Invertebrate community structure, with particular reference to Coleoptera: Carabidae, in Clearfelled and plantation areas of Hamsterley forest, county Durham

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Bolton, Andrew (1995) Invertebrate community structure, with particular reference to Coleoptera: Carabidae, in Clearfelled and plantation areas of Hamsterley forest, county Durham. Masters thesis, Durham University.

INVERTEBRATE COMMUNITY STRUCTURE, WITH PARTICULAR REFERENCE TO COLEOPTERA: CARABIDAE, IN CLEARFELLED AND PLANTATION AREAS OF HAMSTERLEY FOREST, COUNTY DURHAM.

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A dissertation submitted in part fulfilment of the requirements for the degree of Master of Science in Ecology by advanced course.

University of Durham
September 1995

Acknowledgements

I am very grateful to my supervisor, Dr. Tusi Butterfield for all her patience and guidance throughout the project, when she should have been relaxing in hospital. I am grateful to the Forestry Commission for permission to work at Hamsterley forest. Thanks must also go to Mr. Eric Henderson, Mr. Derek Coates, Mr. Brian Preistley, Dr. Judy Allen, and Ms. Gillian Telfer for guidance and assistance during the course of this project, and to Ian Downie who was patient enough to show me how to comprehend a CANOCO output. Finally I must, as always, thank Alex for putting up with me during the production of this dissertation, in a manner above the call of duty yet again.

Summary

1. This study examined the invertebrate populations of two habitat types in Hamsterley Forest, County Durham.

2. Invertebrate populations in mature Sitka spruce plantations and Clearfelled habitats were examined by sampling the soil and surface active fauna.

3. Differences were found to exist abundances of invertebrates at the order level between the habitats, although the responses of the surface active and soil dwelling fauna were different.

4. A larger proportion of the beetles were caught in the clearfelled habitat, although some families were more abundant in the plantation than in the clearfell

5. Significantly more ground beetles were caught in the open clearfell habitat than in the mature plantation.

6. The most abundant carabid species was *Pterostichus adstrictus* contributing over 35% of the carabids caught, and was found almost exclusively on the open habitat.

7. Multivariate analysis revealed that the surface active fauna sampled were distinct in two ways, with the principle axis of ordination relating to habitat type and the second axis of ordination relating to differences in the clearfell sites. At the order level the soil fauna did not separate in a similar manner, and the two habitats are thought to play a minor role in shaping the community.

8. The differences in carabid assemblages in the clearfell sites sampled could not be explained in terms of the environmental variables recorded. It is proposed that the differences between the habitats, and the difference within the open habitat, were related to temperature differences, as a result of the different insulation properties of the habitat types.

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Chapter 1

Introduction

1.1 Upland habitats and their origins

There are no precise dividing lines between the 'uplands' and the 'lowlands' of Britain, although about 30% of the land above the limits of arable farming are generally considered to be upland (Ratcliffe and Thompson 1988). Although relatively small in area and altitudinal ranges compared to the alpine ranges of the world, the British uplands contain a great variety of landscapes and dependent biotic communities (Ratcliffe and Thompson 1988).

Following the retreat of the last Glaciers at the end of the Weichselian period *c.* 11,000 years B.P. the lowland mountain slopes of Britain were covered naturally by forest, except where the ground was to rocky or wet. In the south this was usually composed of Oak (*Quercus* spp), found alone or mixed with other broad leaves. Further north this was typically Scotts Pine (*Pinus sylvestris*), with Birch (*Betula* spp.) on more fertile soils. These differences corresponded to the latitudinal changes from cool temperature broad leaf (nemoral) to boreal coniferous and birch forest (tagia) (Ratcliffe and Thompson 1988). The woodland cover reached a peak during the Atlantic period (Lowe and Walker 1984), about 6000 years ago. The English channel came into existence at the end of the Atlantic period, with an associated lowering of the mean temperature, and the effects of man begin to be detected about this time (Peterken 1981). This led to progressive deterioration in the forest cover, through both climate induced change and man induced clearance (Peterken 1981). After approximately 6000 years now throughout the potential forest zone we have semi natural systems, determined largely by the soil parent material (Gimmingham 1988), as the sub alpine zone of birchwood and medium shrubs has very largely been eradicated (Ratcliffe and Thompson 1988), and the natural tree line can only be seen in a few places, such as the Cairngorms (Nethersole-Thompson and Watson 1981).

The expansion of vegetation following this clearance has been dominated by the acidophilous *Ericaceae* (McVean and Ratcliffe 1962). These are the dwarf shrub heath, with Common Ling (*Calluna vulgaris*), Bell Heather (*Erica cinerea*), Cross leaved Heather, (*Erica tetralix*), Bilberry (*Vaccinium myrtilus*), and Crowberry (*Empetrum nigrum*), extensively found in Britain. This is fragmentary in Europe, and is regarded as an oceanic plant formation (Good 1977, Gimmingham 1975). Many of the invading species have acidifying effect upon the soil, especially *Calluna*, (Miles 1985), and most of these upland soils are infertile, partly intrinsically, due to the acidic underlying rock, and partly due to the pedogenic effects of the plants (Miles 1988a) leading to peat formation.

Dwarf shrub domination of the uplands has been maintained by management practices such as burning, originally to produce more palatable plants for grazing, but also with the effect of increasing Grouse (*Lagopus lagpus scoticus*) populations to the extent of this generating income in itself for grouse shooting. Dating from around 1800, and reaching its peak around 1900 grouse management involved rotational burning, control of sheep (*Ovis aries* L.) or deer (*Cervus elaphus* L.) numbers, and predator numbers (Ratcliffe and Thompson 1988).

Although the communities can be at best described as semi natural, the ericaceous dwarf shrubs have been present for several thousands of years, developing heterogenously both spatially and temporally (Thompson, Stroud, and Pienkowski 1988). This, coupled with the oceanic climatic conditions, has allowed the development of an unusual association of fauna and flora in a world sense (Ratcliffe and Thompson 1988). It is possible that individuals of species in these different areas have developed somewhat specialised adaptations (Thompson, Stroud, and Pienkowski 1988).

1.2 The fauna of the uplands

The dominance of ericaceous dwarf shrubs has been a key factor in shaping the faunal community in the uplands, the growth phases of *Calluna* have been well studied, although little is known of the other dwarf shrub species (Usher and Gardener 1988).

Habitat heterogeneity appears to be an important factor in determining the diversity of invertebrate fauna. Pioneer and degenerate stands of *Calluna,* which exhibit greater floristic diversity in comparison with the building and mature phases, show greater invertebrate diversity (Miller 1974, Gimmingham 1985). Further evidence of the importance of habitat heterogeneity was shown in the comparison of the invertebrate fauna of managed and unmanaged *Calluna* stands (Miller 1974). Unmanaged stands had bushes of all ages, whereas those of the managed stands were all of the same age. Many taxa were found to be more numerous on the unmanaged stands (Gimmingham 1985).

The soil fauna is primarily influenced by the growth phase of *Calluna.* During the pioneer phase the microclimate is harsh because much of the litter is blown away. As the canopy begins to close towards the end of the building phase, the microclimate beneath the plants stabilises and the developing litter layer retains more moisture.

Under these conditions the soil and litter faunas develop rapidly (Chapman and Webb 1978). Litter production begins to decline as the plants reach the degenerate phase, the canopy opens out and the microclimate becomes less humid. Sufficient moisture is, however, retained by existing litter and mosses to enable the soil faunas to retain its high diversity (Chapman and Webb 1978).

Surface active taxa, such as beetles (*Coleoptera*), Springtails (*Collembola*) and some Mites (*Acari*) are usually more abundant in pioneer stands, while the building and mature phases are dominated by shoot and sap feeders. Spiders (*Araneae*), and Ants (*Hymenoptera*) show marked changes in species composition and abundance as Calluna progresses from the pioneer phase to the mature phase (Merret 1976, Brian, Mountford, Abbott and Vincent 1976).

Virtually nothing is known about montane invertebrate community structure and functioning (Ratcliffe and Thompson 1988) although the composition is becoming much better known (Coulsen 1988, Coulsen and Whittaker 1978).

1.3 Afforestation and the uplands

Rates of change in the uplands can vary greatly, from the rapid change in *Calluna* dominated dwarf shrub heath to *Agrostis-Festuca* grass land in only 2 to 3 years following heavy grazing and trampling by livestock, to longer term change to *Betula* and *Pinus* woodland where there is a heavy seed rain (Miles 1988a). Of the recent changes brought about by man afforestation is arguably the most controversial land use change in Britain (Thompson and Usher 1988). The majority of these new forests are different in terms of species composition, structure, nutrient cycling, hydrology and many other features, to both the present upland habitat they replace and the forests which previously occurred (Gimmingham 1988)

The forest cover of Britain is now 10.0% (2,265,000 ha) compared with only 5.3% (1,180,000 ha) in 1924 (Forestry Commission 1987). The census (Forestry Commission 1984) for 1979 to 1982 indicated that the planting during 1971 to 1980 was 60% Sitka Spruce (*Picea sitchensis*), 14% Lodgepole Pine (*Pinus contorta*), 5.5% Japanese/hybrid Larch (*Larix* spp.) 7% other conifers, and only 5.3% broad leafed. The main period of expansion in England was from 1945 to 1950 (Thompson, Stroud, and Pienkowski 1988). Sitka spruce has become an important component of the British landscape

1.5 Aims of the present study

The present study aims to examine the invertebrate community composition of a former heathland site, which has been afforested. The differences in invertebrate community composition between the plantations and the surrounding moors will not be examined *per se*, but within the forest mature plantations and clearfelled areas will be compared.

Two components of the invertebrate community will be examined, the surface active species, and the soil dwelling species. Techniques appropriate to the study these components will be used. Composition of the invertebrate community sampled in this study does not rely directly upon plants as their main source of energy, and hence any difference between the sampled locations will reflect real differences in the macro habitat, rather than reflecting differences in host plant preferences.

Community analysis will be carried out at three levels, the presence and abundance of invertebrate orders, beetle families (*Coleoptera*), and a detailed examination of Ground beetle species (*Coleoptera: Carabidae*) and their abundances. Vegetation and soil analysis will be carried out to allow comparisons both within and between sites, and to characterise the sites themselves.

