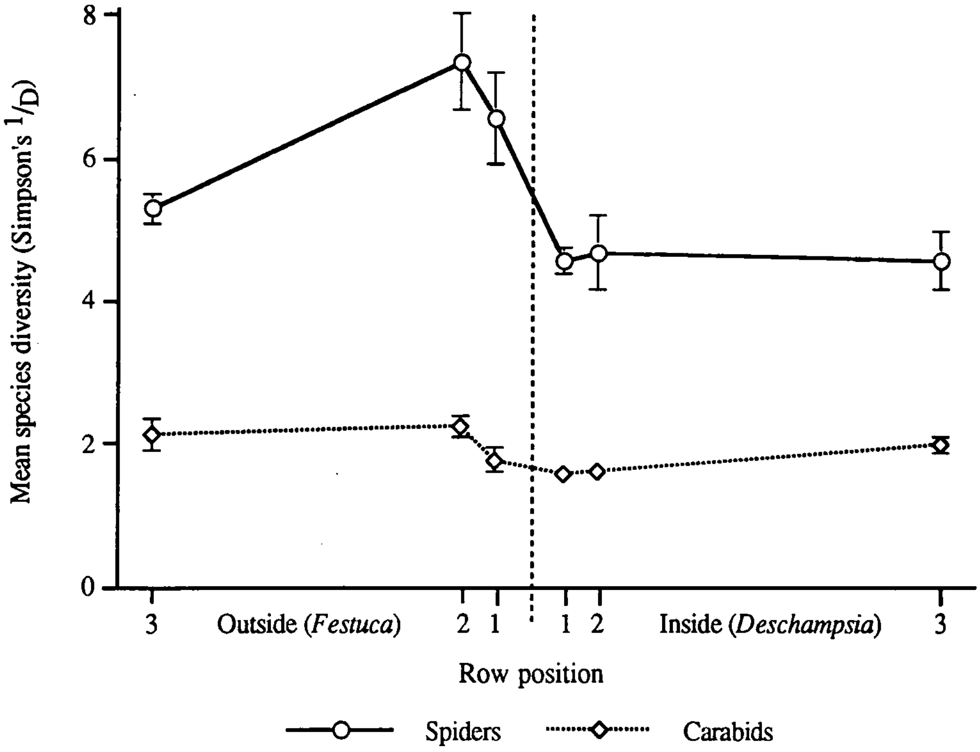


Table 7.6. Duncan's multiple range test for the multiple comparison of row means at Little Dun Fell for significant differences in the number of individuals, species and species diversity of spiders and carabids; * = $p < 0.05$, ** = $p < 0.01$.

Number of individuals

Row	O3	O2	O1	I1	I2	I3	
O3	▨			**	**		
O2		▨		**	**		
O1			▨	*			Carabids
I1				▨		*	
I2	no significant differences				▨		
I3						▨	
			Spiders				

Number of species

Row	O3	O2	O1	I1	I2	I3	
O3	▨						
O2		▨		no significant differences			
O1			▨				Carabids
I1				▨			
I2	no significant differences				▨		
I3						▨	
			Spiders				

Species diversity

Row	O3	O2	O1	I1	I2	I3	
O3	▨			*	*		
O2	**	▨	*	**	*		
O1			▨				Carabids
I1		**	*	▨			
I2		**	*		▨		
I3		**	*			▨	
			Spiders				

There are several possible explanations for the lack of a peak in species richness for either group at the interface on Little Dun Fell;

a. There were no species which have a preference for the ecotone and the same species occurred across the entire transect, and/or

b. There was no overlap of species which have a preference for either grassland or exclosure across the interface, or

c. Equal numbers of specialist species inhabited each area of the transect exclusively.

Although species richness indicated no measurable edge effect in this situation, the variation in the diversity of each group across the transect suggested that the distribution of some of the more common species varied, as close to the interface (row O2) diversity values increased for both groups (Figure 7.5). This increase in diversity could be caused by common species preferring either the *Festuca* or *Deschampsia* grassland habitats and showing a reduction in abundance when close to the interface. Analysing the distribution of each species of both groups using cluster analysis, and defining the potential habitat preferences and degree of spread across the transect of each species (section 7.4.3), can indicate which of the above explanations is the more likely.

Figure 7.6 shows dendrograms constructed using Cluster Analysis of the mean spider composition at each row for both presence/absence and pseudospecies abundance values. Both methods show high levels of similarity in species content and abundance between the row positions. The mean percentage similarity between all rows using presence/absence was 70% (± 1% s.e.), and for pseudospecies abundance was 69% (± 2), which showed that both the species content and abundance did not vary much across the transect. The similarity of the species content between the grazed area (O3) and the ungrazed area (I3) was relatively high (62% with presence/absence), however the similarity reduced to 56% when the abundance values were used. Therefore the clustering of rows based on abundance values does indicate that some species of spider do show a preference for each side of the interface, as the differentiation between *Festuca* grassland and *Deschampsia* grassland row clusters became clearer.

Figure 7.7 shows the same clustering procedures applied to the carabids on Little Dun Fell. The carabid assemblages also showed high levels of similarity for both species content and pseudospecies abundance; the mean percentage similarity for all rows was 74% (± 2) using both levels of abundance. The similarity in species content between grazed and ungrazed areas (O3 and I3) was high for both presence/absence (80%) and pseudospecies abundance values (75%). The results indicate that the interface appeared to have little effect on the distribution of the species or on the abundance of the carabids. The relatively small numbers of species in both groups make the use of cluster analysis in this case questionable, as variation in any single species could have a greater influence on the outcome of the analysis. Nevertheless, they provide a qualitative descriptive tool for observing the differences in species across the transect.

Figure 7.6. Rows clustered according to the similarity of their spider fauna in 1993. Data based on catches from five pitfall traps. Clustering strategies: a) presence/absence values; b) pseudospecies abundance.

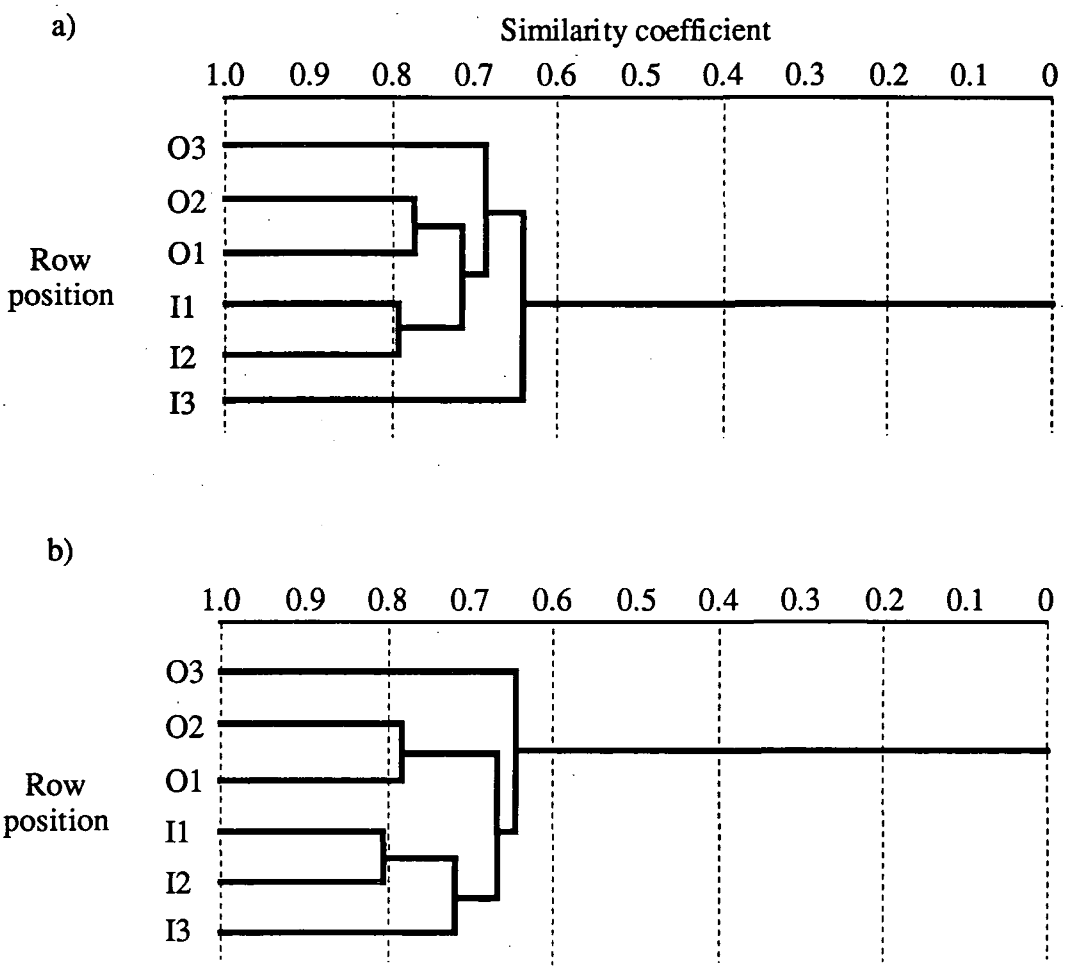
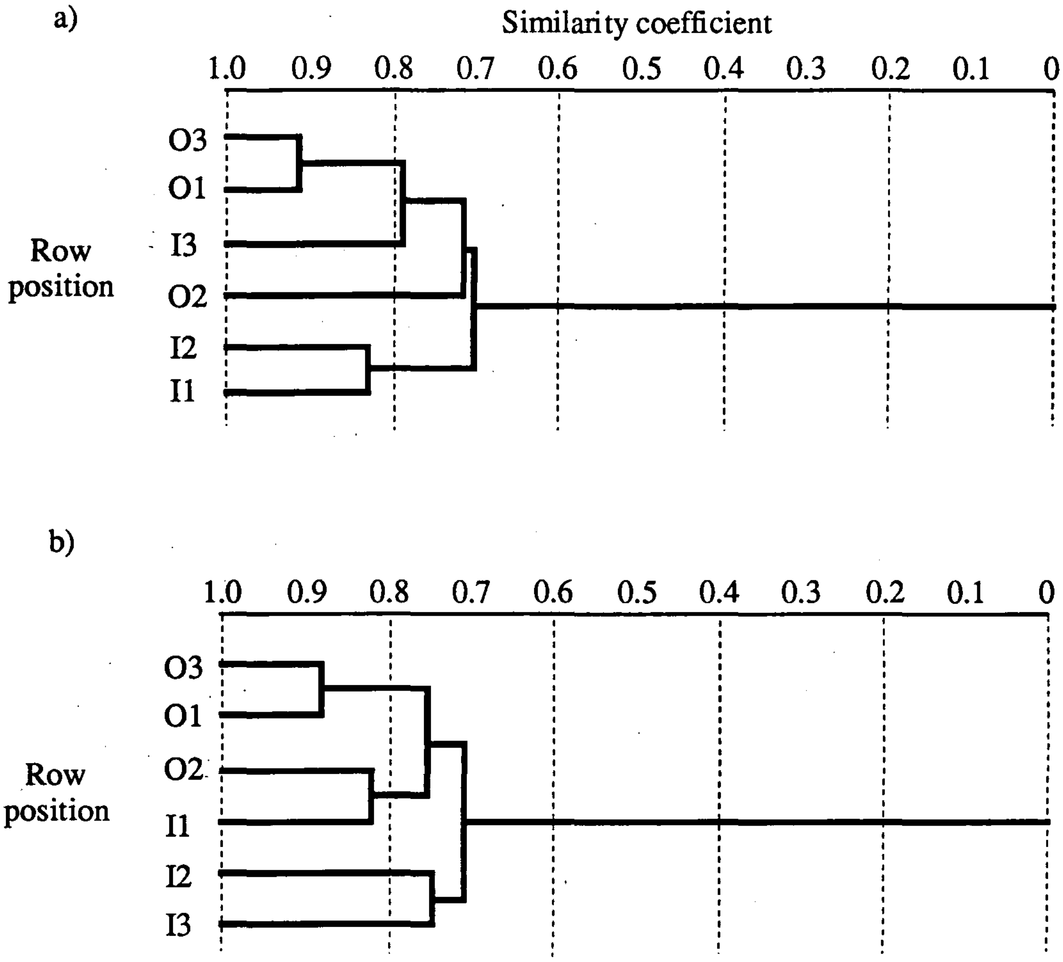


Figure 7.7. Rows clustered according to the similarity of their carabid fauna in 1993. Data based on catches from five pitfall traps. Clustering strategies: a) presence/absence values; b) pseudospecies abundance. Note alteration in row order during clustering in both cases.



7.4.3 Categorisation of the spider and carabid species

Using the same methods as outlined in section 6.3.3, the species (of suitable abundance from both groups) were categorised according to their preferences for *Festuca* grassland, ecotone or *Deschampsia* grassland areas following Duelli *et al.* (1990). Tables 7.7 and 7.8 show the classification applied to 23 species of spider and 8 species of carabid respectively, which accounted for 96% of the spiders and 99% of the carabids trapped. The remaining species were not numerous enough to be categorised.

No species from either group were categorised as preferring the ecotone area between the *Festuca* grassland and the *Deschampsia* grassland exclosure. However, there were differences between the spiders and the carabids based on the categories assigned to the species.

The majority of spider species categorised were classed as preferring the *Deschampsia* grassland exclosure (43%; Table 7.7), although there were several *Festuca* grassland species (26%). The remainder exhibited no preference and were classed as widespread (31%). Most of the species with a preference for either habitat were species which also overlapped at the interface (categories 3 and 4). The total number of spiders (including those species not categorised) did not vary across the transect (Table 7.4), however 67% more species were classed as preferring the *Deschampsia* exclosure than the *Festuca* grassland. This could be a result of variation in both the environmental structure and the trapping efficiency relating to specific species. The increase in structural density within the exclosure could provide more physical space for the spiders to inhabit, resulting in more specimens overall, but this increase could be directly comparable with the numbers per unit area outside the exclosure, where less exclosure individuals were trapped. However the variation in *Deschampsia* preferring species in the three rows outside the exclosure (and the rows inside close to the interface) indicated that they did drop off in abundance approaching and beyond the interface (the basis for classification as category 2, 3 and 4 species), suggesting that they were correctly classed as exclosure species. This explanation applies to species with a *Festuca* preference also.

From a total of 18 species of carabid trapped, only eight were categorised. Four species demonstrated a preference for the *Festuca* grassland, and four preferred the *Deschampsia* exclosure habitat. All were species which overlapped the interface to some degree, either in category 3 or 4. No species demonstrated a widespread distribution.

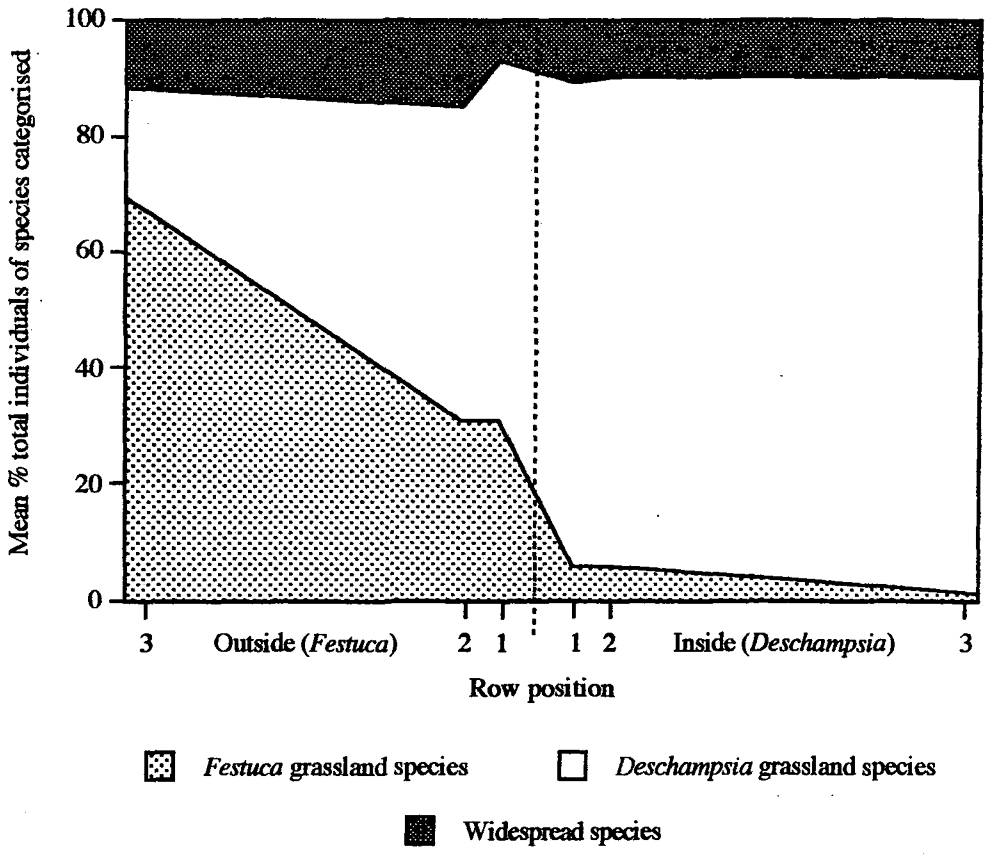
Table 7.7. Categorisation of spider species from Little Dun Fell based on Duelli *et al.* (1990). Category 1 species are hard edge; category 2 species show negative influence towards non-preferred habitat; category 3 species show positive influence; category 4 species show mutual influence and category 6 species are widespread. Note the absence of any category 5 (ecotone) species.

	Preferred habitat		
Species	*Festuca* grassland	*Deschampsia* grassland	Widespread
Pardosa palustris			6
Pardosa pullata		1	
Walckenaeria nudipalpis		3	
Walckenaeria clavicornis			6
Walckenaeria cuspidata			6
Hypomma bituberculatum			6
Gonatium rubens		3	
Oedothorax fuscus	3		
Oedothorax retusus			6
Pelecopsis mengei		2	
Silometopus elegans		3	
Savignya frontata	4		
Erigone dentipalpis	3		
Erigone promiscua	4		
Erigone atra	4		
Hilaira frigida		3	
Centromerus prudens		3	
Centromerita bicolor		3	
Centromerita concinna			6
Oreonetides vaginatus			6
Bathyphantes gracilis	4		
Lepthyphantes angulatus		3	
Allomengea scopigera		2	
Totals	6	10	7

Table 7.8. Categorisation of carabid species from Little Dun Fell based on Duelli *et al.* (1990). Categories as for Table 7.7. Note the absence of both category 5 and category 6 species.

	Preferred habitat	
Species	*Festuca* grassland	*Deschampsia* grassland
Carabus problematicus		4
Leistus rufescens		3
Nebria gyllenhali		3
Notiophilus aquaticus	3	
Notiophilus germinyi	3	
Patrobus assimilis		3
Pterostichus adstrictus	3	
Calathus melanocephalus	3	
Totals	4	4

Figure 7.8. Mean percentage spider composition (number of individuals) per trap along the transect for categorised species (n = 5) during 1993. Position of the interface indicated.



The mean proportionate abundances of the categorised spider species across the transect on Little Dun Fell are shown in Figure 7.8. The proportion of individuals characteristic of each main habitat decreased towards and across the interface. However, the overlap of individuals classed as preferring each main area was unequal. The mean proportion of individuals which preferred the *Festuca* grassland only formed the majority of the individuals categorised at row O3 (69%), furthest away from the *Deschampsia* exclosure. At row O2 the majority of individuals were classed as having a preference for the exclosure (54%), and this majority increased from row O1 (62%) through to row I3 (89%). The proportion of *Festuca* individuals reduced to 6% or less from row I1 in the exclosure. The mean proportion of widespread species did not vary across the transect ($F_{5,24}$ = 1.2, ns), and only accounted for a mean of 11% at each row position. The results suggest that there was an invasion of individuals across the interface in both directions, though there was a bias from the exclosure. The minimal overlap of individuals from the *Festuca* grassland resulted in *Deschampsia* exclosure species composing a 73% majority at the interface (mean from rows O1 and I1). This, coupled with the constancy of the widespread species across the transect, meant that at the interface there was an almost uniform component to the assemblage, which explained the lack of a peak in species richness described earlier (Figure 7.4).

Figure 7.9 shows the mean proportionate abundances of the carabid species categorised. At all row positions, individuals of species which were classed as exclosure were in the majority (98% at row I3 decreasing to 78% at row O3). This uniformity and lack of overlap in the distribution of the individuals could again explain the lack of a peak in species richness, similar to the results found for the spiders.

As described above, the distribution of species and individuals across the transect demonstrated no obvious edge effect. Although those data dealt with the categorised species only (which made up the majority of the assemblages), the remaining species could also influence the species richness across the transect. However, the mean number of non-categorised species of spider and carabid (Figure 7.10) did not vary significantly across the transect, indicating they had no influence on the species richness measurements (spiders, $F_{5,24} = 0.14$, ns; carabids, $F_{5,24} = 0.7$, ns).

Figure 7.9. Mean percentage carabid composition (number of individuals) per trap along the transect for categorised species (n = 15) during 1993. Position of the interface indicated.

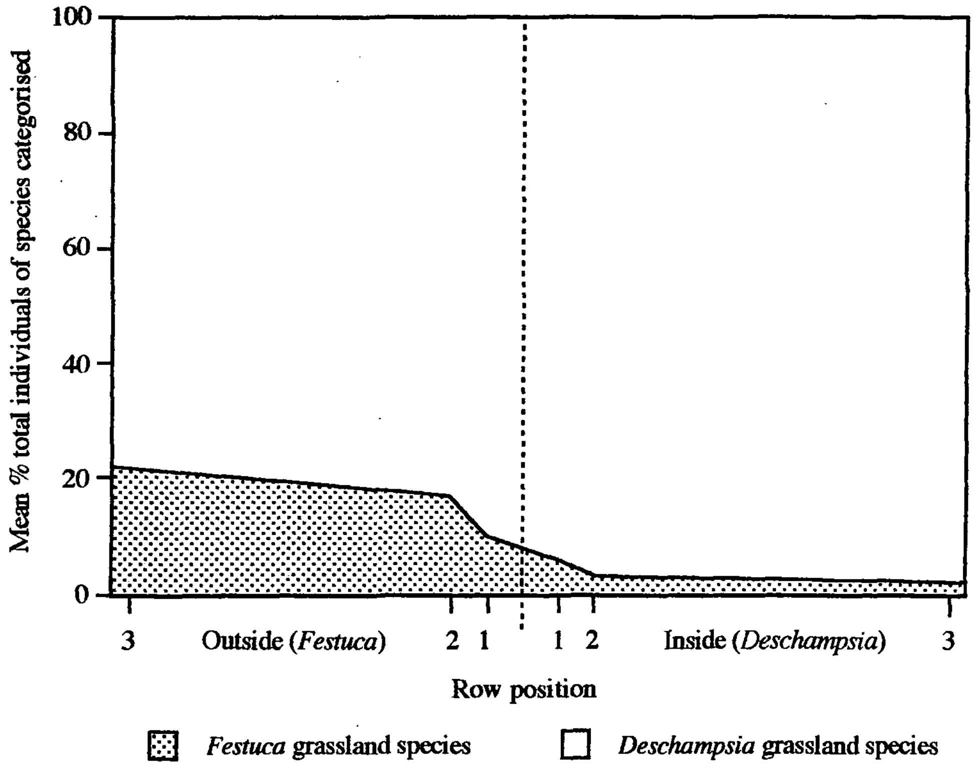
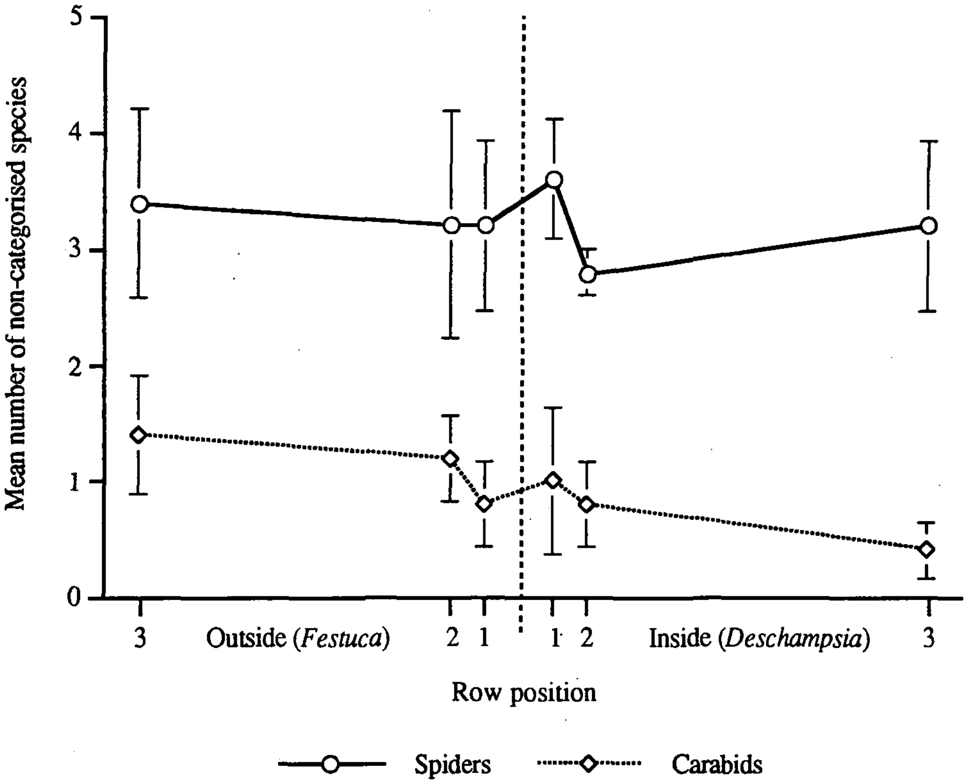


Figure 7.10. Mean number of species of spider and carabid not categorised per trap at each row position on Little Dun Fell during 1993 (± s.e., n = 5). Position of the interface indicated.



7.5 Discussion

7.5.1 Variation in the numbers of invertebrates due to sheep grazing on the vegetation

Sheep are selective feeders and grasses are always their preferential food source when available (McDonald 1990). On the Moor House NNR, sheep tend to concentrate their numbers on the *Agrosto-Festucetum* grasslands (more than 50 times the numbers found on the nearby blanket bog areas) (Rawes and Heal 1978). This type of grassland is primarily associated with the central ridge, around the Cross Fell and Dun Fell summits, but also found in other areas where the soil conditions are suitable (Eddy *et al.* 1969). Within these small areas of preferred grasslands, the high densities of sheep severely affect the plant species composition, percentage cover and also the structural density of the vegetation where they graze (Welch and Rawes 1964, Rawes 1981). These alterations of the local vegetation have also been shown to be detrimental in several ways to the invertebrate fauna, reducing both total numbers and diversity of species, when compared to similarly vegetated areas where sheep grazing has ceased (Morris 1968, Hayward and Whittaker 1979, (similar results from observations on deer grazing by Baines *et al.* 1994)). Grazing pressure has also been show to influence the species composition of both spider (Cherrett 1964, Maelfait and de Keer 1990, Gibson *et al.* 1992, and Gibson, Hambler and Brown 1992), and carabid beetle (Morris and Rispin 1987, McFerran *et al.* 1994a) assemblages.

In this study, there was no significant increase in the number of individual spiders taken in pitfall traps from an ungrazed area compared to a grazed area on the summit of Little Dun Fell, and there were no significant differences in the number of species either. However, the variation in species diversity indicates that there were fluctuations in the distribution of specific species, as diversity increased close to the outside edge of the exclosure, which suggested a more even distribution of the species content at that point in the transect. Cherrett (1964) sampled linyphiid spiders from either side of a sheep-proof fence dividing grazed and ungrazed grassland on the Moor House NNR, within which he found that there was a 79% increase in the total number of individuals found, and also a 100% increase in the species richness in the ungrazed area. He attributed these increases in abundance and richness to the increases in the sward depth following cessation of grazing, finding similar results when he looked at tussocks of grass in unevenly grazed ground. Gibson *et al.* (1992) also found that there were increases in both numbers of individuals and species of spider in ungrazed grassland compared to other areas subjected to several different grazing treatments. Indeed, increases in both numbers of individuals and species of varying degrees were found by Morris (1968), Kajak (1980) and Baines *et al.* (1994) after grazing had ceased. In most studies the spider assemblage attributes can be linked to plant species, either through the effect of food-plants on herbivorous prey abundance or through the architectural properties of particular plant species (Gibson, Hambler and Brown 1992).