Chapter 2

Methods

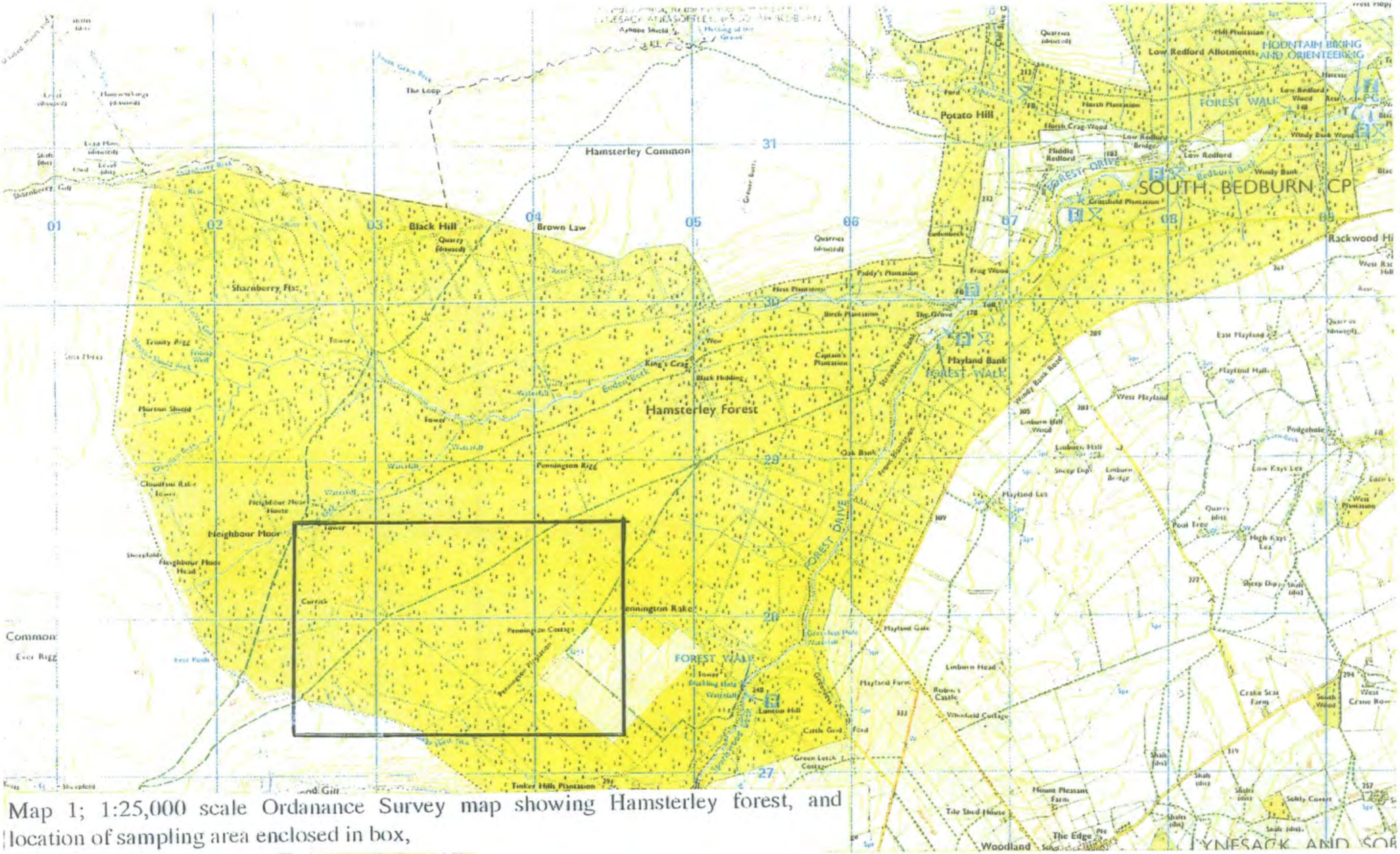
2.1 Study Areas

Hamsterley forest (NZ0530) covers approximately 2500 ha, has an altitudinal range of 150m to 427m, and is mainly plantation blocks of Sitka Spruce, (*Picea sitchensis*), on shallow peats overlying sandstone, Map 1. These blocks are felled as units at different ages, depending upon the demand for wood. This has created a patch work of plantations and clearfelled sites of different ages. The present study was carried out on two open clearfelled sites and two mature plantations. There were two pairs of transects studied in each block, perpendicular to the boundary between the open clearfell and mature plantation habitat, Map 2.

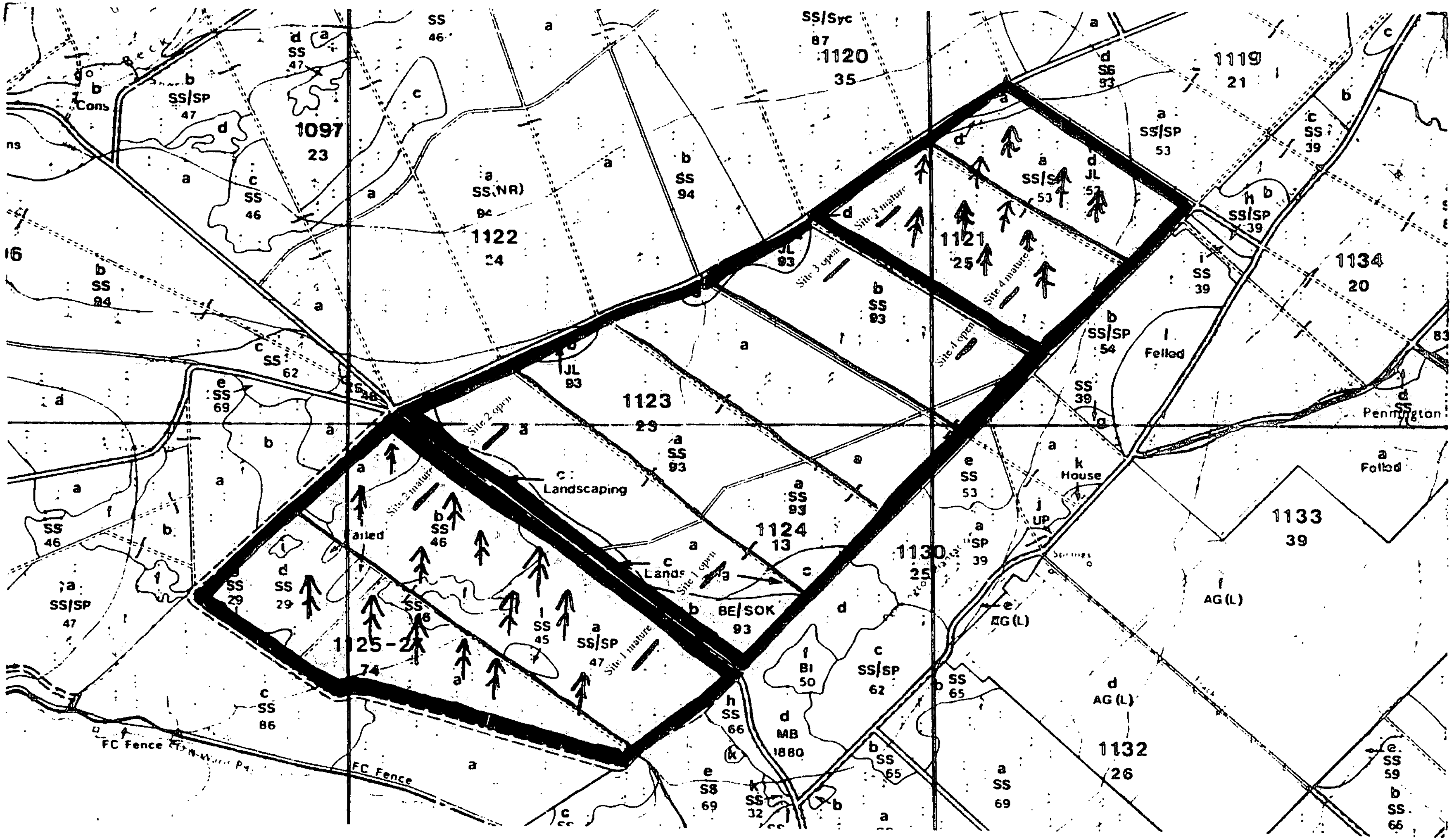
2.1.1 Site descriptions

The mature sites transects were approximately 5m into the habitat. The canopy is closed and low light levels have suppressed plant growth to the point where there is no ground flora, but a carpet of needle litter. Sites 1 and 2, (Plates 1 and 2), were planted approximately 50 years ago, sites 3 and 4, (Plates 3 and 4), were planted approximately 40 years ago, Map 2, and therefore the four sites are approximately the same age. Both plantation blocks are reaching commercial maturity and are due for felling, with sites 1 and 2 due for felling in 1995.

The open sites transects were located approximately 15m into the habitat. There was considerable vegetation cover, up to approximately 50cm in height, with sparse clumps of young spruce of different ages present at sites 1, 3 and 4, (Plates 5, 7, and 8). Less vegetation was found to be present at site 2, (Plate 6) which had some replanting in 1993. This block was felled in 1989, and at the time of the study had been cleared 6 years ago, Map 2. Apart from site 2, these areas had not been mechanically reseeded, but vegetation succession allowed to progress naturally. The boundary between the open and mature of sites 1 and 2 is a road of approximately 2m width, with a drainage ditch on the open side. The boundary between sites 3 and 4 is a grassed over access road of approximately 1.5m.



Map 1; 1:25,000 scale Ordanance Survey map showing Hamsterley forest, and location of sampling area enclosed in box,



Scale 0.5 Km

Map 2; Detailed map of study site, showing position of sample transects, and habitat areas.

Plate 1; Photograph taken facing west, showing the location of the site 1 mature plantation transect. Note the dense carpet of needle litter, and lack of understory vegetation. A pitfall trap can be seen in the foreground.

Plate 2; Photograph taken facing west, showing the location of the site 2 mature plantation transect. Note the dense carpet of needle litter, and lack of understory vegetation.

Plate 3; Photograph taken facing east, showing the location of the site 3 mature plantation transect. Note the dense carpet of needle litter, and lack of understory vegetation. Two of the pitfall traps can be seen in the foreground.

Plate 4; Photograph taken facing east, showing the location of the site 4 mature plantation transect. Note the dense carpet of needle litter, and lack of understory vegetation. Two of the pitfall traps can be seen in the foreground.

Plate 5; Photograph taken facing east, showing the location of the site 1 open transect. Note the dense ground vegetation, and irregular groups of Sitka spruce trees.