The number of carabid specimens taken in pitfall traps from within the exclosure was significantly higher than the numbers taken from the grazed areas. The numbers of species did not, however, show a complimentary increase, suggesting that either some species preferred the exclosure habitat, or that they were more readily retained in the longer vegetation. The latter suggestion seems unlikely because as Greenslade (1964a) pointed out, increases in vegetation close to the trap decreases the trap efficiency for capturing large, ground-dwelling carabids. The pitfall traps might therefore underestimate the real density of large species which show a preference for the denser vegetation type, such as *Carabus problematicus*. Like the spiders, the species diversity of the carabids showed a maximum at row O2, also suggesting some species had preferences for specific parts of the transect.

7.5.2 Variation in the invertebrate species composition due to grazing

Usually in situations where grazing has ceased there is a change in the species composition of the assemblage, as well as an increase in both the numbers of individuals and species (Gibson, Hambler and Brown 1992, McFerran *et al.* 1994a). Differences are usually most noticeable in spiders with the increase of web-spinning species, possibly because the grazed areas lack suitable structures (vegetation, litter) for web attachment (Maelfait and de Keer 1992). Generally, short vegetation species are more suited to unstable communities of spiders (Duffey 1978) such as the small linyphiids. Differences in the carabid assemblages between grazed and non-grazed areas are generally also present (Morton - Boyd 1960), though the controlling factor would seem to be the freedom of movement, but species may show differential susceptibility to trapping according to size, behaviour and the strata in which they are active (Greenslade 1964a).

Initially there appeared to be no real variation in either the spider or carabid species content of the two areas under study, with high levels of similarity between the rows O3 and I3 which were the furthest apart (spiders, 62%; carabids 80% using presence/absence values). The inclusion of abundance values in the analysis, which might indicate any preferences of particular species to any specific area, did not show a large decrease in similarity for the carabids (reduced to 75%), suggesting that the carabid species abundance was essentially the same over the transect. These results highlight the simplistic and fairly crude nature of using cluster analysis and pseudospecies abundance values with so few species, as few differences in species abundance between row positions could have large differences in the overall percentage similarity. The carabid *Patrobus assimilis* was highly abundant at all row positions, well above the value used to indicate the inclusion of pseudospecies (> 29 specimens at one or more row position), therefore no percentage similarity differences were noticeable in the cluster analysis due to differences in the distribution of *P. assimilis*. However, closer analysis of the distribution of *P. assimilis* using ANOVA showed that it is a species which was taken much more abundantly inside the exclosure than outside (65% of the specimens taken from rows I1 to I3). Only two other carabid species (*Carabus problematicus* and *Notiophilus germinyi*) were abundant enough at any of the row positions to merit applying pseudospecies abundance, providing six extra differences in the cluster analysis. These six extra pseudospecies values accounted for the 5% variation from the presence/absence cluster.

As with the carabids, there appeared little variation in the spider species content between the two furthest apart row positions (presence/absence, 62%; pseudospecies abundance 56%). The 6% reduction in similarity between the two methods does, perhaps, indicate that some of the species have a preference for either of the two habitat types, although the cluster analysis probably under-estimates this.

There are several possible explanations for the high levels of similarity in the ground-dwelling spider and carabid assemblages between the two areas surveyed;

1. High edge permeability. The variation between the two vegetation types might not be large enough to inhibit the movement of species across the interface between the habitats. Also, the increase in vegetation structure within the *Deschampsia* grassland might not be different enough to develop a distinct fauna. If changes were going to be found, they probably should be observed after 40 years of exclosure, as would be expected based on other studies (Morris 1968, Gibson *et al.* 1992).

2. Small area. The exclosure size might not be large enough to contain a species assemblage which is large enough to be considered different from the surrounding habitats.

3. Pitfall traps might only be sampling the ground fauna, not the abundance of any additional species which might be utilising the upper layers of the vegetation within the exclosure. However, the fact that there was no increase in the number of species inside the exclosure for either group suggests that this was probably not the case.

The most likely explanation is a combination of points 1 and 2. Using these clustering methods to show differences in species content between habitats is perhaps questionable as they appear relatively insensitive to any variation. However it does have its advantages and the negative result in dissimilarity between the habitats provides important information. In the high altitude situation, few differences were observed using cluster analysis and this in itself implies that most of the species are widespread throughout the study area. This suggests that most of the species are able to utilise both the habitats surveyed, even though ANOVA showed that they have a definite preference for certain areas. It appears therefore that on the summit area, most spider and carabid species have a wide niche, possibly actively foraging in most habitats, but having a preferred area for breeding or sheltering in. It is possible that a number of the species regarded as preferring the short *Festuca* grassland would use the exclosure area as an overwintering site too (as found in field species using woodland edges; Sotherton 1985, Wallin 1985, Maelfait and de Keer 1990).

Although there is usually an increase in the spider family diversity with cessation of grazing (Maelfait and de Keer 1990), this is not realistic for the sub-montane summit. In these high altitude habitats, the proportion of linyphiid spider species compared to other resident families is much higher (Coulson and Butterfield 1986, Downie *et al.* 1995), therefore few species from other families are suited to the local environment, and colonisation of the grazing-free area will be mostly from other linyphiid species.

The common species of carabid which were classified as preferring either outside or inside the exclosure show close similarities with the categories assigned to those species taken from the Moor House NNR by Bauer (1989). Species which Bauer classified as preferring peat habitats were clearly associated with the relatively similar dense vegetation of the *Deschampsia* exclosure, such as *Carabus problematicus*, *Leistus rufescens* and *Patrobus assimilis*. Species which were classed by Bauer as preferring limestone habitats such as *Notiophilus aquaticus*, *N. germinyi* and *Calathus melanocephalus* were classed as preferring the shorter *Festuca* vegetation in this study.

7.5.3 The influence of habitat proximity

Although the two different habitats did not possess species assemblages which were exclusive, even at 50% similarity, there may be some variation in the abundance of particular species approaching and past the interface between the habitats. Previously, species of spider and carabid have been shown to exhibit preferences for habitats with specific vegetation characteristics (e.g. Cherrett 1964, Thiele 1977, Butterfield and Coulson 1983, Coulson and Butterfield 1986 etc.). Chapter 5 showed that this is also the case for spider and carabid beetle species from sub-montane summit areas, with more between habitat variation observed within the spider community than within the carabids. At edges between habitats, populations from both habitats were shown to cross the interface, and most showed a decline across the boundary which is essentially controlled by the interface, and variable responses were shown by different species (chapter 6). In this situation there are clearly some species from both groups which show preferences using pitfall traps for either the *Festuca* or the *Deschampsia* grasslands, and they also show variable levels of abundance across the interface.

It is possible that these species were more readily trapped in the habitat that they have been classified to prefer using the methods employed here, as suggested previously. However, the low number of species which were classified as category 1 from the summit of Little Dun Fell (*Pardosa pullata* only) suggested that most species showed a variation in numbers taken in row positions where the vegetation structure (and subsequent micro-climate associated with that vegetation type) was considered to be similar (category 2, 3 and 4 species). The definition of category 6 species (widespread) is, however, susceptible to the possibilities of trapping error between the two habitats. These species showed a similar abundance in the pitfalls throughout the transect, and therefore showed no variation in numbers where there is clear variation in the habitat. If this category is not valid and any of the widespread species do prefer one of the two main habitats surveyed in real terms, then it would be most likely that the species would show a decrease in abundance using ANOVA, away from the preferred habitat. This was not the case, which suggests that either they were correctly categorised, or that the distance from the interface of the furthest rows was not far enough to observe decreases (possibly highly mobile species) in pitfall trap abundance.

The degree of interaction between the habitats seems to be biased for both groups, with a greater influence arising from the habitat with the greater structural complexity. Generally, these vegetation habitats are the ungrazed areas, particularly in this study, and they contain a surface invertebrate fauna which is considered more stable and able to utilise the dense habitat, and also the surrounding shorter vegetation habitats to a lesser degree. The invertebrates of grazed areas however, are generally unable to utilise the dense vegetation (Duffey 1978, McFerran *et al.* 1994b). It could be inferred that these ungrazed habitats are either more natural compared to the intensively grazed areas, or are simply a later part in the successional sequence.

Most of the spider species with a *Festuca* grassland preference showed a decrease in abundance approaching the interface (67% were category 4), which continued past it into the exclosure habitat too. This trend, accompanied by the fact that most of the species with a preference for the *Deschampsia* exclosure still represented a major part of the number of individuals (though in decreasing numbers further from the interface) in the *Festuca* grassland, accounts for the increase in diversity at rows O2 and O1 in Figure 7.5, as the dominance of the *Festuca* and

Deschampsia species reduced, and the species to number of individuals ratio was highest.

The proportions of species with a preference for either habitat suggested that the species of spider and carabid which prefer the *Deschampsia* vegetation could utilise the *Festuca* grassland vegetation better than those species which prefer the short vegetation could use the denser ungrazed type. These findings suggest that the invertebrate fauna of the dense vegetation habitats which are isolated by the dominant *Festuca* vegetation of the summit areas are well equipped to survive extinction processes, based on their higher dispersal powers (den Boer 1981). However, these findings only apply to a controlled environment, the constant reduction of habitat size (and fragmentation) from overgrazing by sheep will reduce this survival factor in more natural situations.

7.5.4 Comparison of edge permeability studies

Clearly the variation in physical structure between the adjacent habitat types and habitat size are important influences with respect to the movement of invertebrate species crossing the interface (Greenslade 1964b, Baars 1979, Mader 1984, Bauer 1989). In the sharp, abrupt situation of a pasture - plantation interface where the differences are considerable, the species similarities appear low, and the impact of species crossing the interface is low, with species showing large changes in the numbers caught in pitfalls only 1m away from the interface. In the more moderate situation at the boundary between arable fields and deciduous woodland (Bedford and Usher 1994) the distance increased to c. 5m from the interface. This is presumably because the under-storey present in the woodland (c.f. the absence in a conifer plantation) and the increased vegetation structure of the arable field (c.f. a grazed pasture) increases the similarity of the ground-layer of the two habitats, and hence the edge permeability too. In situations with the same sharp boundary but located between two much more similar habitats, the assemblage composition of the two vegetation types tends to be very similar, and the impact of species crossing the interface is higher, even deeper into each habitat. However in both these situations, the specific groups of invertebrates show variation between species too. Spiders show much greater internal species variation between the habitats, while carabid species, which are not associated with the vegetation for web attachment etc., show this variation to a much lesser degree.

The general results obtained and presented in this chapter were those expected. The softer edge between the two upland grassland habitats appears to increase the edge permeability compared to the harder forest edge, and the edge effect was much more reduced. Stamps *et al.* (1987) suggested that in soft edge situations, patch size and shape have a greater influence on the degree of interchange between the habitats than they do in hard edge situations. This could be true of this survey, as the study exclosure was relatively small (40m x 40m). However, it should also be noted that the entire study area is essentially an island itself, the summit plateau of Little Dun Fell being only about 0.2km^2 (above the 800m contour). Therefore the exclosure comprises a relatively large part of the entire area from which most of the invertebrates would be sampled. Any species which have managed to colonise the exclosure vegetation are under the influences of two factors, firstly, they must have the high altitude tolerance typical of all the invertebrates associated with the summit, and secondly, they must be able to withstand the competitive influences of species from the surrounding *Festuca* grassland. However, the fact that the common species associated with the short *Festuca* are more typical of unstable, succession vegetation (Duffey 1978, Maelfait and de Keer 1990), and their low levels of dispersal across the interface compared to the *Deschampsia* preferring species suggests that they represent an impoverished fauna compared to the more natural exclosure species assemblage (although this is perhaps diluted).

Chapter 8. General discussion

The main purpose of this study was to understand the effect and impact of habitat heterogeneity on the resident invertebrate fauna in an upland area of particular importance for its conservation value. Habitat heterogeneity is a term which can be used to describe environmental patterns across a variety of spatial scales. though in this study, habitat heterogeneity has been taken at a scale which represents the variation in dominant vegetation types, where each 'type' consists of relatively homogeneous plant species and structures (e.g. *Festuca* grassland, *Eriophorum* mire or forestry plantation). This is a simplistic approach which takes no account of heterogeneity within a particular type of vegetation, but it is probably the scale most suited to studying surface-dwelling invertebrate distribution, especially when the sampling method is partially influenced by activity.

Studying heterogeneous habitats is a relatively new branch of ecological research (recently termed "Landscape Ecology"), which focuses on the complex spatial structure of the environment and how it affects ecological patterns and processes (Bell *et al.* 1991, Hansson *et al.* 1995). Rather than concentrating on the biology of isolated habitat types which are generally deemed homogeneous, this discipline attempts to address questions such as "How does landscape structure affect movement patterns or foraging dynamics?", "How does the landscape structure affect the demography of populations, or species interactions such as predation and competition?", or "How should an understanding of spatial processes affect our use or management?" (Wiens 1995). These are broad-ranging questions, hardly within the scope of a single thesis, and more suited to several studies. However, one of the more positive aspects of research on invertebrate distribution is the ability to ask several questions and receive coherent answers from a relatively small scale study.