Plate 6; Photograph taken facing east, showing the location of the site 2 open transect. Note the absence of dense ground vegetation, and high amount of wood debris.

Plate 7; Photograph taken facing west, showing the location of the site 3 open transect. Note the bare ground vegetation, with regular groups of Sitka spruce trees.

Plate 8; Photograph taken facing west, showing the location of the site 4 open transect. Note the dense ground vegetation, and high number of Cotton grass seed heads.

2.2 Field Survey Methods

Four survey methods were employed, to obtain information on the distribution and abundance of soil dwelling and surface active invertebrates, the abundance and distribution of plant species on the open site, and soil chemistry.

2.2.1 Invertebrate Surveys

Animal population sampling methods can be of two types. The first is an absolute population estimation method, that is population estimates per unit area. These types of estimate can be converted to measures such as density. The second type is a relative population estimation method, that is population estimates per unit effort. These types of measures are not estimates per unit area, and can not be converted to measures such as density (Southwood 1971). The invertebrate survey in this study focused on sampling two components of the total invertebrate community, specifically the soil dwelling and the surface active components, using both types of population estimation methods. This allowed collection of data using the same technique in both the mature and open sites for each of the components. The plant inhabiting species and aerial species were not collected directly but may have been incidentally collected.

2.2.1.1 Surface Active Invertebrate Survey

Surface active invertebrates can be collected in several ways, such as by 'grubbing', or hand searching, by vacuum sampling, or by trapping, (Southwood 1971). As 'grubbing' is extremely time consuming, and not very quantitative, it is not a usual method of collecting samples (Southwood 1971). Although quantitative samples can be collected using the vacuum sampling method (Southwood 1971, Wright & Stewart 1992) the differences in habitat types between the open and mature sites is such that the efficiency of the vacuum sampler is not constant, due to the needle litter in plantations blocking the sample bag and reducing suction power (I. Downie, pers comm.). Therefore, this method was rejected. It was decided that a trapping method would be used, as these may be left on site and then collected at a later date allowing a larger number of samples to be collected.

The method used in this study involves traps sunk into the ground with the rim just below the soil surface, known as pitfall traps. This method relies upon surface active invertebrates falling into the trap as they walk around, although invertebrates which predominately fly are also be caught. This method has been used extensively for surface active invertebrates (Southwood 1971) and has proved useful in the study of ground beetles (Greenslade 1964, Butterfield and Coulson 1983), and has been used in previous studies with similar aims, (Day and Carthy 1988, Lenski 1982). The data collected is not per unit habitat, and is therefore a relative population estimation method. The traps used were plastic vending cups 91mm deep and with a mouth diameter of 65mm. These were placed in a transect of six traps within each site, at a distance of 2m apart. This arrangement both increases the efficiency and the independence of the traps (Luff 1975). This gave a total of 24 traps in the each habitat type and a total of 48 traps in total.

Each transect was perpendicular to the boundary between the open and mature component of each site, see Map 2. The transect in the open clearfell site was located approximately 10m to 15m from the edge, the transect in the mature plantation was located 5m and 10m from the edge. Each trap was individually numbered, with the closest trap to the boundary labelled as number one and the furthest trap from the boundary numbered six. Each trap was filled to approximately one third depth with ethylene glycol to act as a preserving agent, with a small amount of detergent added to reduce the surface tension. The ethylene glycol is known to have an attracting effect on ground beetles (Holopainen 1992). This mainly affects the sex ratio of the catch, which is not under consideration in the current study, (Holopainen 1992). The traps were left *in situ* for two week periods. The contents of each trap were decanted off on site, into screw cap plastic bottles labelled with the time period, site number, habitat type, and trap number. The traps were collected for 5 trapping periods, or 10 weeks, from the 28th of April to the 7th of July 1995, table 1, giving a total of 240 traps.

2.2.1.2 Soil Inhabiting Invertebrates Survey

The soil inhabiting invertebrates were surveyed by collecting a soil sample of 17cm wide by 17cm long by 7cm deep, giving a sample size surface area of 289cm^2. A spade was used to collect the samples to avoid any compression damage that may occur when a 'corer' is used (Southwood 1971). This allowed many samples to be transported complete and undisturbed, which is desirable when using a behavioural method of extraction. At each site 10 replicate samples were taken at random, from between 2 and 5m of the pitfall transect. Each sample was stored separately in a plastic bag and labelled with sample number, site and sampling period, before transportation back to the laboratory for extraction. Samples were taken at three time period corresponding to periods 1, 3 and 5 of the pitfall survey, and 80 samples were taken per time period, table 1.

A behavioural method, rather than mechanical method such as sieving or flotation, was used as it allowed many samples to be processed simultaneously, thus increasing the sample size. Extraction of animals from a substrate containing a high amount of organic matter is possible with this method, which is usually found to be problematical using other mechanical differential separation techniques (Southwood 1971).

Behavioural methods rely upon a stimulus being applied to a sample, which then causes a movement response from the invertebrates inhabiting the sample (Southwood 1971). The standard and most commonly used is the dry extractor, such as the Berlese-Tullgren funnel, which has been used and modified considerably (Hammer, 1944, Haarlov, 1947, Macfadyen, 1953, 1955, 1961, 1962) although the basic principle remains the same. Heat is applied to the sample from above, causing the water to evaporate, driving the animals out. The animals then fall through a grill support into a collecting funnel and then a collecting bottle. Two factors must be taken into consideration to maximise the efficiency of this process. The first is that the sample be placed with the upper most surface pointing down towards the collecting funnel and bottle, to allow the animals to escape by their natural passage ways (Hammer, 1944). The second is that there should be a space between the edge of the core and the sides of the funnel apparatus, to avoid condensation, which can result in serious loss of invertebrates (Haarlov, 1947). Both of these considerations were fulfilled in this study.

The 'Large Berlese funnels' in the Department of Biological Sciences, Durham University were used, with a 100W pearlescent light bulb as a heat source and 95% ethanol used as a preservative. The cores were subjected to extraction for seven calendar days, after which all samples were dry. After extraction the collection bottles were decanted into labelled screw cap plastic vials before identification and counting of the invertebrates present. The data collected are per unit habitat and are, therefore, an absolute population estimation method.

Table 1; Time periods of pitfall trapping and soil sample collection used in this study.

Dates	Pitfall time period	Soil sample time
28/4/95-12/5/95	1	1
12/5/95-26/5/95	2	
26/5/95-9/6/95	3	2
9/6/95-23/6/95	4	
23/6/95-7/7/95	5	3

2.2.2 Laboratory Sorting and Identification

The process of sorting and identification applied equally to samples collected by soil extraction and pitfall traps. Each sample was examined under a binocular microscope, in a plastic petri dish. Graph paper was selotaped to the lower surface of the petri dish to ensure that the entire sample was viewed. The samples were illuminated with fibre optic lights to reduce alcohol evaporation. Each sample was sorted into orders (Tilling 1987) and the numbers noted. Coleoptera larvae and adults were identified to family (Luff 1991, and Unwin 1988 respectively) and the numbers noted. Carabid adults and larvae were then identified to species (Lindroth 1974, and Luff 1974 respectively) and the numbers noted, where not explicitly stated in the text the authorities may be found in Appendix 3. Coleoptera adults, Coleoptera larvae and 'other orders' were stored in labelled plastic capped vials, with 95% ethanol as the preservative, for future reference.

2.2.3 Vegetation Survey

As there is no understory vegetation in the mature plantation site, a vegetation survey was carried out on the open clearfell site only. Using standard 1m by 1m quadrats the plants present were identified to species in the field (Fitter, Fitter and Blamey 1985, Fitter, Fitter and Farrer 1984) and scored for abundance in line with the National Vegetation Classification on the DOMIN scale (Rodwell 1992). Two additional features were recorded, the presence and DOMIN score of bare peat and the presence and DOMIN score of wood debris, resulting from the harvesting process, as it was thought these may be important. This survey was carried out to identify any features that the transect sites had in common, and to quantify any differences that may exist.

The quadrats were located at random between 2 and 5m from the transect, 6 quadrats were recorded from each transect site, with a total of 24 quadrats taken in total. The aim of the survey was not to locate and identify all the plant species present but to determine vegetative environment around the pitfall transect. Six quadrats would also allow the comparison of results from the plant survey to the results from the pitfall trapping after TWINSPAN (Hill 1979a) analysis . The data were collated and analysed in the laboratory.

2.2.4 Soil Chemistry analysis.

Soil samples were taken from each site in the same manner as the soil invertebrate survey. The samples were air dried in the laboratory until they became friable. Surface plant debris were removed before sieving through a 850μm sieve, to generate a constant particle size. The sieved residue was then analysed for the pH, water content, organic carbon content and inorganic carbon content, following Hesse (1971).

The pH was determined by weighing 5g of sieved residue and adding 25ml of distilled water. After thorough mixing this was allowed to stabilise for 1 hour before the pH was determined using a calibrated electronic pH probe and meter. The reading for each site was recorded for use in further analysis.

Soil water content was determined by weighing approximately 1g of sieved residue in a small labelled crucible of known weight, and noting the weight to four decimal places. The sample was then dried at 105°C in an air circulation oven for 12 hours, forcing the water in each sample to evaporate. The samples were then cooled to room temperature in a desiccator to prevent reabsorption of air borne moisture, before reweighing. The soil water content was then calculated by subtracting the soil weight after heating from the original weight, and converted to a percentage.

The organic carbon content was determined by reheating the samples used for the soil water analysis, in a muffle furnace at 480°C for 12 hours. Any organic carbon present in the sample ignites and burns away, the samples were then allowed to cool to 105°C in the furnace before being removed and placed in the dessicator to cool to room temperature. The samples were then reweighed and the weights noted. The organic carbon content was then be calculated by subtracting this new weight from that obtained after the soil water analysis, and converted to a percentage.

The inorganic carbon content was calculated by reheating the samples, in the muffle furnace, to 950°C for 1 hour. This forces inorganic carbon compounds such as calcium and magnesium carbonate to ignite and burn away. The samples were then allowed to cool to 105°C in the furnace before being removed and placed in the dessicator to cool to room temperature. The samples were then reweighed and the weights noted. The inorganic carbon content was then calculated by subtracting this new weight from that obtained after the organic carbon analysis, and converted to a percentage.

The residue left after this process is mainly minerals such as silica, as well as metal oxides such as iron and aluminium. Although determination of these is important in the study of soil physiognomy, it was deemed beyond the scope of the current study. The percentage of this mineral residue was determined, and noted.