8.1 How does landscape structure influence invertebrate distribution?

The invertebrates of the north Pennine sub-montane plateaux have seldom been examined, although extensive studies on the vegetation and climate of the local area (Manley 1942, Welch and Rawes 1964, Eddy *et al.* 1969, Rawes 1981) have provided an excellent source of information for understanding the invertebrate distribution. The sub-montane plateaux sampled comprised several different vegetation types forming a mosaic, which contained a relatively diverse spider fauna which showed variation in species content between the habitats. The carabid fauna appeared to be less heterogeneous, with species apparently more widespread between the different vegetation types. An important consideration in any study relating invertebrate distribution to the environment is that a functional interaction between the habitat structure and the organisms of interest must be demonstrated (McCoy and Bell 1991), and that the scale of the investigation be suitable to meaningfully observe movement or distribution patterns. In most community studies, differences can be seen at several scales, whether sampling within or between habitats, large or small. However, the differences observed in this small scale study are still evident when included in a much larger scale community study (see Figures 5.12 - 5.14 and Coulson *et al.* 1995), with the summit spider community showing larger variation in species distribution on the plateaux (using DCA) than the carabids showed. The summit staphylinid community also showed slightly more internal variation than the carabids, but not as much as was found in the spider community. Different spider and carabid species assemblages were also observed in two highly-contrasting habitats at lower altitude (sheep pasture and forestry plantation) which were relatively close to each other, again indicating invertebrate habitat selection.

This study has shown that whilst different invertebrate species assemblages associated with the different vegetation types can be demonstrated, the influence of different surrounding vegetation types affects the species content of that habitat close to the border, and this influence decreases away from the boundary. The influence was found to be much higher between the sub-montane plateaux sites than was found between the lower altitude pasture/plantation sites. Factors which could control the level of influence have been mentioned previously, and include edge permeability, habitat similarity and size. Both the boundaries studied were maintained by a fence for experimental purposes, though linear boundaries like this produce, if anything, a narrower edge effect and ecotonal area than would be found between two habitats where the boundary is not man-made. In artificial experiments (e.g. fenced areas), the distance of mixing of the two vegetation types at the edge is kept to a minimum through grazing, succession and canopy cover, whilst usually in nature, the border is rarely as sharp. Therefore, the more natural ecotone zone would be expected to be considerably wider, usually dependent on the degree of difference and mixing between the two habitat types, but also influenced by the size (and subsequent percentage resident species composition) of each habitat (Stamps *et al.* 1987).

Much of the variation in species preference found in the invertebrate groups studied is attributable to their dependency (or independency) on the vegetation for foraging. The larger degree of variation in the spider community compared to that found in the carabids was to be expected, spiders are generally much more dependent on the habitat vegetation structure for web placement (Schaefer 1978, Robinson 1981) or 'perches' for non-web-building species (Greenquist and Rovner 1976), and between the different habitat types of the sub-montane plateaux this was the main environmental difference. Vegetation structure is not considered directly important in controlling carabid species distribution, but it may influence their prey distribution. Habitat moisture is however considered one of the most important factors (Butterfield and Coulson 1983, Gardner 1991), though in this wet, high altitude environment, the variation in moisture between habitats was low and much less than would be found between differing habitat types at lower altitudes; a result of the extremity of the climate. The cluster analysis and classification results from this thesis confirm these findings, that the carabid species contents are more similar between habitats than the spiders in all three studies. Carabids have been shown to engage in two contrasting types of movement (Baars 1979). In a favourable environment 'random walk' predominates, where the beetles cover short distances in a continually changing direction within the habitat. Where adjacent habitat types are strongly contrasted with a well defined interface they are able to avoid crossing the boundary (Greenslade 1964b, Rijnsdorp 1980, Mader 1984). When the transition between habitats is more gradual, carabids continually cross boundaries in random walk until the increasingly unfavourable terrain encountered prompts a bout of rapid 'directed movement' designed to bring the individual back into a more amenable locality (Baars 1979, Lloyd 1987). This would indeed indicate that most vegetation types within the mosaic on the three summits were favourable habitats to the majority of the carabid species. Movement in invertebrate species can be a result of several different stimuli, operating at different spatial scales (Ims 1995). Table 8.1 gives a summary of the most probable movement types and the type of spatial structure associated with them. In this study, the two most important landscape scales would be the habitat patch and the patch mosaic. Movement at the resource patch scale is essentially within habitat and too small for the scope of this study. In contrast, movement at regional scale is too large, perhaps more associated with larger more mobile invertebrates and vertebrates. In conclusion, any movement between the habitat patches in this study would most likely be a result of foraging (and possibly dispersal) processes across boundaries.

As previously discussed, habitat heterogeneity can influence the spatial distribution and preferences of invertebrate populations and also the movement patterns between different landscape elements. However, the degree of heterogeneity in the local environment can also influence the size, stability and demography of invertebrate populations according to the equilibrium theory of island biogeography (MacArthur and Wilson 1967). The theory states that the number of species found on an island (or, in this case, an isolated vegetation type) is a function of the rate of immigration and the rate of extinction of species. The survival time of small and isolated populations will often be relatively low, and the survival of species living in such a way will depend on powers of dispersal sufficiently high to result in a rate of population establishment that compensates the rate of population extinction (den Boer 1981). Although spider and carabid populations can easily disperse to the surrounding areas (as shown in chapters 5, 6 and 7), these habitats may be unfavourable because of biotic or physical factors. The physical size of habitat patches may influence both immigration and extinction rates, immigration increases with size because the target is larger, and extinction decreases with size because there should be more opportunity to escape competition or predators in a larger area (Colinvaux 1986). Larger populations in large areas also face less chance of random extinction. This could partly explain the bias in movement of individuals from the smaller patch of *Deschampsia* grassland on the top of Little Dun Fell, as smaller populations should possess a much higher dispersal rate, as suggested by den Boer (1981) above.

Table 8.1. Animal movement modes and influential spatial structures classified according to the spatial scale (after Ims 1995).

Spatial scale	Movement type (Life process)	Spatial structures
Resource patch	Food item searching (foraging)	Food item distribution Food patch shape and size Small-scale obstructions
Habitat patch	Patch searching, traplining (webs etc.), territory patrolling	Food patch configuration Shelter Abiotic factors and topography
Patch mosaic (landscape)	Dispersal	Patch parameters (e.g. size, shape, isolation) Landscape parameters (e.g. connectivity, dispersion)
Region	Migration	Large-scale topography Large-scale barriers

Young (1995) suggested that within a landscape a combination of habitat type and spatial arrangement could influence the population dynamics of species, although this is surely linked to the movement capabilities of the animal (Ims 1995). The habitat structure of specific outcrops has been shown to influence both the size and diversity of certain invertebrate populations (reviewed in chapter 7), and the distances between suitable habitats could have an influence on the degree of interchange (dispersal and immigration) between those habitats. For example, the configuration of habitat patches appeared relatively unimportant to patch immigration rates for butterflies which dispersed over large distances (Fahrig and Paloheimo 1988), whereas Lawrence (1988) found that both immigration and emigration rates were affected by patch isolation for milk weed beetles with a more restricted dispersal ability. The type of habitat between the preferred habitats is important (connectivity), with unfavourable habitats creating barriers to ground dispersal in non-aerial animals.

In summary, the differences between vegetation types on the plateaux were not large enough to inhibit most spiders or carabids from crossing at the boundary. Presumably this is an artifact of the high structural similarity of the vegetation and wider niche of the invertebrates. However, the spiders, with their greater vegetation dependency, showed some degree of species-vegetation fidelity. Between more contrasting habitats with greater structural dissimilarity, the species-vegetation fidelity is characteristically higher and invertebrate movement between habitats lower in both groups.

8.2 Communities within the landscape

A widely used descriptor in ecological theory is the term 'community', but despite a vast literature on both its definition and use in ecology, the accepted definition is obscure. Southwood (1987) attempted to address the question of "what is a community?", and found that the current uncertainties and controversies in the field of community ecology fall into two broad areas:

1. Are communities mere assemblages of organisms in a location or are they tightly linked and structured groups of interacting species?
2. To what extent is the nature of the community 'organism-driven' or 'environment-driven'?

He concluded that within both of the above questions neither alternative would provide the whole answer. This suggests that use of the term 'community' is unscientific to say the least, and indeed the question of "is a community anything more than an abstraction made by ecologists from continuously varying vegetation?" has been proposed (Krebs 1985). Clearly there is much debate which still needs to be resolved, however the purpose of this discussion was not to review the current theory on community characteristics, but to clarify its practical use in this study.

In the production of the National Vegetation Classification (NVC), Rodwell (1991) used the term 'community' to describe the principle vegetation types in Britain. He used community in a practical sense based on the repeated nature of the vegetation associations, and used 'sub-community' to describe close variants of the main vegetation types. The methods avoided the construction of a hierarchical classification which would have introduced problems of scale. The differences in vegetation type have been shown to be one of the major factors controlling spider and carabid species distribution, and using these habitat differences as a template for animal communities is a common approach (Southwood 1977, 1987). Using the concept of a community as a repeatable association of species could also describe invertebrate communities, and it would fit the scale of the investigation used in this study.

Throughout this thesis I have used ‘community’ to describe the widest possible scenario within the sampling area, e.g. the entire invertebrate fauna of a particular vegetation type was labelled the ‘invertebrate community’. This description has also been sub-divided to account for the different groups being surveyed, e.g. the spider and carabid communities. The most important source of difference in describing these communities was the level of similarity in species content (and also relative abundance) between pitfall trap catches at each site. However, pitfall traps are well known for sampling the invertebrate ground fauna, which is ideal in the short vegetation types associated with the summit vegetation. It seems reasonable to assume that this method accurately samples certain aspects of the spider and carabid communities in these areas such as species richness. However, in a different situation, such as within one of the plantation habitats sampled for its edge qualities, the pitfall traps must take a lower proportion of the total spider fauna associated with the ground and canopy. To this end I have used the term ‘assemblage’ when considering the pitfall trap catch from any set of traps, regarding this ‘list’ as part of the larger, all encompassing community. At the scale of this study this definition is well suited, as comparison with invertebrate communities from other areas which might indicate higher levels of either similarity or dissimilarity between the assemblages is useful, but not a prime concern.

Animal communities are inherently more difficult to identify than plant communities due to their mobility, particularly the spider and carabid communities. While they sometimes show close associations with the vegetation, the gradient between invertebrate assemblages trapped in different vegetation communities is on the whole much wider and indistinct, with much overlap at the boundaries. The question of what separates two communities which are not as defined as the vegetation requires more rigorous conditions. For this purpose the multivariate approach was employed to identify separate assemblages which represented part of each community. Although they bring in a degree of hierarchical structure to the separation, they can account for the transient nature of the invertebrates, and reliably indicate when two habitats contain separate assemblages, possibly communities. In this study, the degree of overlap and similarity between the invertebrate species content suggests that there was only one carabid community associated with the summit areas, while the spider community may be identified as a selection of sub-communities because it showed much more variation between habitats.

8.3 How does our knowledge of landscape patterns affect our use or management in these areas?

The vegetation heterogeneity on the summit plateaux is important for the conservation of the invertebrate community associated with the vegetation. Several species of spider are restricted to habitats with particular environmental conditions, and although the majority of carabid species utilise a broader range of habitats, some species showed preferences for certain areas. The habitat heterogeneity therefore increases the diversity of the invertebrates in an environment with an already elevated rarity factor (diversity and rarity being two of the major criteria in assessing the value of a particular area for nature conservation; Ratcliffe 1977, Usher 1986). Similarly, patches of woodland within monotonous agricultural areas also produce a local increase in species diversity (Bedford and Usher 1994).

More specifically, the study on the distribution of predatory invertebrates at the boundary between forest and pasture has important implications for studies on field margins and crop pest control. Field margins are considered important reservoirs of many predatory arthropod species which feed on pests in crop fields (Sotherton 1985, Dennis and Fry 1992) and although these margins also act as reservoirs for the prey species/crop pests, the presence of the margins and their associated predatory species reduce the pest numbers (Mader 1988). Although the numbers of potential invertebrate predators crossing boundaries between habitats is not important when considering woodland and sheep pastures (this boundary was chosen for its physical properties, not its management and applied potential), it is important when the sheep pasture is replaced by a more valuable crop. Clearly the differences between a pasture or wheat field (low structural complexity) and a forest are too large to allow species from either main habitat to utilise the other (this study and Bedford and Usher 1994). However a narrow belt of vegetation with structural density intermediate between the two monocultures on either side of it could provide a refuge of species which would be more able to move into either habitat type as the structural differences between the margin and the monocultures are less extreme. Such habitats provide the main source of refugia to overwintering predators which alternate between field margins and arable crops on a seasonal timescale (Sotherton 1985). Dennis and Fry (1992) concluded that the margin vegetation cover that favoured arthropods and was beneficial from an agronomic viewpoint, comprised a dense, low herb layer, because such cover excluded the aggressive annual weeds of arable land which were harboured in disturbed field margins (Greaves and Marshall 1987).

The results in this thesis indicate that spiders might be a more useful group to study from a conservation perspective. They show much clearer variation between habitats (at both low and high altitudes), a necessary requirement for quantifying and monitoring environmental change (Rushton and Eyre 1992).

Summary

1. Aspects of the distribution and ecology of surface-dwelling spiders (Araneae) and carabid beetles (Coleoptera; Carabidae) were examined on different high-altitude vegetation communities in the north Pennines, England. The influence of boundaries between habitats on the spider and carabid communities within heterogeneous environments was also investigated.

2. The advantages and disadvantages of pitfall trapping are discussed, concluding that for this study they were the best method of sampling surface-dwelling spiders and carabid beetles. Also, a review of some of the common community analysis techniques was carried out, and the most appropriate species diversity index and methods of multivariate analysis were chosen in light of the aims of this study.

3. Thirteen sites representing the dominant vegetation types above 820m on the sub-montane plateaux of the Cross Fell and Dun Fell summits, Cumbria, were sampled by pitfall traps to examine their invertebrate fauna during 1991. This area is internationally important for its peatland and upland grassland habitats, and the summits form the largest area of high plateaux in England.

4. At each site, six pitfall traps (70mm mouth diameter) were placed in a line 2m apart. Several environmental variables were also collected, including aspects of local topography, soil characteristics and vegetation structure.

5. A total of 5921 spiders (including immatures) from six families and 56 species, and 3690 carabids from 22 species were taken from all 13 sites. The majority of spider species belonged to the family Linyphiidae (84%). All three fell tops showed high species similarity in their spider and carabid species composition (all comparisons using Sørensen's Index were greater than 70% similarity).

6. The average numbers of individuals, species richness and species diversity were calculated for both spiders and carabids from the pitfall catch. The mean number of spiders per pitfall at each site during 1991 varied from 34 - 122, and the carabids from 6 - 81. The mean number of species varied from 8 - 15 (spiders) and 3 - 9 (carabids), and species diversity using the reciprocal of Simpson's D, varied from 2.6 - 7.6 (spiders) and 1.6 - 4.5.