2.3 Data analysis

The statistical methods used in the study follow Zar (1984) with the multivariate analysis methods following Hill (1979a, 1979b) ter Braak (1988).

The normality of the data were checked by two methods, by visual inspection following the plotting of a histogram, and by comparison of the variance to the arithmetic mean. If the data looked visibly skewed, or the variance was much larger than the mean, it was normalised by either the $x'=\log(x+1)$ or the $x'=\surd x+0.5$, where x is the datum from the data set and x' is the value to be used in the statistical analysis. The normality of the transformed data were checked by the methods outlined above.

Three factors were thought to have an effect on the invertebrate populations of interest in this study, firstly the effect of habitat, with two habitat types, secondly the effect of time, with samples taken at different time periods, and finally the effect of site, examining the four sampling locations. For this reason three factor analysis of variance was used, using the computer program SPSS for Windows to analyse the data for individual orders. This allows both the analysis of the factors in question and their interactions. For the data which could not be normalised the equivalent non parametric analysis of variance method, the Kruskal-Wallis test, was used. The t-test was used for direct comparisons between two population means, using the computer program Excel for Windows.

Simultaneous analysis of the invertebrate populations was achieved by using the multivariate analysis computer programs TWINSPAN (Hill 1979a), DECORANA, (Hill 1979b), and CANOCO (ter Braak 1988).

TWINSPAN (Two Way Indicator Species Analysis) (Hill 1979a), is a polythetic divisive cluster analysis program which was originally designed to classify vegetation data. The program is designed to split the principle ordination axis in two, giving two groups of samples, and indicating which species are used to make the split, termed the indicator species. The two groups produced are subsequently split again following the same process, until an arbitrary point is reached. The process uses 'pseudospecies' (Hill, Bunce and Shaw 1975) a concept where the abundance of a species can be broken into discreet units which represent biologically different responses to an environment. The pseudo species cut levels were set in the programs, reflecting the transformation used in the earlier analysis.

DECORANA (DEtrended CORrespondance ANAlysis) (Hill 1979b), is an extension of the earlier reciprocal averaging technique, but removes the correlations between the first and later axes, and thus removes the effect of arching the data. This is most pronounced in the second axis, with the third and subsequent axes sometimes related to the first. Eigen values are generated for each axis, and if they are considerably less in the third and subsequent axes, they are usually considered not significant. In the simplest sense, the data is analysed by generating scores for the species, and using these to generate scores for samples, and then recalculating the species scores to recalculate the sample scores. This procedure is repeated many times until stable values are obtained for both the sample and species scores. The scores can be plotted, and any gradient effects in the axis noted.

CANOCO (CANOnical Community Ordination) (ter Braak 1988), is an extension of DECORANA, and is used to analyse the relationship between species abundances and external variables. Canonical Correspondance Analysis was used, where scores are calculated for both environmental variables and samples by a mixture of ordination and multiple regression. The multiple regression component is carried out during the two way calculations for sample and species scores by regressing the sample scores on the environmental variables. The significance of the resulting environmental and samples scores can be tested using Monte Carlo analysis permutation test. By plotting the sample scores and environmental scores on the same axis the direction and effect of the environmental variables can be seen.

Chapter 3

Results:

Environmental Characterisation

3.1. Vegetation Survey of the open clearfell sites.

Only seven species of plant were encountered in the survey of the open site, all were identified to species and the DOMIN score recorded, see Appendix 1. This low number of species was an underestimate of the floristic diversity of the open sites, as other species were seen, but did not fall within the quadrats recorded. However, the aim was to characterise the plant communities around each of the pitfall transects.

The data was analysed using TWINSPAN, with the psuedospecies cut levels altered to reflect the DOMIN Scale, that is, with all values up to DOMIN 3 represented by psuedospecies 1, DOMIN value 4 represented by psuedospecies 2, DOMIN value 5 represented by pseuodospecies 3, DOMIN value 7 represented by pseuodospecies 4, and DOMIN value 10 represented by pseuodospecies 5, table 2. A dendrogram was constructed, showing the division at each level of the analysis for the sites, fig 1.

Table 2; TWINSPAN analysis results of transformed vegetation DOMIN values, n=24, Samples 1 to 6 are from site 1, 7 to 12 site 2, 13 to 18 site 3, and 19 to 24 site 4.

```
                          111111222111221
                         798201876043394215546312
Chamerion angustifolium  5443--4-4333-1----------  0000
Wood debris              44454534442-111---------  0001
Bare ground              445454233-231--433343---  0010
Picea sitchensis         334---34------1--3-3-3--  0011
Calluna vulgaris         -44445555555535555555555  010
Eriophorum vaginatum     ------44445545-543444444  011
Deschampsia flexuosa     -3--------3--------43443  10
Vaccinium myrtilus       ------------------3-3333  110
Erica tetralix           -------------------34334  111
                         000000000000000111111111
                         000000111111111000011111
                         000111000011111001101111
                         0110110111000010101 0011
                          01 01 0110111      0101
                                 01 011
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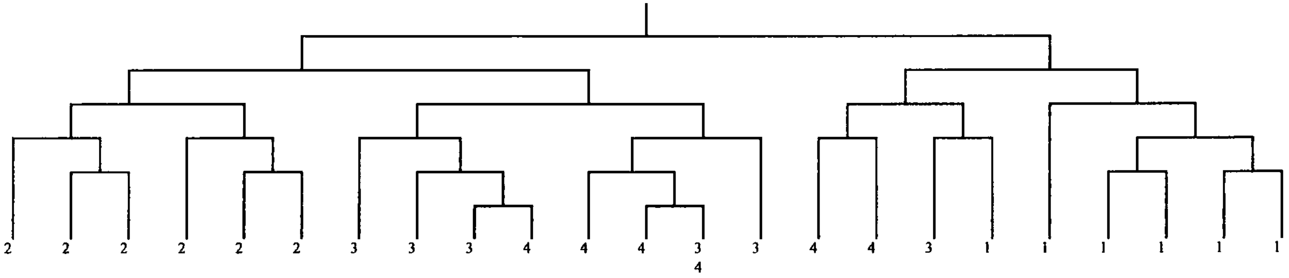
Site 1, along with quadrats 15, 21 and 22 from sites 3 and 4, were separated from the rest of the sites at the first division. This was due to the absence of *Erica tetralix*, and *Vaccinium myrtilus* at sites 2, 3, and 4, and both these species were positive indicators at this division. Site 2 splits away from the rest of the samples in its entirety at division two. This was the only site were *Eriophorum vaginatum* did not occur, and to have high scores for wood debris and bare ground. Sites 3 and 4 never separated into distinct, cohesive units in the classification. Using the classification at the second division it would be possible to determine 4 plant community types on the open clearfell;

Community 1 was dominated by *Calluna vulgaris* and *Eriophorum vaginatum*, with *Erica tetralix* and *Deschampsia flexuosa*, characterised by site 1. Community 2 was dominated by *Calluna vulgaris* and *Eriophrum vaginatum*, without *Erica tetralix* and *Deschampsia flexuosa.* Community 3 was dominated by *Calluna vulgaris*, with varying amounts of bare ground and *Eriophorum vaginatum*, but no *Erica tetralix.* These two communities were found at sites 3 and 4. Community 4 was composed of *Calluna vulgaris* with bare ground and wood debris, characterised by site 2.

Fig 1; Dendrogram drawn from the results of the TWINSPAN analysis of plant species abundances on the open clearfell habitat, showing the hierarchical classification of sites. n=24



3.2. Soil Analysis

All the soil samples taken were analysed for the water content, both organic and inorganic carbon content and the final mineral residue proportions. The percentage composition of each soil sample can be found in table 3, along with the pH values.

Table 3; Percentage composition of water content, organic Carbon, inorganic Carbon, and mineral residues, and pH values of soil samples collected from open clearfell and mature plantation habitats.

	Mature plantation				Open clearfell			
	1	2	3	4	1	2	3	4
$H_2$0	15.29%	22.86%	7.89%	23.25%	8.56%	7.17%	3.48%	7.68%
$C_{organic}$	71.52%	71.68%	87.03%	71.81%	31.79%	81.27%	44.15%	66.17%
$C_{inorganic}$	0.55%	0.32%	0.34%	0.81%	0.77%	2.97%	0.54%	0.46%
Mineral Residue	12.64%	5.14%	4.74%	4.74%	59.08%	8.59%	51.83%	25.69%
pH	3.2	3.0	3.2	3.1	3.4	3.1	3.2	3.2

All the pH values recorded were in a range from 3.0 to 3.4, which is very acidic, but typical of peat soils (Heal and Smith 1978). There was a range of 3.0 to 3.2 in the mature plantation habitats, with a range of 3.1 to 3.4 in the open clear fell habitats. The organic Carbon content was the bulk constituent of the soil samples in all cases except site 1 and site 3 open, which had relatively high mineral residues. The mineral residues remaining were a mixture of quartz, and metal oxides (pers. obs.).

3.3. Discussion

Clearfelling operations have effects which vary from place to place and have been studied in many parts of the world (Hill *et al.* 1983). The felling regime in Britain, and the responses of afforestation is however different to that of other northern European countries (Hill *et al.* 1983). Nevertheless there are well known immediate effects of clearfelling on the environment, relating to light incidence, temperature variation, and stump/root behaviour (Hill *et al.* 1983). Clearfelled sites can be considered as secondary succession sites, with a mixture of buried seed (Competitors, *sensu* Grime 1979) and invasive colonising seed (Ruderals *senu* Grime 1979) germinating. Both of these categories of plants were found during the current study. It is well known that plants modify their environment (Miles 1988b) and in particular the soil, and this may be expected to occur more under long-lived species such as trees (Howard and Howard 1983, Zinke 1962). Regeneration failure is thought to be one of the most limiting factors in the geographical ranges of species (Grime *et al* 1990). If modification of the local conditions has occurred to a point whereby the seed bank fails to regenerate, a paucity of the local species will occur. All the species found in the current study have been found in disturbed upland habitats before (Mile 1988a, Hill 1986).

Sitka Spruce (*Picea sitchensis*) regenerates readily, and is now the most abundant conifer in the county (Graham 1988). Rosebay Willowherb (*Chamerion angustifolium*) is not an upland plant species but is a characteristic plant of disturbed ground. This species has a very high dispersive power but does not persist in long established communities (Grime *et al.* 1990). It is found extensively in the county, and has undergone a rapid expansion since the early part of this century (Graham 1988). Wavy hair Grass (*Deschampsia flexuosa*) and Bilberry (*Vaccinium myrtilus*) are both upland plant species, typical of low soil pH and nutrient supply, like Sitka Spruce and Rosebay Willowherb have no persistent seed bank and rely upon seed dispersal (Grime *et al* 1990). These species can only be present at the site now by seed rain from the surrounding area. Common Ling (*Calluna vulgaris*) Cotton Grass (*Eriophorum vaginatum*) and Cross Leaved Heath (*Erica tetralix*) all maintain a persistent seed bank, which germinates on disturbance and exposure to the soil surface (Grime *et al* 1990, Hill 1986). Common Ling seeds can survive being buried throughout a plantation's lifetime, and so could be relicts from the original plants present on the site. It is thought that Cotton Grass and Cross Leaved Heath seeds would not survive the rotation length (Hill 1986). All the species have been recorded previously in the 8 surrounding tetrads to the tetrad investigated (Graham 1988) and so could have colonised the site by seed.

The communities were matched with National Vegetation Classification types with TABLEFIT (Hill 1990) these fell into two upland community types, Calluna-Eriophorum blanket bog, (M19c), and Calluna-Racomitrium lanuginosum heath, (H14). Both of these communities occur within the county. Although *Racomitrium lanuginosum* was not recorded in this work, it has been recorded from the tetrads immediately to the north of the study site (Graham 1988). The lack of an understory in the mature plantation sites is typical of Sitka Spruce stands (Miles 1988). The effects of the trees on the soil pH and surface organic matter tends to change with the age of the stand, peaking in acidity with the closure of the canopy before generally returning to the original values. The acidifying effects of the spruce plantations on the soil are comparable to those of Common Ling, although there is accelerated podsolization under the spruce stands, which is not broken up naturally by the soil fauna (Miles 1988).

The main effects of clearfelling the plantation at this particular site have been to allow plant communities to recolonise which are of a comparable nature to those of the general surrounding upland areas. This study did not aim to quantify the vegetative outcome of clearfelling but to quantify the habitat available to the invertebrates studied within Hamsterley Forest itself. This only allows the results to be taken as a guide to the general effects of clearfelling, within the framework of previous, and more rigorous work.

Chapter 4

Results:

Invertebrate Community Composition

From a total of 240 pitfall traps and 229 soil cores ($6.62m^2$) 17 orders of invertebrates were sampled, table 4, with 11 orders common to both techniques of collection. Approximately 20,000 invertebrates were collected by Berlese extraction and 11,000 invertebrates in pitfall traps. Three orders were collected only by soil extraction, the Oligochaeta, Orthoptera, and Polydesmida, and three orders were collected only by pitfall traps, the Pulmonata, Dermaptera, and Lithobiomorpha.

In both methods only two of the orders contributed the bulk of the catch. Collembola and Acari accounted for *c.* 80% of the catch from the soil cores, while Diptera and Coleoptera accounted for *c.* 70% of the catch from the pitfall traps.

Table 4; Total and Percentage abundance of each order caught in Pitfall traps, and collected by Berlese extraction, summed for all habitats.

	Pitfall Traps		Berlese Extraction	
Order	Abundance	Percentage	Abundance	Percentage
Oligocheata	0	0	314	1.71
Pseudoscorpionidae	2	0.02	96	0.52
Araneae	1899	16.85	714	3.90
Opiliones	464	4.12	58	0.32
Acari	7	0.06	7139	38.97
Polydesmida	0	0	1	0.01
Lithobiomorpha	3	0.03	0	0
Collembola	246	2.18	8121	44.33
Orthoptera	0	0	5	0.03
Dermaptera	4	0.04	0	0
Hemiptera	118	1.05	227	1.24
Thysanoptera	1	0.01	31	0.17
Lepidoptera	22	0.19	19	0.10
Diptera adults	5247	46.56	741	4.05
Diptera larvae	0	0	74	0.40
Diptera pupae	0	0	36	0.20
Hymenoptera	573	5.08	120	0.66
Coleoptera	2654	23.55	399	2.18
Coleoptera larvae	0	0	223	1.22
Pulmonata	28	0.24	0	0
total	11268	100	18318	100

4.1. Oligocheata

Oligochaeta were the sixth most abundant order collected by Berlese extraction, with a total of 314 individuals collected from 35 of the 240 samples, and contributed approximately 2% of the catch. The majority of individuals were collected from time period 1, when approximately 90% of the total number of oligocheates were caught (n=278, 88%). Only 2% and 10% caught in time periods 2 and 3 respectively. No oligocheata were found in pitfall traps.

4.2. Acari

Only seven mites were caught in pitfall traps, but there were 7139 Acari extracted from the soil cores by Berlese extraction, contributing almost 40% of the total Berlese catch, and were the second most abundant order collected by this method. The data was not normally distributed and transformed following section 2.3.

There was generally an increase in the density of Acari with time, in one case almost a 400% difference from time period 1 to 3 (site 3 mature).

The density of acari in the soil cores was generally higher in the mature plantations than in the open clearfell, table 5. In fact in the open sites there were only two samples with densities over $1,000m^2$, site 1 open, time periods 1 and 2, whereas in the mature sites only three sites had densities of less than $1,000m^{-2}$.

Table 5; Mean density (m^2)±1s.e. of Acari collected by Berlese extraction, calculated from transformed abundance data, n=229.

	Mature Plantation				Open Clearfell			
time period	1	2	3	4	1	2	3	4
1	854.48 ±13.00	1030.12 ±10.43	501.06 ±7.60	1159.61 ±15.92	1190.73 ±5.23	579.99 ±2.22	513.46 ±5.47	256.90 ±12.61
2	1335.49 ±11.03	1420.72 ±3.08	1499.42 ±10.73	727.30 ±10.66	1320.61 ±25.64	684.37 ±12.68	612.73 ±4.36	819.37 ±1.78