7. Two-way indicator species analysis (TWINSPAN) and detrended correspondence analysis (DCA) were used to classify and ordinate the sites based on their spider and carabid composition. Logarithmic counts were used throughout all analyses.

8. The 13 sites were split into three groups based on their spider fauna using TWINSPAN and DCA. Group A comprised four sites (dense vegetation sites), and the remainder (primarily shorter grassland sites) were split into Group B (two sites) and Group C (seven sites). The species which proposed this initial split was *Erigone dentipalpis*, which was relatively uncommon at Group A sites. Group B sites were separated from the Group C sites based on the higher abundance of *Centromerus prudens* in the Group B sites. The DCA ordination showed a similar separation of the sites, but indicated a higher degree of variation in species patterns within Group A.

9. TWINSPAN also produced three groups of sites based on their carabid fauna. Group A comprised two sites, and the remainder were split into Group B (three sites) and Group C (eight sites). The species producing the separation were *Notiophilus aquaticus* (absent at Group A sites) and *Pterostichus diligens* which showed a preference for Group B sites. The DCA ordination showed similarities with the classification, indicating Group A was different from the other groups, and that Group B sites were different from Group C sites.

10. Canonical correspondence analysis (CCA) was used to assess the influence of the measured environmental variables on the distribution of the spider and carabid species. Due to high multicollinearity, only three variables were used in the CCA; vegetation density, soil depth and site slope. This produced only three ordination axes.

11. The spider distribution was attributable to the three variables used in the CCA (Monte Carlo permutation test; $p < 0.01$ for both axis one and all three axes combined), with vegetation density having the most influence, then soil depth and slope in that order. The CCA ordination showed close similarities to the DCA, indicating a realistic assessment of the variables influencing the spider distribution.

12. The carabid distribution also showed a relationship with the three variables (Monte Carlo permutation test; $p < 0.02$ for axis 1. All three axes combined proved not significant). The lack of significance of the three axes and low

similarity with the DCA suggested that the carabid distribution was not realistically influenced by the three variables.

13. Three spider associations for the plateaux were proposed based on their common species composition. Two short *Festuca* grassland assemblages and a *Nardus/Eriophorum* assemblage associated with higher vegetation density. The species composition of the plateaux sites was compared to other upland habitats (from northern England and Sutherland, Scotland) using DCA. Strong differences were observed based on the summit study areas higher altitude. A comparison with high altitude spider communities from the Cairngorms, Scotland was also made.

14. Three carabid assemblages were also identified, although the degree of variation was lower than was found for the spiders, suggesting that most species were widespread. The species composition of the summit areas were however noticeably different in comparison with the other habitats from northern England and Scotland.

15. The influence of altitude on the species composition of the sub-montane areas and their high conservation importance are discussed in light of these findings.

16. To investigate the influence of the boundary between different habitat types on spider and carabid distribution, three study sites comprising a grass pasture used for sheep grazing bordering on a coniferous plantation were chosen to represent a sharp gradient between two structurally dissimilar habitats. Sampling was carried out during 1992.

17. The three sites were situated at Hamsterley, Bedburn and Standalone in west County Durham. The interface between the two habitat types was kept abrupt by a fence which allowed free movement of invertebrates crossing the boundary.

18. At each site 30 pitfall traps were operated, 15 in each habitat on either side of the interface. The traps were arranged in six rows of five traps in a line, 3m apart within each row. Row G3 was placed 11m from the interface in the grass pasture, row G2 was placed 1m from the interface and row G1 placed at the interface. Rows P1, P2 and P3 were placed at corresponding positions inside the plantation.

19. The spider and carabid catches from each site were compared, and then considered replicates and combined. Seasonal trends within both groups using pitfall traps were similar at each site, though there was variation in the total numbers taken.

20. A total of 14 143 adult spiders belonging to 127 species (13 families) and 11 859 carabid beetles belonging to 46 species were taken from all three sites. A total of 1844 immature spiders were also taken but not identified. The majority of the spider species belonged to the family Linyphiidae (71%).

21. Significantly more specimens of spiders and carabids were taken from the pasture trap rows than were taken from the plantation rows (102% more spiders and 165% more carabids). The variation across the transect was further broken down into the different row positions and significant differences between row positions was shown using ANOVA and Duncan's multiple range tests.

22. The mean number of individuals of spiders per pitfall trap progressively decreased from the pasture across the interface to the plantation habitat. The number of carabids trapped was highest at the pasture side of the interface (row G1), and lowest in the plantation. The mean number of species in both groups was highest close to the interface on the pasture side (spiders 36 ± 3 at row G1; carabids 17 ± 1 at row G2). Mean species diversity in the spiders was similar to the species richness results, but the carabids indicated a drop in diversity at the interface.

23. Cluster analysis on the spider distribution indicated that most species were present at all row positions, but that several species were considered common at specific areas of the transect. The carabids showed similar results, but the species taken were more widespread across the rows than the spiders. Distinct species assemblages were found in the pasture and plantation habitats based on the relative abundance from pitfall traps.

24. The common spider and carabid species were classified into six categories based on their habitat preference and also the influence of the non-preferred habitat (50 spider species and 23 carabid species were categorised). It was found that the variations in species richness and diversity across the transect were primarily attributable to both the overlap of pasture and plantation preferring species at the interface. The proportion of species in both groups classed as preferring the

ecotone was low, never comprising the majority of species at any row including the interface.

25. It was concluded that the variation in physical and biological characteristics which the interface induced were the main influences on the spider and carabid species. Factors such as edge permeability, habitat size and structural similarity are important in controlling their distribution and movement.

26. The same methods were used to investigate the influence of the boundary between two much more similar habitats, at an exclosure on the *Festuca* grassland dominated summit of Little Dun Fell during 1993. The fenced exclosure measured 40m by 40m, and excluded sheep from grazing that area. Pitfall traps rows were labelled O1 to O3 (outside the exclosure) and I1 to I3 (inside).

27. The exclusion of sheep in the exclosure since 1955 had altered the vegetation content and structure of the plants, increasing the diversity and structural density within it. This produced a pronounced three-fold increase in density and four-fold increase in sward height within the exclosure. The gradient between these habitats was considered more similar in structure and microclimate than the extreme variation between pasture and plantation.

28. The seasonal distribution of the spiders and carabids showed peaks in total numbers trapped in June, and spiders showed a second peak in late August and September.

29. A total of 3972 adult spiders belonging to 56 species (5 families) and 2426 carabids from 18 species were taken in the pitfall traps. A total of 387 immature spiders were also taken but not identified. As found in other upland spider studies, the majority of species belonged to the Linyphiidae (88% of the species and 99% of the specimens trapped).

30. Significantly more specimens of carabid were trapped inside the denser vegetation of the exclosure (69%), but the numbers of spider taken inside was not significantly larger (19%).

31. There were no significant differences in mean number of individuals of spider or species richness at each row position across the transect, but diversity was greatest outside the exclosure at row O2 ($F_{5,24} = 6.2$, $p < 0.01$). The numbers of

individuals of carabids was significantly greater inside the exclosure, but species richness did not significantly vary across the transect. Carabid species diversity was greatest at row O2, and there was significant variation across the transect, with the lowest value at row I1.

32. Cluster analysis indicated that most species of spider and carabid were present at all row positions and that only a few species showed preferences for specific parts of the transect. Most of the common species were abundant at all rows and the cluster analysis could not differentiate at this high level of abundance.

33. A total of 23 spider species and 8 carabids were categorised as having a specific distribution across the transect. No species in either group were found to prefer the ecotone. The majority of spider and carabid species showed a preference for the exclosure vegetation, and they were found in high numbers at row O3, furthest from the exclosure. Festuca grassland species in both groups reduced in numbers approaching the interface, and were extremely low inside the exclosure. There were 7 widespread spider species (31%), but no widespread carabids.

34. The high similarity of the vegetation and therefore high edge permeability was considered the most important reason for the general widespread nature of the invertebrate communities across the transect.

35. The implications that this study has for understanding the effects of habitat heterogeneity at the landscape level are discussed, such as invertebrate movement patterns, population dynamics and management aspects.

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Appendix 1a. The numbers of different adult spider species recorded at 13 sites from Cross Fell (CF1 - 7), Little Dun Fell (LDF1 - 3) and Great Dun Fell (GDF1 - 7) during 1991.

Appendix 1b. The numbers of different carabid species recorded at 13 sites from Cross Fell (CF1 - 7), Little Dun Fell (LDF1 - 3) and Great Dun Fell (GDF1 - 7) during 1991.

Appendix 2a. The numbers of different adult spider species recorded at each row position at boundary site A, during 1992.

Appendix 2b. The numbers of different adult spider species recorded at each row position at boundary site B, during 1992.

Appendix 2c. The numbers of different adult spider species recorded at each row position at boundary site C, during 1992.

Appendix 2d. The numbers of different carabid species recorded at each row position at boundary site A, during 1992.

Appendix 2e. The numbers of different carabid species recorded at each row position at boundary site B, during 1992.

Appendix 2f. The numbers of different carabid species recorded at each row position at boundary site C, during 1992.

Appendix 3a. The numbers of different adult spider species recorded at each row position at the Little Dun Fell boundary transect during 1992.

Appendix 3b. The numbers of different carabid species recorded at each row position at the Little Dun Fell boundary transect during 1992.

Appendix 1a. The numbers of different adult spider species recorded at 13 sites from Cross Fell (CF1 - 7), Little Dun Fell (LDF1 - 3) and Great Dun Fell (GDF1 - 3) during 1991.

	CF1	CF2	CF3	CF4	CF5	CF6	CF7	LDF1	LDF2	LDF3	GDF1	GDF2	GDF3	Total
CLUBIONIDAE														
Clubiona diversa O.P.-Cambridge, 1862				1										1
THOMISIDAE														
Xysticus cristatus (Clerck, 1757)	1		1		1				1				1	5
Xysticus sabulosus (Hahn, 1832)			1											1
LYCOSIDAE														
Pardosa monticola (Clerck, 1757)	3	4	5		12			2	2		2		1	31
Pardosa pullata (Clerck, 1757)		4			1	2	1			2	2		1	13
Alopecosa pulverulenta (Clerck, 1757)		4			4	1		1			1		1	12
Pirata piraticus (Clerck, 1757)						1								1
HAHNIIDAE														
Antistea elegans (Blackwall, 1841)							1							1
THERIDIIDAE														
Robertus lividus (Blackwall, 1836)												1		1
LINYPHIIDAE														
Ceratinella brevipes (Westring, 1851)			1					1			1			3
Walckenaeria nudipalpis (Westring, 1851)	8		2		1	3	1	1	3		2	1		22
Walckenaeria antica (Wider, 1834)	1							1		1				3
Walckenaeria clavicornis (Emerton, 1882)	26	40	21	7	3	4	19	16	10	18	8	8	30	210
Walckenaeria cuspidata (Blackwall, 1833)			1	1	57	14	10	1	1	1		15	5	106
Walckenaeria capito (Westring, 1861)				1										1
Walckenaeria acuminata Blackwall, 1833										1				1
Dicymbium nigrum f. *brevisetosum* Locket, 1962	1						1			3		2		7
Dicymbium tibiale (Blackwall, 1836)								1					3	4
Hypomma bituberculatum (Wider, 1834)	1													1
Gonatium rubens (Blackwall, 1833)											1			1
Oedothorax fuscus (Blackwall, 1834)	2		7	3	8		2	3	5	3			1	34
Oedothorax agrestis (Blackwall, 1853)										1				1
Oedothorax retusus (Westring, 1851)	9		4	1	1	1	1	2	3	1			1	24
Pelecopsis mengei (Simon, 1884)	1	2		2			2	5	2	2	1	1		18

cont.

	CF1	CF2	CF3	CF4	CF5	CF6	CF7	LDF1	LDF2	LDF3	GDF1	GDF2	GDF3	Total
Silometopus elegans (O.P.-Cambridge, 1872)	6	2	32	118		28	36	116	51	1	3		2	395
Tiso vagans (Blackwall, 1834)		1				1	1	1	1				1	6
Monocephalus fuscipes (Blackwall, 1836)	2													2
Monocephalus castaneipes (Simon, 1884)								1						1
Lophomma punctatum (Blackwall, 1841)													1	1
Micrargus herbigradus (Blackwall, 1854)		8									1			9
Erigonella hiemalis (Blackwall, 1841)		2			2									4
Savignya frontata (Blackwall, 1833)	3		10	8	7	3	3	3	10	9	1	3	10	70
Diplocephalus permixtus (O.P.-Cambridge, 1871)				1		73	34	3			27			138
Araeoncus crassipes (Westring, 1861)				2				1	1	2		1		7
Typhochrestus digitatus (O.P.-Cambridge, 1872)									2	1			1	4
Erigone dentipalpis (Wider, 1834)	77	6	75	42	60	5	26	118	133	82	3	9	67	703
Erigone promiscua (O.P.-Cambridge, 1872)	263	4	72	7	90	5	32	95	98	443	18	90	237	1454
Erigone atra (Blackwall, 1841)	59	3	56	18	55	12	31	56	81	89	3	29	29	521
Rhaebothorax morulus (O.P.-Cambridge, 1873)				1	1			1	1	1				5
Semljicola caliginosa (Falconer, 1910)	1		1			15			6	1	79	7	2	112
Leptorhoptrum robustum (Westring, 1851)													2	2
Drepanotylus uncatus (O.P.-Cambridge, 1873)		1			2	10	2		2		19	19		55
Leptothrix hardyi (Blackwall, 1850)	1													1
Hilaira frigida (Thorell, 1872)	63	105	73	51	19	27	18	41	33	15	17	8	88	558
Hilaira nubigena Hull, 1911					1	7					36	2		46
Porrhomma pallidum Jackson, 1913				1				1	1					3
Agyneta conigera (O.P.-Cambridge, 1863)			1											1
Meioneta gulosa (L. Koch, 1869)	1		3	4			1	4	6	2			1	22
Centromerus prudens (O.P.-Cambridge, 1873)		1	8	19	3	1	1	10	4	3			2	52
Centromerita bicolor (Blackwall, 1833)	20	17	4	3	17	64	39	5	12	15	24	2	15	237
Centromerita concinna (Thorell, 1875)	18	35	28	14	33	3	1	20	16	27	2	3	13	213
Oreonetides vaginatus (Thorell, 1872)	14	3	1	3	7	1	1	14	22	4			38	108
Bathyphantes gracilis (Blackwall, 1841)	3	3	5		1	4	1	3	3	1	22	1	7	54
Lepthyphantes mengei Kulczynski, 1887			1			1	1		2					5
Lepthyphantes angulatus (O.P.-Cambridge, 1881)		28		1	1	2	1	1		1	6		1	42
Allomengea scopigera (Grube, 1859)											1			1
Total at each site	584	273	413	307	387	288	267	528	512	730	280	202	560	5334
Number of species	24	20	24	23	24	25	26	30	28	27	24	18	27	56

Appendix 1b. The numbers of different carabid species recorded at 13 sites from Cross Fell (CF1 - 7), Little Dun Fell (LDF1 - 3) and Great Dun Fell (GDF1 - 3) during 1991.

	CF1	CF2	CF3	CF4	CF5	CF6	CF7	LDF1	LDF2	LDF3	GDF1	GDF2	GDF3	Total
Carabus problematicus Herbst, 1786	19	31	9	6	36	37	75	46	27	24	25	3	36	374
Leistus rufescens (Fabricius, 1775)								6		8	8			22
Nebria gyllenhali (Schoenherr, 1806)	103	188	205	248	36	65	105	7	1	14	3	1	67	1043
Nebria salina Fairmaire & Laboulbene, 1856		1	3											4
Notiophilus aestuans (Motschulsky, 1864)	1				3	1		1					1	7
Notiophilus aquaticus (Linnaeus, 1758)	57	14	49	10	158	2	13	25	28	10			22	388
Notiophilus biguttatus (Fabricius, 1779)	16	8	2	2	21	13	15	3	1		2		4	87
Notiophilus germinyi Fauvel, 1863	17	1	6	1	82	1	3	136	26	119	1	5	97	495
Loricera pilicornis (Fabricius, 1775)	3	21	1		6	73	136	1		1	36	3	11	292
Miscodera arctica (Paykull, 1798)													1	1
Patrobus assimilis Chaudoir, 1844	62	57	48	42	115	53	62	90	63	90	16	12	86	796
Trechus obtusus Erichson, 1837	26	23	13	3	7		1	2	5	2	1		12	95
Bembidion aeneum Germar, 1824												1	2	3
Bembidion guttula (Fabricius, 1792)											1	5		6
Bembidion lunulatum (Fourcroy, 1785)												1		1
Pterostichus adstrictus Eschscholtz, 1823		1							1	1				3
Pterostichus diligens (Sturm, 1824)	1				1	1		14	6	8	3	2	2	38
Pterostichus madidus (Fabricius, 1775)									1					1
Calathus melanocephalus (Linnaeus, 1758)			2	3	20			2	2				1	30
Olisthopus rotundatus (Paykull, 1790)		1											1	2
Amara lunicollis Schiödte, 1837													1	1
Bradycellus harpalinus (Serville, 1821)													1	1
Total at each site	305	346	338	315	485	246	410	333	161	277	96	33	345	3690
Number of species	10	11	10	8	11	9	8	12	11	10	10	9	16	22

Appendix 2a. The numbers of different adult spider species recorded at each row position at boundary site A, during 1992.

	G3	G2	G1	P1	P2	P3	Total
AMAUROBIIDAE							
Amaurobius fenestralis (Stroem, 1768)	1	5	69	244	44	38	401
SEGESTRIIDAE							
Segestria senoculata (Linnaeus, 1758)			1				1
GNAPHOSIDAE							
Drassodes cupreus (Blackwall, 1834)		22	43	17	4		86
Haplodrassus signifer (C.L.Koch, 1839)		14	31	28	9		82
Micaria pulicaria (Sundevall, 1831)		8	21	1			30
CLUBIONIDAE							
Clubiona lutescens Westring, 1851	1	1					2
Clubiona compta C.L.Koch, 1839					1	1	2
Clubiona diversa O.P.-Cambridge, 1862					1		1
Agroeca proxima (O.P.-Cambridge, 1871)		3	8	3	3	1	18
Scotina gracilipes (Blackwall, 1859)				1	1		2
ZORIDAE							
Zora spinimana (Sundevall, 1833)	1					1	2
THOMISIDAE							
Xysticus cristatus (Clerck, 1757)	5	29	14	6	1		55
Oxyptila atomaria (Panzer, 1810)		2	2	2			6
SALTICIDAE							
Heliophanus flavipes (Hahn, 1832)			1				1
Neon reticulatus (Blackwall, 1853)				1			1
LYCOSIDAE							
Pardosa monticola (Clerck, 1757)	9	1	5	1	1		17
Pardosa palustris (Linnaeus, 1758)	33	39	14	9	4		99
Pardosa pullata (Clerck, 1757)	43	404	204	106	27	9	793
Pardosa amentata (Clerck, 1757)	7	9	9	11	2		38
Pardosa nigriceps (Thorell, 1856)	8	7	2	3	1	1	22
Pardosa lugubris (Walckenaer, 1802)				2			2
Alopecosa pulverulenta (Clerck, 1757)	36	82	59	20	6	3	206
Trochosa terricola Thorell, 1856	5	53	12	5	7	1	83

cont.

	G3	G2	G1	P1	P2	P3	Total
AGELENIDAE							
Textrix denticulata (Olivier, 1789)					2		2
Coelotes atropos (Walckenaer, 1825)	2	39	104	84	117	125	471
Cryphoeca silvicola (C.L.Koch, 1834)		3	16	107	112	18	256
MIMETIDAE							
Ero furcata (Villers, 1789)				1	1		2
THERIDIIDAE							
Enoplognatha ovata (Clerck, 1757)		1		1			2
Pholcomma gibbum (Westring, 1851)						1	1
TETRAGNATHIDAE							
Pachygnatha clercki Sundevall, 1823	3						3
Pachygnatha degeeri Sundevall, 1830	575	803	166	22	5	1	1572
Meta segmentata (Clerck, 1757)			2	3			5
Meta mengei (Blackwall, 1869)		1			2		3
LINYPHIIDAE							
Ceratinella brevipes (Westring, 1851)			2			1	3
Walckenaeria vigilax (Blackwall, 1853)	1						1
Walckenaeria cucullata (C.L.Koch, 1836)			2	2			4
Walckenaeria unicornis O.P.-Cambridge, 1861		1					1
Walckenaeria monoceros (Wider, 1834)			1				1
Walckenaeria acuminata Blackwall, 1833	3	4	12	7	8	12	46
Dicymbium nigrum f. *brevisetosum* Locket, 1962	14	47	18	10	1		90
Dicymbium tibiale (Blackwall, 1836)		2					2
Dismodicus bifrons (Blackwall, 1841)			1				1
Gonatium rubens (Blackwall, 1833)					1	1	2
Pocadicnemis juncea Locket & Millidge, 1953		1					1
Oedothorax fuscus (Blackwall, 1834)	377	32	4	1	1		415
Oedothorax retusus (Westring, 1851)	12	2	4	1			19
Silometopus elegans (O.P.-Cambridge, 1872)	5				1		6
Cnephalocotes obscurus (Blackwall, 1834)	1	15	3	2			21
Tiso vagans (Blackwall, 1834)	3	13	18		2		36
Tapinocyba praecox (O.P.-Cambridge, 1873)		17	2	1			20
Tapinocyba pallens (O.P.-Cambridge, 1872)		6	3	3	17	20	49
Monocephalus fuscipes (Blackwall, 1836)		2	4	7	6	5	24
Gongylidiellum vivum (O.P.-Cambridge, 1875)	1						1

cont.

	G3	G2	G1	P1	P2	P3	Total
Micrargus herbigradus (Blackwall, 1854)		3			2	2	7
Micrargus apertus (O.P.-Cambridge, 1870)					2		2
Erigonella hiemalis (Blackwall, 1841)		4	3			1	8
Savignya frontata (Blackwall, 1833)	12	10	7	6	1		36
Diplocephalus cristatus (Blackwall, 1833)			1				1
Diplocephalus picinus (Blackwall, 1841)					2		2
Milleriana inerrans (O.P.-Cambridge, 1884)	8	4	1				13
Erigone dentipalpis (Wider, 1834)	438	155	26	2	2	1	624
Erigone atra (Blackwall, 1841)	57	11	12	7	4		91
Porrhomma pygmaeum (Blackwall, 1834)			1	1			2
Porrhomma pallidum Jackson, 1913	1		1				2
Agyneta subtilis (O.P.-Cambridge, 1863)	1						1
Agyneta conigera (O.P.-Cambridge, 1863)						1	1
Meioneta rurestris (C.L.Koch, 1836)	3	1	2	3	1		10
Centromerus sylvaticus (Blackwall, 1841)						2	2
Centromerus prudens (O.P.-Cambridge, 1873)		5	5	9	10	2	31
Centromerus dilutus (O.P.-Cambridge, 1875)					1	2	3
Centromerita bicolor (Blackwall, 1833)	3	6	6	1			16
Centromerita concinna (Thorell, 1875)	1	4	6	2			13
Sintula cornigera (Blackwall, 1856)						1	1
Oreonetides vaginatus (Thorell, 1872)			1				1
Saaristoa abnormis (Blackwall, 1841)			2		2	6	10
Macrargus rufus (Wider, 1834)			1		4	7	12
Bathyphantes gracilis (Blackwall, 1841)	5	1			3	2	11
Bathyphantes parvulus (Westring, 1851)				1			1
Diplostyla concolor (Wider, 1834)			1	2			3
Drapetisca socialis (Sundevall, 1832)				2	1	2	5
Tapinopa longidens (Wider, 1834)		1	3	2	9	4	19
Labulla thoracica (Wider, 1834)				4	2		6
Stemonyphantes lineatus (Linnaeus, 1758)		2	8	5	2		17
Bolyphantes luteolus (Blackwall, 1843)			1				1
Bolyphantes alticeps (Sundevall, 1832)		2	2	8	10	3	25
Lepthyphantes minutus (Blackwall, 1833)			3	10	6	18	37
Lepthyphantes alacris (Blackwall, 1853)				2	3	1	6
Lepthyphantes obscurus (Blackwall, 1841)		1					1

cont.

	G3	G2	G1	P1	P2	P3	Total
Lepthyphantes tenuis (Blackwall, 1842)	9	23	6	14	21	4	77
Lepthyphantes zimmermanni Bertkau, 1890		2		14	73	112	201
Lepthyphantes tenebricola (Wider, 1834)					1		1
Lepthyphantes ericaeus (Blackwall, 1853)	2	1	2	3	8	10	26
Lepthyphantes pallidus (O.P.-Cambridge, 1871)	2	2	2	8	11	11	36
Lepthyphantes expunctus (O.P.-Cambridge, 1875)					1		1
Linyphia triangularis (Clerck, 1757)			3	1	1		5
Linyphia hortensis Sundevall, 1829				1	1		2
Neriene clathrata (Sundevall, 1829)			2		2		4
Neriene peltata (Wider, 1834)		2			1		3
Total at each site	1688	1908	965	820	575	431	6387
Number of species	70	118	119	120	118	113	99

Appendix 2b. The numbers of different adult spider species recorded at each row position at boundary site B, during 1992.

	G3	G2	G1	P1	P2	P3	Total
AMAUROBIIDAE							
Amaurobius fenestralis (Stroem, 1768)		1	3	1	18	9	32
GNAPHOSIDAE							
Drassodes cupreus (Blackwall, 1834)			3	2			5
Haplodrassus signifer (C.L.Koch, 1839)			1	1			2
Micaria pulicaria (Sundevall, 1831)				1			1
CLUBIONIDAE							
Clubiona lutescens Westring, 1851					1		1
Clubiona compta C.L.Koch, 1839						1	1
Agroeca proxima (O.P.-Cambridge, 1871)			2	9			11
LYCOSIDAE							
Pardosa monticola (Clerck, 1757)	1						1
Pardosa palustris (Linnaeus, 1758)	2	1					3
Pardosa pullata (Clerck, 1757)	8	28	9	15	1		61
Pardosa amentata (Clerck, 1757)	12	39	44	63			158
Pardosa nigriceps (Thorell, 1856)	1	6	2	1			10
Pardosa lugubris (Walckenaer, 1802)				3	1		4
Alopecosa pulverulenta (Clerck, 1757)	3	13	9	2			27
Trochosa terricola Thorell, 1856			1				1
AGELENIDAE							
Coelotes atropos (Walckenaer, 1825)			1	1		1	3
Cryphoeca silvicola (C.L.Koch, 1834)				3	103	127	233
MIMETIDAE							
Ero furcata (Villers, 1789)			1				1
THERIDIIDAE							
Robertus lividus (Blackwall, 1836)	1				1		2
TETRAGNATHIDAE							
Pachygnatha degeeri Sundevall, 1830	28	19	15	1			63
Meta mengei (Blackwall, 1869)				1			1
LINYPHIIDAE							
Ceratinella brevipes (Westring, 1851)		1		2			3
Walckenaeria nudipalpis (Westring, 1851)				1			1