3	1513.40 ±4.98	1326.51 ±11.23	1846.28 ±8.93	1068.39 ±9.98	897.69 ±0.92	434.29 ±14.83	908.81 ±2.09	881.30 ±8.17

A three factor analysis of variance was carried out on the transformed abundance data, table 6. There were significant differences in the abundance of extracted acari between the time periods (F=7.43, df 2, 228, p=0.001) there were significant differences in the abundance of extracted acari between habitats (F=28.30, df 1, 228, p=.0000). The sites were also significantly different in the abundance of extracted acari (F=4.48, df 3, 228, p=.005).

Table 6; Summary of results of three factor analysis of variance calculated from transformed Acari Berlese extraction abundances using all time periods, n=229.

Berlese extraction			
	df	F	Sig. of F
Main Effects			
TIME	2	7.43	.001
HABITAT	1	28.30	.000
SITE	3	4.48	.005
2-Way Interactions			
TIME HABITAT	2	1.251	.289
TIME SITE	6	1.944	.075
HABITAT SITE	3	2.786	.042
3-Way Interactions			
TIME HABITAT SITE	6	3.081	.007

The data from each habitat and site were pooled together into the three time periods, and tested with a one way analysis of variance allowing analysis using the Tukey Honestly significant difference test (Tukey test).

There were no significant interactions between time with habitat and time with site, suggesting that the effect of time is constant across the habitats and sites. There were, as expected, significant differences between the three time periods, (One way ANOVA, F=7.19, df 2, 228, p=0.0009), with the Tukey test showing that all the time periods were significantly different from each other at the 0.05 level. This suggests that a very rapid increase occurred in the population levels during the course of this study.

4.3. Araneae

Araneae were the fourth most abundant order collected by Berlese extraction, with 714 collected in total representing approximately 4% of the total catch. The data was not normally distributed and was normalised following section 2.3.

Table 7; Mean density (m^2), ±1 s.e. of Araneae collected by Berlese extraction, calculated from transformed abundance data, n=229.

	Mature Plantation				Open Clearfell			
Time period	1	2	3	4	1	2	3	4
1	44.64 ±1.00	47.81 ±0.96	35.47 ±0.91	7.49 ±1.08	9.05 ±1.24	13.32 ±1.12	35.63 ±1.26	5.39 ±0.86
2	25.24 ±1.62	19.77 ±1.00	111.16 ±0.77	12.04 ±1.06	23.21 ±1.08	6.99 ±2.16	29.36 ±0.77	42.42 ±1.30
3	154.41 ±0.17	68.65 ±0.71	31.59 ±1.15	42.27 ±0.89	69.98 ±0.97	4.73 ±2.92	29.85 ±1.16	100.65 ±0.30

The mean density of spiders were much higher in the mature habitats than in the open habitats, table 7, and the mean density of spiders in general increased with time.

A three factor analysis of variance carried out on the transformed data, table 8, showed that there were significant differences between the different time periods (F=3.257, df 2, 228, *p*=0.040) and between habitats (F=4.220, df 1, 228, *p*=0.41). No significant differences were found between sites (F=2.297, df 3, 228, *p*=0.079).

A one way ANOVA conformed the significant differences in abundance between the time periods, (F=3.4128, df 2, 228, p=0.0347), and the Tukey test was applied, showing that all three time periods significantly different from each other at 0.05 level. There seems to be no simple linear pattern to this, as some sites increase, while others decrease with time.

Table 8; Summary of three factor analysis of variance results for pooled transformed Araneae data from pitfalls (N=240) and Berlese extractions, (N=229)

Pitfall traps				Berlese extraction			
	df	F	p		df	F	p
Main Effects				Main Effects			
TIME	4	48.52	.000	TIME	2	3.257	.050
HABITAT	1	90.29	.000	HABITAT	1	4.220	.047
SITE	3	2.38	.070	SITE	3	2.297	.122
2-Way Interactions				2-Way Interactions			
TIME HABITAT	4	1.02	.398	TIME HABITAT	2	0.020	.820
TIME SITE	12	1.82	.047	TIME SITE	6	1.935	.068
HABITAT SITE	3	4.29	.272	HABITAT SITE	3	1.711	.078
3-Way Interactions				3-Way Interactions			
TIME HABITAT SITE	12	.69	.760	TIME HABITAT SITE	6	1.118	.637

The Araneae were the third most abundant order trapped in pitfall traps, with a total of 1899 collected representing approximately 17% of the catch. The data was normalised following section 2.3.

Examining the data in table 9 it can see that in all but one sample sites the abundance of spiders is much higher in the open habitats than in the mature habitats, and there is a general decrease in density with time.

There was significant differences between the time periods (F=48.5, df 4, 239, p=.000) and between habitat (F=90.294, df 1, 239, p=.000) but not between the sites (F=2.387, df 3, 239, p=0.070).

Table 9; Mean ±1s.e. abundance calculated from transformed Araneae data from pitfall trap collection, n=6, N=240.

	Mature Plantation				Open Clearfell			
Time period	1	2	3	4	1	2	3	4
1	5.11 ±0.16	15.67 ±0.27	11.54 ±0.18	7.26 ±0.25	12.22 ±0.26	26.89 ±0.22	14.60 ±0.08	16.14 ±0.28
2	2.10 ±0.18	4.00 ±0.12	6.60 ±0.11	3.73 ±0.20	10.07 ±0.33	16.62 ±0.23	7.35 ±0.58	17.88 ±0.36
3	1.73 ±0.33	1.68 ±0.40	1.66 ±0.26	2.14 ±0.17	4.64 ±0.70	4.41 ±0.44	3.70 ±0.22	5.42 ±0.35
4	3.43 ±0.15	3.44 ±0.14	1.87 ±0.28	3.06 ±0.35	16.99 ±0.19	6.46 ±0.44	4.95 ±0.31	10.44 ±0.19
5	0.35 ±0.22	0.82 ±0.35	1.40 ±0.24	0.96 ±0.34	3.27 ±0.28	4.08 ±0.34	1.08 ±0.26	3.17 ±0.20

The data were pooled into the five time periods, and a one way ANOVA confirmed the significant differences in abundances between the time periods, (F=33.0968, df 4, 239, p=0.000), with the Tukey test showing that three significant homogenous subsets existed at the 0.05 level. Time period 1 was distinct from all other times, and times 2 and 4, times 3 and 5 forming two homogenous groups respectively. This suggests that there was no simple linear decrease in spider abundances throughout the survey period, or that there was not an decrease to a trough and then a rise, but that the sites behaved differently, this is supported by the significant interaction between these two factors, table 8.

4.4. Opiliones

Only 9 soil core samples contained Opiliones, and no analysis will be carried out on these data. A total of 464 Opiliones were caught in pitfall traps, accounting for approximately 4% of the total catch, and were the fifth most abundant order collected. The data was normalised following section 2.3.

Table 10; Mean ±1s.e. abundance of Opiliones calculated from transformed data for Pitfall traps in each habitat and time period, n=240

	Mature plantation				Open Clearfell			
Time period	1	2	3	4	1	2	3	4
1	0.15 ±0.16	0.36 ±0.44	0.22 ±0.25	0.50 ±0.65	0.27 ±0.31	0.41 ±0.51	0.34 ±0.40	0.33 ±0.39
2	0.27 ±0.31	0.27 ±0.31	0.28 ±0.33	0.26 ±0.30	0.15 ±0.16	0.20 ±0.22	0.27 ±0.31	0.21 ±0.23
3	0.32 ±0.37	0.12 ±0.12	0.55 ±0.74	0.35 ±0.41	0.36 ±0.43	0.30 ±0.35	0.41 ±0.51	0.20 ±0.22
4	0.25 ±0.28	0.18 ±0.19	0.45 ±0.58	0.39 ±0.47	0.26 ±0.29	0.41 ±0.50	0.38 ±0.46	0.54 ±0.71
5	0.20 ±0.22	0.38 ±0.47	0.42 ±0.53	0.19 ±0.21	0.58 ±0.79	0.36 ±0.43	0.27 ±0.31	0.47 ±0.61

The data, see table 10, are very variable and in all cases the standard errors are at least equal to, if not greater than, the mean. A three factor analysis of variance was carried out on the transformed abundance data, table 11.

There was significant differences in the abundance of opiliones trapped between the time periods (F=17.173, df 4, p=0.000) and between the sites (F=3.399, df 3, p=.024) but not between the habitat types (F=1.123, df 1, p=.371), table 11.

Table 11; Results of three factor analysis of variance, on transformed Opiliones abundance data from all sites, habitats and time periods collected in pitfall traps, n=240.

Pitfalls			
	df	F	p
Main Effects			
TIME	4	17.173	.000
HABITAT	1	1.123	.371
SITE	3	3.399	.024
2-Way Interactions			
TIME HABITAT	4	2.668	.053
TIME SITE	12	0.547	.224
HABITAT SITE	3	7.437	.148
3-Way Interactions			
TIME HABITAT SITE	12	1.848	.469

There were no significant interactions and the transformed abundance data from the time periods were pooled and a one way ANOVA confirmed the significant differences in abundance, (F=15.0267, df 4, 239, p=0.000). A Tukey test showed that there were three significantly different homogenous subsets. Times 5 and 4 were significantly different to all other times (group 3), time 3 significantly was different to all other time periods (group 2), and times 1 and 2 were significantly different to all other time periods, (group 1) at the 0.05 significance level. Relating these groups to table 10 there seems to be clear pattern.

The significant differences in abundance between the sites was confirmed (one way ANOVA, F=2.4078, df 4, 239, p=0.0679). and all the sites were significantly different from each other at the 0.05 level from the Turkey test, this would suggest that local environmental factors are more important than the effects of two major habitat types.

4.5. Pseudoscorpionidae

Only two Psuedoscorpions were caught in pitfall traps, and very few Pseudoscorpionidae were extracted from the soil cores, with 96 extracted in total, from 49 of the total of 229 soil cores. Due to the low number of samples containing

Pseudoscorpionidae it was decided to test only those samples that contained psuedoscorpions for differences between the open clearfell and mature plantation habitat. The data were analysed using a t-test, there was no difference between abundances in the mature plantation and open clear felled habitats with a *p* value of 0.30, (t=-1.0479, n=49, df 47).

4.6. Collembola

59 of the 240 pitfalls contained Collembola and the majority (*c.* 75 %) were caught in the first sampling period. There is little point in testing for differences between time periods. However, when the abundance for habitat was examined the majority (*c.* 90 %) are also trapped in the mature plantations, with 29 caught in the open, and 157 the mature plantation. No Collembola caught in pitfall traps in the open habitat after the first time period.

In contrast Collembola were the most abundant order extracted from the soil cores, with 8121 extracted, accounting for 44% of the total catch. The data was transformed following section 2.3.

If table 12 is examined there is a general increase in density with time, although this is neither uniform with samples, nor constant across the sites. The pooled transformed data were analysed using three factor analysis of variance, and the numbers extracted from the cores were significantly different from the three time periods (F=23.100, , df 2, 228, p=.000). There was significant differences in the numbers extracted from each habitat (F=4.298, df 1, 228, p=.000) with generally more collected in the mature plantation. There was significant differences between the numbers of Collembola caught between the sites (F=11.630, df 2, 228 p=.000), see table 13.

Table 12; Mean density (m^{-2})±1s.e. of Collembola in each habitat type collected by Berlese extraction, n=229.

	Mature plantation				Open Clearfell			
Time Period	1	2	3	4	1	2	3	4
1	548.60 ±5.56	249.17 ±3.84	1781.21 ±35.46	277.38 ±4.55	709.98 ±32.99	717.25 ±42.18	139.47 ±7.96	152.61 ±1.88
2	453.98 ±3.38	885.46 ±11.19	2593.14 ±8.68	2240.39 ±17.89	1135.00 ±6.92	583.48 ±10.08	2011.59 ±31.39	146.54 ±5.18
3	1420.10 ±7.15	2295.61 ±7.52	2079.65 ±19.22	1513.26 ±17.56	822.05 ±16.49	1828.20 ±14.60	1599.57 ±51.56	499.26 ±7.19

There were no significant interactions between time and habitat, suggesting that an underlying biological mechanism applying to both habitats, however there were significant interactions between both time and site, and habitat and site, suggesting that the four sites did not respond in a similar manor.

Table 13; Summary results of three factor analysis of variance on transformed Collembola data.

Berlese			
	df	F	p
Main Effects			
TIME	2	23.100	.000
HABITAT	1	4.298	.000
SITE	2	11.630	.000
2-Way Interactions			
TIME HABITAT	2	1.004	.481
TIME SITE	4	5.769	.000
HABITAT SITE	2	6.835	.000
3-Way Interactions			
TIME HABITAT SITE	4	5.299	.000

4.7. Hemiptera

A total of 118 hemipterans, true bugs, were trapped in 61 of the 240 pitfall traps, contributing approximately 1% of the catch, and were the seventh most abundant order caught. Only 11 samples (11%) from the mature sites contained hemipterans, with a total of 14 caught, the vast majority were caught in the open habitats, with 50 samples containing 104 hemipterans, approximately 90% of the total pitfall catch.

A total of 227 hemipterans were extracted from 57 of the 229 soil cores, accounting for approximately 1% of the total catch, and again was the seventh most abundant order. Only 7 cores of the 57 cores containing hemipterans were found in the mature plantation, with only 10 of the 227 hemipterans caught. Most of the hemipterans were collected in the open habitat, accounting for 96% of the hemipterans caught. There was a significant decrease in the numbers of hemipterans caught with time (one-way ANOVA, df 2, n=50, *p*=0.009) with a five fold difference (time 1 n=150, time 2, n=40, time 3 n=27).

4.8. Lepidoptera

A total of 22 adult Lepidoptera were caught in the pitfall traps, accounting for less than 1% of the catch. There was little pattern to those collected, other than only one Lepidoptera was ever found in a trap at a time. There was not enough data to justify individual analysis of this data.

4.9. Diptera

There were only adults in the pitfalls traps, but both pupae and larvae were collected by Berlese extraction.

A total of 74 larvae were extracted for the soil cores accounting for 0.4% of the catch, and were the eleventh most abundant 'order'. There were not enough collected to analyse the differences between the replicate sites or the different time periods, however pooling the data there were significantly higher abundances per sample in the open habitat (t-test, t=3.657 n=35, df 28, p=.0001).

There were a total of 36 diptera pupae extracted from the soil cores, which accounted for 0.2% of the catch, and was the thirteenth most abundant 'order'. The pupae were only extracted from time period 1, this suggests that eclosure had occurred between time periods 1 and 2. There were more pupae found in the open sites than in the mature site, with 28 collected from the open sites compared to 8 from the mature sites.

The diptera adults were the third most abundant order, with 714 adult diptera extracted from the soil cores, accounting for *c.* 4% of the catch. The data was normalised following section 2.3, three factor analysis of variance was carried out on the transformed data, table 14. There were significant differences in the abundance of between the habitats (F=8.444, df 1, p=0.002) between the sites (F=2.701, df 3, p=0.028) but there was no significant differences between the time periods, (F=2.225, df 2, p=.119).

In general the open sites had a higher density of diptera than the mature sites, the main exception is site 4 had higher densities constantly in the mature habitat throughout the sampling season.

Table 14; Mean Density(m^{-2})±1s.e. of Diptera calculated from the transformed abundances extracted from the soil cores, n=229

	Mature Plantation				Open Clearfell			
time period	1	2	3	4	1	2	3	4
1	0.15 ±0.05	0.35 ±0.08	0.67 ±0.06	0.27 ±0.11	0.51 ±0.15	0.58 ±0.10	0.60 ±0.08	0.12 ±0.05
2	0.52 ±0.09	0.49 ±0.11	0.18 ±0.08	0.40 ±0.10	0.68 ±0.17	0.68 ±0.05	0.46 ±0.04	0.34 ±0.09
3	0.35 ±0.08	0.14 ±0.07	0.30 ±0.08	0.42 ±0.08	0.65 ±0.09	0.27 ±0.09	0.40 ±0.12	0.34 ±0.36

The diptera were the most abundant order caught in pitfall traps, with 5247 individuals caught, accounting for 46.56% of the total pitfall catch. The data was normalised following section 2.3.

There was not a general pattern to the mean abundances for each site, other than in the majority of sites the mean abundance caught decreases with time.

There were significant differences in the abundance of diptera caught through time (F=7.389, df 4, 228 p=.000). There were significant differences in the abundance of diptera caught in pitfall traps between the habitats (F=66.874, df 1, 228 p=.000) and significant differences in the abundances between each site(F=17.746 df 1, 228 p=.000) however this is complicated by significant interaction effects, both at the two way interaction level and at the three way interaction level, table 16.

Table 15; Mean abundance±1s.e. of adult Diptera calculated from transformed abundances in pitfall traps, n=240

	Mature Plantation				Open Clearfell			
Time period	1	2	3	4	1	2	3	4
1	8.03 ±0.27	40.16 ±0.31	11.34 ±0.42	37.06 ±0.11	31.95 ±0.34	48.90 ±0.41	9.93 ±0.10	9.52 ±0.32
2	11.49 ±0.34	70.20 ±0.20	19.98 ±0.33	39.84 ±0.09	9.52 ±0.27	25.34 ±0.40	8.57 ±0.17	5.52 ±0.40
3	12.62 ±0.41	31.64 ±0.07	11.62 ±0.28	39.01 ±0.18	5.45 ±0.33	15.23 ±0.27	9.68 ±0.24	7.54 ±0.24
4	13.23 ±0.17	37.07 ±0.09	20.01 ±0.08	27.15 ±0.30	8.31 ±0.27	10.43 ±0.55	10.83 ±0.11	7.01 ±0.26
5	17.95 ±0.53	26.54 ±0.39	10.23 ±0.20	11.94 ±0.30	4.17 ±0.51	5.10 ±0.62	11.66 ±0.31	3.59 ±0.48

Table 16; Summary of results of three factor analysis of variance on transformed diptera adult pitfall abundances, for pitfall trap data (N=240) and Berlese extraction data (N=229).

Pitfall				Berlese			
	df	F	p		df	F	p
Main Effects				Main Effects			
TIME	4	7.389	.000	TIME	2	2.225	.119
HABITAT	1	66.874	.000	HABITAT	1	8.444	.002
SITE	3	17.746	.000	SITE	3	2.701	.028
2-Way Interactions				2-Way Interactions			
TIME HABITAT	4	4.527	.002	TIME HABITAT	2	0.070	.901
TIME SITE	12	2.053	.022	TIME SITE	6	6.549	.000
HABITAT SITE	3	9.485	.000	HABITAT SITE	3	4.098	.004
3-Way Interactions				3-Way Interactions			
TIME HABITAT SITE	12	2.790	.019	TIME HABITAT SITE	6	0.968	.568

4.10. Hymenoptera

A total of 120 hymenopterans were extracted from 37 of the 229 soil cores, accounting for only 0.66% of the catch, and were the ninth most abundant order collected. There was an increase in the number of samples containing hymenopterans with time (t=1 n=9, t=2 n=8, t=3 n=20), with only 18 of the hymenoptera collected in the mature plantation.

Hymenopterans were the fifth most abundant order collected in pitfalls and a total of 573 were collected in 181 of the 240 pitfall traps (c. 75 %), contributing approximately 5% of the catch. The abundance values obtained were not normally distributed, and could not be normalised using any of the standard methods outlined in section 2.3.

The data was therefore analysed using the non parametric Kruskal-Wallis test. A three factor analysis was carried out in line with the previous analysis of variance tests, see table 17, there was significant differences between the time periods, between the habitats and sites, but no significant interactions.

Table 17; Summary of results of three factor Kruskal-Wallis analysis of variance for untransformed hymenoptera pitfall abundances, n=240.

Pitfalls		
	df	p
Main Effects		
TIME	4	$p < 0.001$
HABITAT	1	$p < 0.001$
SITES	3	$p < 0.001$
2-Way Interactions		
TIME HABITAT	4	$p > 0.05$
TIME SITES	12	$p > 0.05$
HABITAT SITES	3	$p > 0.05$
3-Way Interactions		
TIME HABITAT SITES	12	$p > 0.05$

There was no general pattern in the data, although the total number recorded in each habitat and each time period differed from random ($\aleph^2=24.77$, df 4, $p<0.001$) with two distinct peaks in the data one in time period 2 and one in time period 5, due to high numbers of Bees collected (Hymenoptera: Aculeata) in the open habitat (*pers. obs.*).

4.11. Discussion

Springtails (Collembola) and mites (acari), the two most abundant orders collected from the soil cores, play an important role in the decomposition process (Swift *et al.* 1979). Free living mites occur in a great variety of habitats, and they are especially abundant where there is organic detritus. Block (1966) studied the mites of moorland peat and mineral soils, at altitude at Moor House Nature Reserve. Before his work it had been reported that the peak abundance in mite populations was during autumn and winter, except in alpine and arctic soils (Block 1966). He found that there were considerable variations in the peak mite populations, with the common species peaking in summer in 1961, but in autumn in 1962. It was thought that 1961 represented a more usual response as there was a late spring in 1962. The mean densities found in this study were much lower than those in the Moor House study, but are not strictly comparable as were obtained by different extraction techniques. The main factor limiting the population abundances was thought to be the low temperature, restricting the length of the breeding season, with two possible responses, namely species having one generation per year and species having two generations per year (Block 1966). The higher densities in the mature habitat and open clearfell in this study is probably a true reflection of a difference in numbers, and not and effect of the sampling method, as the soil characteristics were so similar. The peak abundances in the mature habitat were constant across the sites, in time period 3, at the end of June, but the peak abundances in the soil of the open clearfell sites were much more variable, with half of the sites having peak abundance in the earlier time periods. This could be related to temperature effects as it is known that plantations are less susceptible to extreme temperature variation (Grace and Unsworth 1988) and across the four sites the conditions may be more constant, whereas the difference in vegetation cover in the open sites leads to temperature variation (Grace an Marks 1978) which would be reflected in the peak populations of the mites.

Springtails (Collembola) are one of the main biological components of the soil fauna (Swift *et al.* 1979) and indeed were by far the most abundant order extracted from the soil in this study. There was a rapid increase in the numbers of springtails throughout the period of the study, and although all four plantation sites did not respond in the same manner, the transects within each plantation block responded in the same manner. The springtails were much more abundant in the plantation blocks than in the open sites, with the only comparable abundances being in the open sites with the low vegetation cover and high amount of wood debris, site 2. The tree stumps were an important component of this habitat (*c.f.* plate 6) which are known to be a habitat 'refugia' for springtails (Setälä and Marshall 1994). It is known that population cycles and the rate of development in springtails are related more to temperature than to an internal biorhythm, with the effect of moisture playing an important role. Usher (1970) found only one peak in the collembolan population in the litter layer in Pine forests in Scotland, but Hale (1966) showed two peaks in moorland collembolan populations at Moor House Nature Reserve, Usher (1970) attributed these differences to the more severe climatic conditions in Scotland. Badejo and van Straalen (1993) showed that there were large differences in the number of springtails in forest and deforested cassava plots in Nigeria, with different genera peaking in density at different times. However, although these differences were attributable to differences in soil moisture, the replicates within the cassava site did not behave homogeneously. Changes in collembolan densities varied from year to year in Holland, in a site specific manner, (Hogervorst *et al.* 1993) and found that different families reacted in different ways to changes in the needle litter. In Huhta and Mikkonen (1982) it was found that one species (*Lepidocyrtus lignorum* FABR.) had extremely high densities (over 10,000m^2), but most species had densities comparable with those of the present study. The main species (Genus *Entomobyra* L.) found reacted differently to clear cutting, with the species peaking in abundance at slightly different times and of different magnitudes under the tree canopy and in the clear cuts. From the single peaks observed by Huhta and Mikkonens' (1982) study they suggested that the open clear cuts are much more variable in the temperature regime, as during the day the litter layer open sites were approximately 3^{o}C higher than the Spruce stands, but at night approximately equal, with a maximum of 7^{o}C difference. As temperature is known to affect the development time this suggests that 'stable' temperature and moisture regimes under the mature plantation blocks allow more regular population growth, to a higher level, and that the population peak would be earlier in the open clearfell site and at levels more dependent upon the local environment factor.