cont

	G3	G2	G1	P1	P2	P3	Total
Walckenaeria cucullata (C.L.Koch, 1836)				18	11	9	38
Walckenaeria cuspidata (Blackwall, 1833)			1	1	1	1	4
Walckenaeria acuminata Blackwall, 1833			1	4			5
Dicymbium nigrum f. *brevisetosum* Locket, 1962	2	6	5	1		1	15
Dismodicus bifrons (Blackwall, 1841)		1		1			2
Metopobactrus prominulus (O.P.-Cambridge, 1872)			1				1
Gonatium rubens (Blackwall, 1833)		1		8		1	10
Maso sundevalli (Westring, 1851)		1		20	2		23
Pocadicnemis pumila (Blackwall, 1841)			1	2			3
Pocadicnemis juncea Locket & Millidge, 1953		1	3	14			18
Oedothorax fuscus (Blackwall, 1834)	353	41	20				414
Oedothorax retusus (Westring, 1851)	4	1	3				8
Trichopterna thorelli (Westring, 1861)		1	1				2
Silometopus elegans (O.P.-Cambridge, 1872)		1	1				2
Cnephalocotes obscurus (Blackwall, 1834)		2	2	4			8
Tiso vagans (Blackwall, 1834)		1	1				2
Minyriolus pusillus (Wider, 1834)						2	2
Tapinocyba praecox (O.P.-Cambridge, 1873)				2	1		3
Tapinocyba pallens (O.P.-Cambridge, 1872)			1	16	20	32	69
Monocephalus fuscipes (Blackwall, 1836)	1	3		31	20	37	92
Gongylidiellum vivum (O.P.-Cambridge, 1875)		1	1				2
Micrargus apertus (O.P.-Cambridge, 1870)				1			1
Savignya frontata (Blackwall, 1833)	7	6	6	6			25
Diplocephalus latifrons (O.P.-Cambridge, 1863)				1	1	2	4
Diplocephalus picinus (Blackwall, 1841)					6	5	11
Araeoncus humilis (Blackwall, 1841)			1				1
Milleriana inerrans (O.P.-Cambridge, 1884)	2	1	5			1	9
Erigone dentipalpis (Wider, 1834)	271	213	109				593
Erigone atra (Blackwall, 1841)	60	68	53		2		183
Leptorhoptrum robustum (Westring, 1851)		1					1
Porrhomma pygmaeum (Blackwall, 1834)	3	4		1		2	10
Porrhomma pallidum Jackson, 1913	1	5	1	3	2	1	13
Porrhomma campbelli F.O.P.-Cambridge, 1894		1	2	2			5
Porrhomma microphthalmum (O.P.-Cambridge, 1871)	2		1	2			5
Meioneta rurestris (C.L.Koch, 1836)	4	10	15	3		1	33

cont

	G3	G2	G1	P1	P2	P3	Total
Meioneta saxatilis (Blackwall, 1844)		2	2	24			28
Centromerus sylvaticus (Blackwall, 1841)				2			2
Centromerus prudens (O.P.-Cambridge, 1873)					1		1
Centromerita bicolor (Blackwall, 1833)		2	2	1			5
Sintula cornigera (Blackwall, 1856)	1				2		3
Saaristoa abnormis (Blackwall, 1841)			1		3	1	5
Macrargus rufus (Wider, 1834)			1	3	7	1	12
Bathyphantes gracilis (Blackwall, 1841)	21	44	30	34	1		130
Bathyphantes parvulus (Westring, 1851)	4	5	3	16			28
Bathyphantes nigrinus (Westring, 1851)		1		2			3
Diplostyla concolor (Wider, 1834)		1	1	7			9
Drapetisca socialis (Sundevall, 1832)					2	3	5
Tapinopa longidens (Wider, 1834)				5	5	2	12
Labulla thoracica (Wider, 1834)				3	4	6	13
Stemonyphantes lineatus (Linnaeus, 1758)		1	1	4			6
Bolyphantes alticeps (Sundevall, 1832)				23	1		24
Lepthyphantes minutus (Blackwall, 1833)				1	5	1	7
Lepthyphantes alacris (Blackwall, 1853)					4	2	6
Lepthyphantes obscurus (Blackwall, 1841)				1	1	6	8
Lepthyphantes tenuis (Blackwall, 1842)	42	47	47	61	8	13	218
Lepthyphantes zimmermanni Bertkau, 1890	7	5	9	111	107	79	318
Lepthyphantes mengei Kulczynski, 1887				2	1		3
Lepthyphantes tenebricola (Wider, 1834)				5	2	9	16
Lepthyphantes ericaeus (Blackwall, 1853)			4	26	2	2	34
Lepthyphantes pallidus (O.P.-Cambridge, 1871)	1	2	3	29	32	23	90
Lepthyphantes expunctus (O.P.-Cambridge, 1875)					1	1	2
Helophora insignis (Blackwall, 1841)				1			1
Pityohyphantes phrygianus (C.L.Koch, 1836)				3	2	2	7
Linyphia triangularis (Clerck, 1757)					1		1
Linyphia hortensis Sundevall, 1829				2			2
Neriene clathrata (Sundevall, 1829)		1	5	5	5	2	18
Neriene peltata (Wider, 1834)		4	5	3	1		13
Allomengea scopigera (Grube, 1859)		1	2	2			5
Total at each site	842	594	442	624	389	386	3277
Number of species	26	43	50	63	39	33	91

Appendix 2c. The numbers of different adult spider species recorded at each row position at boundary site C, during 1992.

	G3	G2	G1	P1	P2	P3	Total
AMAUROBIIDAE							
Amaurobius fenestralis (Stroem, 1768)		2				1	3
SEGESTRIIDAE							
Segestria senoculata (Linnaeus, 1758)			1				1
GNAPHOSIDAE							
Drassodes cupreus (Blackwall, 1834)	1	2	9	2		1	15
Haplodrassus signifer (C.L.Koch, 1839)			10			1	11
Micaria pulicaria (Sundevall, 1831)			1				1
CLUBIONIDAE							
Clubiona reclusa O.P.-Cambridge, 1863			1				1
Clubiona lutescens Westring, 1851				1			1
Clubiona diversa O.P.-Cambridge, 1862	1		1				2
Agroeca proxima (O.P.-Cambridge, 1871)		3	17	3			23
THOMISIDAE							
Xysticus cristatus (Clerck, 1757)	2						2
LYCOSIDAE							
Pardosa monticola (Clerck, 1757)	2		1				3
Pardosa palustris (Linnaeus, 1758)	23		1				24
Pardosa pullata (Clerck, 1757)	43	4	6	1	1		55
Pardosa amentata (Clerck, 1757)	3	3	4		2		12
Pardosa nigriceps (Thorell, 1856)	16	8	6	3	3		36
Alopecosa pulverulenta (Clerck, 1757)	5	1					6
Trochosa terricola Thorell, 1856	2	5	3	1			11
AGELENIDAE							
Coelotes atropos (Walckenaer, 1825)			2	3		2	7
Cryphoeca silvicola (C.L.Koch, 1834)	1	1	2	2	3		9
MIMETIDAE							
Ero furcata (Villers, 1789)			6	3		4	13
THERIDIIDAE							
Robertus lividus (Blackwall, 1836)	2	2	15	32	16	14	81
Robertus neglectus (O.P.-Cambridge, 1871)			1	1			2
Pholcomma gibbum (Westring, 1851)	1	1			2	5	9

cont.

	G3	G2	G1	P1	P2	P3	Total
TETRAGNATHIDAE							
Pachygnatha degeeri Sundevall, 1830	37	27	28	5			97
Meta segmentata (Clerck, 1757)			4	2			6
Meta mengei (Blackwall, 1869)			2		4	2	8
LINYPHIIDAE							
Ceratinella brevipes (Westring, 1851)	2	7	38	14	4	14	79
Walckenaeria nudipalpis (Westring, 1851)	1		9	3	2	1	16
Walckenaeria vigilax (Blackwall, 1853)	2	2	2				6
Walckenaeria antica (Wider, 1834)			1				1
Walckenaeria cucullata (C.L.Koch, 1836)			1	1			2
Walckenaeria cuspidata (Blackwall, 1833)			4		2	1	7
Walckenaeria unicornis O.P.-Cambridge, 1861	1		6	1	1	4	13
Walckenaeria acuminata Blackwall, 1833		9	40	27	9	15	100
Dicymbium nigrum f. *brevisetosum* Locket, 1962	11	13	13				37
Dismodicus bifrons (Blackwall, 1841)					1		1
Metopobactrus prominulus (O.P.-Cambridge, 1872)		1	11	10	3	4	29
Gonatium rubens (Blackwall, 1833)	1	2	14	13		5	35
Maso sundevalli (Westring, 1851)					2	5	7
Pocadicnemis pumila (Blackwall, 1841)	2	3	7	5	1	2	20
Pocadicnemis juncea Locket & Millidge, 1953		1		1			2
Oedothorax fuscus (Blackwall, 1834)	98	38	3				139
Oedothorax retusus (Westring, 1851)	5	5	1				11
Pelecopsis mengei (Simon, 1884)				1			1
Silometopus elegans (O.P.-Cambridge, 1872)	4						4
Cnephalocotes obscurus (Blackwall, 1834)		4	5	1	1	1	12
Evansia merens O.P.-Cambridge, 1900			1				1
Tiso vagans (Blackwall, 1834)	2						2
Minyriolus pusillus (Wider, 1834)			1	1		2	4
Tapinocyba praecox (O.P.-Cambridge, 1873)			2	1			3
Tapinocyba pallens (O.P.-Cambridge, 1872)			18	45	20	4	87
Monocephalus fuscipes (Blackwall, 1836)		3	16	15	6	13	53
Gongylidiellum vivum (O.P.-Cambridge, 1875)			1				1
Micrargus herbigradus (Blackwall, 1854)	1		3		2	2	8
Micrargus apertus (O.P.-Cambridge, 1870)	1	1	5	1	1	1	10
Micrargus subaequalis (Westring, 1851)	1						1

cont.

	G3	G2	G1	P1	P2	P3	Total
Erigonella hiemalis (Blackwall, 1841)		7	1			1	9
Savignya frontata (Blackwall, 1833)	38	73	82	15	3	2	213
Diplocephalus latifrons (O.P.-Cambridge, 1863)	1		1	1		1	4
Diplocephalus picinus (Blackwall, 1841)					2	2	4
Milleriana inerrans (O.P.-Cambridge, 1884)	2	2	1	1			6
Erigone dentipalpis (Wider, 1834)	715	297	59	1			1072
Erigone atra (Blackwall, 1841)	101	125	53	5	2		286
Ostearius melanopygius (O.P.-Cambridge, 1879)	1	2					3
Porrhomma pygmaeum (Blackwall, 1834)	3	1	5	3			12
Porrhomma pallidum Jackson, 1913	6	1	6	4	3	1	21
Porrhomma campbelli F.O.P.-Cambridge, 1894		2	1	2			5
Porrhomma microphthalmum (O.P.-Cambridge, 1871)		1	1	1			3
Agyneta subtilis (O.P.-Cambridge, 1863)	3			1			4
Agyneta conigera (O.P.-Cambridge, 1863)		3	67	44	36	12	162
Meioneta rurestris (C.L.Koch, 1836)	21	3	2	1	1		28
Meioneta saxatilis (Blackwall, 1844)		1	2				3
Microneta viaria (Blackwall, 1841)		1	1	1	1	3	7
Centromerus sylvaticus (Blackwall, 1841)		1	8	1	1	3	14
Centromerus prudens (O.P.-Cambridge, 1873)		1	6	2	1	1	11
Centromerus dilutus (O.P.-Cambridge, 1875)				4	5		9
Centromerita bicolor (Blackwall, 1833)	3		9				12
Centromerita concinna (Thorell, 1875)			3				3
Sintula cornigera (Blackwall, 1856)		3	30	42	22	12	109
Saaristoa abnormis (Blackwall, 1841)			2	5	3	2	12
Macrargus rufus (Wider, 1834)			3				3
Bathyphantes gracilis (Blackwall, 1841)	2	7	11	7	2		29
Bathyphantes parvulus (Westring, 1851)	1		16		2	2	21
Diplostyla concolor (Wider, 1834)		5	20	7	1		33
Poeciloneta globosa (Wider, 1834)		1	4	1	1	1	8
Drapetisca socialis (Sundevall, 1832)				1	2	5	8
Tapinopa longidens (Wider, 1834)			14	12	5	9	40
Labulla thoracica (Wider, 1834)			14	5	3	2	24
Stemonyphantes lineatus (Linnaeus, 1758)			2	1			3
Bolyphantes alticeps (Sundevall, 1832)			13	4			17
Lepthyphantes minutus (Blackwall, 1833)			1		1	2	4

cont.

	G3	G2	G1	P1	P2	P3	Total
Lepthyphantes alacris (Blackwall, 1853)			1	2	5	7	15
Lepthyphantes obscurus (Blackwall, 1841)		1		2	4	3	10
Lepthyphantes tenuis (Blackwall, 1842)	12	34	80	49	23	22	220
Lepthyphantes zimmermanni Bertkau, 1890	3	23	189	172	115	207	709
Lepthyphantes mengei Kulczynski, 1887		1		1	1		3
Lepthyphantes tenebricola (Wider, 1834)				1	1		2
Lepthyphantes ericaeus (Blackwall, 1853)	1		6	9	6	10	32
Lepthyphantes pallidus (O.P.-Cambridge, 1871)			13	16	8	5	42
Lepthyphantes expunctus (O.P.-Cambridge, 1875)		1	3		1	3	8
Helophora insignis (Blackwall, 1841)		1	5	4	10	44	64
Pityohyphantes phrygianus (C.L.Koch, 1836)						1	1
Linyphia triangularis (Clerck, 1757)			4	8	2		14
Neriene clathrata (Sundevall, 1829)		2	4	2	1	2	11
Neriene peltata (Wider, 1834)		1	2	1	2		6
Microlinyphia pusilla (Sundevall, 1829)		1				1	2
Allomengea scopigera (Grube, 1859)		1	4	1	1		7
Total at each site	1184	751	1072	639	363	470	4479
Number of species	44	55	85	68	55	51	107

Appendix 2d. The numbers of different carabid species recorded at each row position at boundary site A, during 1992.

	G3	G2	G1	P1	P2	P3	Total
Carabus problematicus Herbst, 1786	5	12	9	33	30	23	112
Carabus violaceus Linnaeus, 1758	1						1
Nebria brevicollis (Fabricius, 1792)	483	209	70	60	40	18	880
Notiophilus aquaticus (Linnaeus, 1758)		1				1	2
Notiophilus biguttatus (Fabricius, 1779)	13	12	45	19	12	34	135
Loricera pilicornis (Fabricius, 1775)	44	129	29	6	4	3	215
Clivina fossor (Linnaeus, 1758)	7						7
Patrobus septentrionis (Dejean, 1828)	3						3
Trechus obtusus Erichson, 1837		1			2		3
Trechus quadristriatus (Schrank, 1781)	1				1		2
Bembidion lampros (Herbst, 1784)	2	2	5				9
Bembidion aeneum Germar, 1824	1						1
Bembidion guttula (Fabricius, 1792)	1	1	3	1		1	7
Pterostichus adstrictus Eschscholtz, 1823		5	1	2		13	21
Pterostichus cristatus (Dufour, 1820)	1						1
Pterostichus cupreus (Linnaeus, 1758)	2	10	1	2		1	16
Pterostichus diligens (Sturm, 1824)	11	6	1				18
Pterostichus madidus (Fabricius, 1775)	114	155	74	12	25	53	433
Pterostichus melanarius (Illider, 1798)		2			3	5	10
Pterostichus niger (Schaller, 1783)	3	1	2	1			7
Pterostichus strenuus (Panzer, 1796)	9	7	1				17
Calathus fuscipes (Goeze, 1777)	115	201	262	100	46	17	741
Calathus melanocephalus (Linnaeus, 1758)		18	21	6	1	1	47
Calathus micropterus (Duftschmid, 1812)	1			8	4	1	14
Calathus piceus (Marsham, 1802)	1			1	5	2	9
Agonum dorsale (Pontoppidan, 1763)	8	2					10
Agonum muelleri (Herbst, 1784)	6	16	7	1	1		31
Amara aenea (Degeer, 1774)	61	30	6	2	3		102
Amara communis (Panzer, 1797)	47	30	13	1	2		93
Amara familiaris (Duftschmid, 1812)	77	55	41	38	31	4	246
Amara lunicollis Schiödte, 1837	25	4	9	1	1		40
Amara plebeja (Gyllenhal, 1810)		1					1

cont.

	G3	G2	G1	P1	P2	P3	Total
Harpalus affinis (Schrank, 1781)		1			1		2
Badister bipustulatus (Fabricius, 1792)				1			1
Dromius angustus Brullé, 1834					1		1
Total at each site	1042	911	600	295	213	177	3238
Number of species	26	25	19	19	19	15	35

Appendix 2e. The numbers of different carabid species recorded at each row position at boundary site B, during 1992.

	G3	G2	G1	P1	P2	P3	Total
Cychrus caraboides (Linnaeus, 1758)					1		1
Carabus problematicus Herbst, 1786	1	3	6	22	18	7	57
Carabus violaceus Linnaeus, 1758				2			2
Leistus ferrugineus (Linnaeus, 1758)		1		11	4	1	17
Nebria brevicollis (Fabricius, 1792)	373	365	690	86	27	9	1550
Notiophilus biguttatus (Fabricius, 1779)	7	9	8	30	17	14	85
Notiophilus germinyi Fauvel, 1863		1				1	2
Loricera pilicornis (Fabricius, 1775)	56	73	29	5		1	164
Clivina fossor (Linnaeus, 1758)	17	11	22	2		1	53
Patrobus septentrionis (Dejean, 1828)	2	1					3
Trechus obtusus Erichson, 1837	6	7	5	6			24
Trechus quadristriatus (Schrank, 1781)	28	34	189	24	1	1	277
Bembidion lampros (Herbst, 1784)	7	30	53	12	4		106
Bembidion quadrimaculatum (Linnaeus, 1761)					1		1
Bembidion aeneum Germar, 1824	53	3	2	1			59
Bembidion guttula (Fabricius, 1792)	29	9	3	4		1	46
Pterostichus adstrictus Eschscholtz, 1823	1	6	2	2		1	12
Pterostichus diligens (Sturm, 1824)	2	10	8	18	3		41
Pterostichus madidus (Fabricius, 1775)	7	22	41	207	34	10	321
Pterostichus melanarius (Illider, 1798)	74	57	58	21	4	2	216
Pterostichus niger (Schaller, 1783)	6	1	4	1			12
Pterostichus strenuus (Panzer, 1796)	3	9	4	9			25
Abax parallelepipedus (Piller & Mitterpacher, 1783)				3		3	6
Calathus fuscipes (Goeze, 1777)	28	70	334	104	11	7	554
Calathus melanocephalus (Linnaeus, 1758)	17	44	55	134	21	5	276
Calathus micropterus (Duftschmid, 1812)				8	41	36	85
Calathus piceus (Marsham, 1802)				15	26	25	66
Agonum albipes (Fabricius, 1796)						1	1
Agonum dorsale (Pontoppidan, 1763)			1				1
Agonum muelleri (Herbst, 1784)	61	54	14		1		130
Amara aenea (Degeer, 1774)	7	8	8	3	1		27
Amara communis (Panzer, 1797)	2	25	9				36

cont.

	G3	G2	G1	P1	P2	P3	Total
Amara familiaris (Duftschmid, 1812)	3	13	5	11	8		40
Amara lunicollis Schiödte, 1837			1				1
Amara plebeja (Gyllenhal, 1810)			3				3
Total at each site	790	866	1554	741	223	126	4300
Number of species	23	25	25	25	18	18	35

Appendix 2f. The numbers of different carabid species recorded at each row position at boundary site C, during 1992.

	G3	G2	G1	P1	P2	P3	Total
Cychrus caraboides (Linnaeus, 1758)		1					1
Carabus problematicus Herbst, 1786		1		5	6	2	14
Leistus ferrugineus (Linnaeus, 1758)		2	26	13	2	1	44
Leistus rufescens (Fabricius, 1775)			1				1
Nebria brevicollis (Fabricius, 1792)	15	220	76	2	2	3	318
Notiophilus aquaticus (Linnaeus, 1758)	1		5				6
Notiophilus biguttatus (Fabricius, 1779)	6	32	188	30	27	4	287
Notiophilus germinyi Fauvel, 1863						1	1
Loricera pilicornis (Fabricius, 1775)	14	59	33	3	1	2	112
Clivina fossor (Linnaeus, 1758)	3	39	33	7	1		83
Patrobus septentrionis (Dejean, 1828)				3			3
Trechus obtusus Erichson, 1837			8	25	4		37
Trechus quadristriatus (Schrank, 1781)	3	10	52		2		67
Bembidion lampros (Herbst, 1784)		1	4				5
Bembidion quadrimaculatum (Linnaeus, 1761)	2	1				1	4
Bembidion aeneum Germar, 1824	1	1					2
Bembidion guttula (Fabricius, 1792)	3	1	8	1			13
Bembidion unicolor Chaudoir, 1850		1					1
Pterostichus adstrictus Eschscholtz, 1823		2					2
Pterostichus diligens (Sturm, 1824)	2	10	13	3	1		29
Pterostichus madidus (Fabricius, 1775)	82	35	60	67	48	65	357
Pterostichus melanarius (Illider, 1798)	1	2	2	1	2		8
Pterostichus niger (Schaller, 1783)		3	2				5
Pterostichus strenuus (Panzer, 1796)		1	8	3			12
Abax parallelepipedus (Piller & Mitterpacher, 1783)			1				1
Calathus fuscipes (Goeze, 1777)	264	95	192	39	22	35	647
Calathus melanocephalus (Linnaeus, 1758)	165	191	614	286	113	59	1428
Calathus micropterus (Duftschmid, 1812)	1	17	97	106	100	191	512
Calathus piceus (Marsham, 1802)	2	6	48	67	20	89	232
Agonum muelleri (Herbst, 1784)	7	7	2	1			17
Amara aenea (Degeer, 1774)	9	3	2	1	2	4	21
Amara communis (Panzer, 1797)	7	2	2			2	13

cont.

	G3	G2	G1	P1	P2	P3	Total
Amara familiaris (Duftschmid, 1812)	14	3	4	1	3	2	27
Amara lunicollis Schiödte, 1837	1						1
Amara plebeja (Gyllenhal, 1810)	1	1					2
Trichocellus placidus (Gyllenhal, 1827)			1				1
Bradycellus harpalinus (Serville, 1821)	1	1	3	1			6
Dromius melanocephalus Dejean, 1825		2					2
Total at each site	605	750	1485	665	356	461	4322
Number of species	23	30	27	21	17	15	38

Appendix 3a. The numbers of different adult spider species recorded at each row position at the Little Dun Fell boundary transect during 1993.

	O3	O2	O1	I1	I2	I3	Total
GNAPHOSIDAE							
Gnaphosa leporina (L. Koch, 1866)		1					1
CLUBIONIDAE							
Clubiona diversa O.P.-Cambridge 1862					1		1
THOMISIDAE							
Xysticus cristatus (Clerck, 1757)		1					1
LYCOSIDAE							
Pardosa palustris (Linnaeus, 1758)	2	1		1		3	7
Pardosa pullata (Clerck, 1757)				3	3	4	10
Alopecosa pulverulenta (Clerck, 1757)					1		1
Pirata piraticus (Clerck, 1757)						2	2
LINYPHIDAE							
Ceratinella brevipes (Westring, 1851)						1	1
Walckeaeria nudipalpis (Westring, 1851)	2	4	11	14	20	16	67
Walckeaeria vigilax (Blackwall, 1853)		1					1
Walckeaeria clavicornis (Emerton, 1882)	35	34	45	49	49	42	254
Walckeaeria cuspidata (Blackwall, 1833)	1	3	1	1	5		11
Walckeaeria acuminata Blackwall, 1833		1		1	2	1	5
Dicymbium tibiale (Blackwall, 1836)	1			1	2	1	5
Dismodicus bifrons (Blackwall, 1841)		1		1			2
Hypomma bituberculatum (Wider, 1834)	2	3		1	4	2	12
Gonatium rubens (Blackwall, 1833)		1		3	1	3	8
Oedothorax gibbosus (Blackwall, 1841)					1		1
Oedothorax gibbosus f. *tuberosus* (Blackwall, 1841)		1				1	2
Oedothorax fuscus (Blackwall, 1834)	2	1	7	1	1		12
Oedothorax retusus (Westring, 1851)	15	9	9	5	8	13	59
Pelecopsis mengei (Simon, 1884)		1			2	7	10
Pelecopsis parallela (Wider, 1834)			1			9	10
Silometopus elegans (O.P.-Cambridge, 1872)	68	118	199	272	372	327	1356
Tiso vagans (Blackwall, 1834)		1	1	2	1		5
Monocephalus fuscipes (Blackwall, 1836)				1			1
Micrargus herbigradus (Blackwall, 1854)	1						1

cont.

	O3	O2	O1	I1	I2	I3	Total
Micrargus apertus (O.P.-Cambridge, 1870)				1			1
Erigonella heimalis (Blackwall, 1841)		2	1	1			4
Savignya frontata (Blackwall, 1833)	10	7	5	6	1		29
Diplocephalus permixtus ((O.P.-Cambridge, 1871)	1				2		3
Araeoncus crassiceps (Westring, 1861)		1	2				3
Typhochrestus digitatus ((O.P.-Cambridge, 1872)	1		2				3
Milleriana inerrans (O.P.-Cambridge, 1884)		1					1
Erigone dentipalpis (Wider, 1834)	172	49	106	11	25	1	364
Erigone promiscua (O.P.-Cambridge, 1872)	172	58	60	6	12	1	309
Erigone atra (Blackwall, 1841)	52	16	26	6	7	1	108
Rhaebothorax morulus (O.P.-Cambridge, 1873)	4						4
Semljicola caliginosa (Falconer, 1910)		1	1				2
Hilaira frigida (Thorell, 1872)	16	15	27	47	48	57	210
Ostearius melanopygius (O.P.-Cambridge, 1879)		1	1				2
Porrhomma pygmaeum (Blackwall, 1834)	2					1	3
Porrhomma pallidum Jackson, 1913				1	1	2	4
Porrhomma campbelli F.O.P.-Cambridge, 1894	3			2			5
Mieoneta rurestris (C.L.Koch, 1836)						1	1
Mieoneta gulosa (L.Koch, 1896)	3	2		1	1		7
Centromerus prudens (O.P.-Cambridge, 1873)	18	52	95	59	98	67	389
Centromerita bicolor (Blackwall, 1833)	5	39	77	71	97	93	382
Centromerita concinna (Thorell, 1875)	2	2	8	6	4	1	23
Oreonetides vaginatus (Thorell, 1872)	15	14	8	21	16	27	101
Bathyphantes gracilis (Blackwall, 1841)	4	2	2	2	2		12
Bathyphantes parvulus (Westring, 1851)	1		2	2		1	6
Bathyphantes nigrinus (Westring, 1851)		1					1
Lepthyphantes tenuis (Blackwall, 1852)						1	1
Lepthyphantes ericaeus (Blackwall, 1853)				1			1
Lepthyphantes angulatus (O.P.-Cambridge, 1881)	1	3	6	21	30	63	124
Allomengea scopigera (Grube, 1859)			1	5	6	11	23
Total at each row	611	448	704	626	823	760	3972
Number of species	28	35	26	34	31	30	57

Appendix 3b. The numbers of different carabid species recorded at each row position at the Little Dun Fell boundary transect during 1993.

	O3	O2	O1	I1	I2	I3	Total
Carabus problematicus Herbst, 1786	17	36	23	36	69	83	264
Leistus rufescens (Fabricius, 1775)	1	6	13	29	18	13	80
Nebria gyllenhali (Schoenherr, 1806)	4	1	9	12	15	21	62
Notiophilus aestuans (Motschulsky, 1864)	2				1	1	4
Notiophilus aquaticus (Linnaeus, 1758)	16	4	3	5	1		29
Notiophilus biguttatus (Fabricius, 1779)	1	1		2			4
Notiophilus germinyi Fauvel, 1863	30	28	22	32	14	4	130
Loricera pilicornis (Fabricius, 1775)				1			1
Patrobus assimilis Chaudoir, 1844	167	166	294	476	423	275	1801
Trechus obtusus Erichson, 1837	2		2			1	5
Trechus quadristriatus (Schrank, 1781)					1		1
Bembidion lampros (Herbst, 1784)					1		1
Pterostichus adstrictus Eschscholtz, 1823	2	7	2		1	2	14
Pterostichus diligens (Sturm, 1824)	3	1	2	1			7
Calathus melanocephalus (Linnaeus, 1758)	4	3	8	2	1		18
Amara lunicollis Schiödte, 1837		1					1
Trichocellus cognatus (Gyllenhal, 1827)		1		1	1		3
Bradycellus ruficollis (Stephens, 1828)		1					1
Total at each site	249	256	378	597	546	400	2426
Number of species	12	13	10	11	12	8	18