Spiders (Araneae) are known to be important predators in the uplands (Coulson and Whittaker 1978) but the communities present are primarily influenced by vegetation 'architecture' (Coulson and Butterfield 1986), and most upland spiders have a wide geographical distribution (Otto and Svensson 1982). The proportion of hammock web builders (Linyphiidae) to other spider families increases with increasing altitude, with this family the dominant at high altitude (Downie *et al.* 1995). In this study there was generally an increase in the numbers of spiders extracted from the soil cores over the duration of the sampling period, but there was a decrease in the numbers of spiders caught in the pitfall traps. In both cases there were significant differences between the two habitats, but there were more spiders extracted from the soil cores in the mature plantation, whereas there were more spiders collected in the pitfalls in the open clearfell habitat. This would suggest that either there are two separate communities of spiders being collected, or that the pitfall traps were ineffective in catching spiders in this study. As pitfall traps have been used successfully in previous studies (Downie *et al.* 1995, Bultman and Utez 1982) it is probable that there are differing responses in the soil dwelling and surface active components of the spider community. As previously discussed with the mites and springtails, the effects of temperature in the plantation may be important, with the spiders inhabiting the soil litter having a more consistent prey resource, behaving in a more predictable manner. The structure of the litter layer is known to affect the spider communities found (Bultman and Utez 1982) and litter depth rather than litter nutritional quality affects the abundances caught, this combination is fulfilled in the mature plantation, with a deep, structurally complex nutritionally poor litter layer. If the surface active component *are* influenced by the vegetation structure, which has been shown very locally (Bell 1993), this would explain the differences in the abundances between the open clearfell and mature plantation sites, with the more complex vegetation architecture of the open clearfell (as opposed to no ground flora in the mature plantation) supporting a greater number of niches, and hence spiders (Krebs 1985). The differences in plant species composition between the four open sites may be reflected in the plant architecture, and although this was not measured their were differences in the vegetation height and structure (pers obs, *c.f.* Plates 5-8). This may account for the differences in numbers caught in pitfalls between the sites, with sites with generally the highest amount of vegetation, 1 and 4, having the highest abundances of spiders.

Harvestmen (Opiliones) are surface active invertebrate predators, feeding on soil litter species. Low numbers were found during the course of this study, and there were no differences in the numbers caught between the two habitat types. However there were significant differences in the numbers caught between the site. It would seem that there were overriding differences between the four sampled areas rather than between the mature and open habitats. The reasons behind this would appear to be the reliance of harvestmen on the vegetation structure, to a lesser extent reflecting the same ecological constraints as the spiders. No equivalent harvestmen component in the litter layer was discovered.

There were a low number of Hymenopterans recorded in the study with very few and most of those caught being bumble bees (Hymenoptera: Aculeata) which were utilising the heather (pers. obs.). Low number of parasitoids were caught which fits with the general idea of a decline in parasitoids with altitude (Randall 1982), although neither method of data collection in this study is particularly ideal for the study of parasitic wasps. The utilisation of open habitats by bees may be an important factor in retaining genetic links between plants within the forest and from the moorlands in the vicinity, with regards to pollination. If the seeds germinating in the open clearfell are over 50 years old there is a high potential for cross generation reproduction.

True flies (Diptera) were the most abundant order caught in pitfall traps, and had a high abundance in the soil cores. The presumed eclosure of the flies from time period 1 to 2 may be an artefact of the extraction method as the Berlese Tullgren funnels are, as described in Chapter 2, a behavioural method and rely upon the response of the fauna in the sample. Pupae in general have limited response capability usually related to movement, such as from parasitoid probing, and not to environmental factors. However, this emergence would agree with the 'spring peak' (*sensu* Coulson 1988, Coulson 1978) in diptera abundances in the uplands. The higher numbers of larvae, pupae and adults from the soil cores collected in the open would suggest that habitat may either support higher numbers of flies, or a wider range of species, but the 'spring peak' in abundance was not recorded in the soil cores. There appears to be no clear cut explanation for the differences in this data other than the high mobility of this order. This coupled with this orders high diversity and the different site characteristics may mean that several different components of the diptera community may have been sampled simultaneously. This would be particularly important if mainly fungivorous flies are being sampled in the mature plantation, and mainly carnivorous and detritovorous species sampled in the open habitat. The diversity of fly species in both habitats needs to be assessed, as the differences noted (suffered!) were of high numbers of *Hydrotaea irritans* (Diptera Muscidae) in the open clearfell, which were absent from the mature plantations (pers. obs.).

Chapter 5

Results:

Coleoptera

The Coleoptera were the fifth most abundant order extracted from the soil cores, with 399 adults extracted, accounting for *c.* 3% of the catch. Coleoptera larvae were extracted, with 233 extracted, and were the eighth most abundant order. The Coleoptera were the second most abundant order collected by pitfall trapping, with 2654 collected, approximately 25% of the pitfall catch. This order was chosen for more detailed analysis, namely at the family and species level. Although data was collected on both adults and larvae, only the adult data will be considered here.

5.1. Analysis of Coleoptera Families.

As previously outlined the aims of the study were to distinguish differences amongst habitats, and so the data from each time period has been pooled together.

There were seven families of beetles extracted from the soil cores. One family, the Staphylinidae accounted for 68% of the catch. The Carabidae were the second most abundant order extracted accounted for *c.* 30% of the number extracted. Almost all of the adult carabids collected were of one species, *Trechus obtusus*, with only two other individuals recorded, one *Calathus melanocephalus* and one P*terostichus adstrictus*. Two families accounted for less than 5% of the total number extracted, the Endomychidae (2.5%) and Curculionidae (1.5%). The other families, the Dryopidae, Rhizophagidae and Cryptophaigdae all accounted for less than 1% of the total number extracted. The dominance by the Staphylinids was examined, comparing the two habitat types, were there was no significant difference, (t test, t=-1.45, df 95, p=0.145).

There were 2654 beetles collected in pitfall traps, which belonged to nine families, table 18. Two families contributed over 90% of the catch (Carabidae 76.18 %, Staphlynidae 16.47%). Four of the families sampled contributed less than 1% of the catch (Curculionidae 0.41%, Leiodidae, 0.11%, Erotylidae 0.04%, Psephenidae 0.23%), and the remaining three families contributed less than five percent of the catch, (Silphidae 3.69%, Coccinelidae 1.70%, Endomychidae 1.17%).

Table 18; Showing Abundance and Percentage abundance of each Beetle family collected in the pitfall trap, n=48

Family	Abundance	Percentage Abundance
Silphidae	98	3.69
Staphylinidae	437	16.47
Carabidae	2022	76.19
Coccinelidae	45	1.70
Curculionidae	11	0.41
Leiodidae	3	0.11
Erotylidae	1	0.04
Psephenidae	6	0.23
Endomychidae	31	1.17
Total	2654	100

Graph 1, page 41, shows the number of families in each pitfall traps, in the correct spatial orientation, although the x and y axis are not to scale. There were significantly more beetles caught in the open habitat, table 19, than in the mature habitat (t test, t=-6.76, df 28, n=48, p=0.000) although there were not significantly more families caught in each pitfall trap, table 20, in the open habitat than the mature habitat (two tailed t test, t=-0.501, df 46, n=48, p=0.618).

Table 19; Showing mean±1s.e. abundance of Coleoptera in open clearfell and mature plantation, n=48

Site	Mature plantation	Open clearfell
1	15.83 ±3.28	110.83 ±18.60
2	30.67 ±2.80	85.83 ±5.17
3	39.17 ±4.75	57.17 ±6.14
4	40.67 ±3.56	62.17 ±9.41

Table 20; Mean number±1s.e. of beetle families in each site from pooled time pitfall trap data, n=48

Site	Mature plantation	Open clearfell
1	2.50 ±0.27	3.17 ±0.38
2	2.83 ±0.49	3.17 ±0.20
3	3.67 ±0.68	2.83 ±0.38
4	3.17 ±0.38	3.50 ±0.42

5.1.2. Coleoptera: Staphylinidae.

There were 437 staphylinid beetles collected in pitfall traps, contributing approximately 17% of the total pitfall catch and were the second most abundant beetle family collected. Graph 2, page 41 shows the spatial pattern of Staphlynid beetles caught in each pitfall trap, and although the x and y axis are not to scale the abundance bars are in the spatially correct orientation in relation to each other. There were significantly more staphylinids in the mature plantation than in the open habitat (t test, t=3.6817, df 46, n=48, p=0.000) with a mean±1s.e. abundance per pitfall trap of 12.13±1.07 in the mature habitat, and 6.08±1.29 in the open habitat. Within the habitats there were significant differences between the mature sites (one way ANOVA, F=3.138, df 3, n=24, p=0.048) with significantly more at site 3 (17.00±1.95) than at sites 1, 2 and 4 (9.83±2.42, 11.17±2.40, and 10.50±2.32 respectively). Sites 2, 3 and 4 in the open habitats had much lower mean±1s.e. abundance per pitfall trap of staphylinds than site 1, table 21.

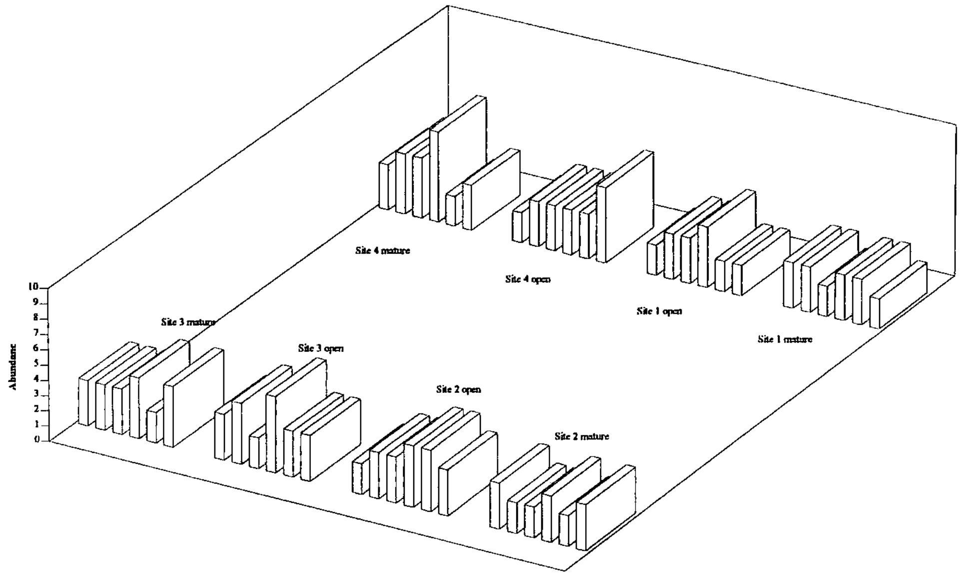
Table 21; Mean ±1s.e. of Staphylinid beetles caught in pitfall traps in Open clearfell and Mature plantation habitats, n=48.

Site	Mature plantation	Open clearfell
1	9.83 ±2.42	14.00 ±3.39
2	11.17 ±2.40	2.17 ±0.74
3	17.00 ±1.95	3.33 ±1.29
4	10.50 ±2.32	4.83 ±1.99

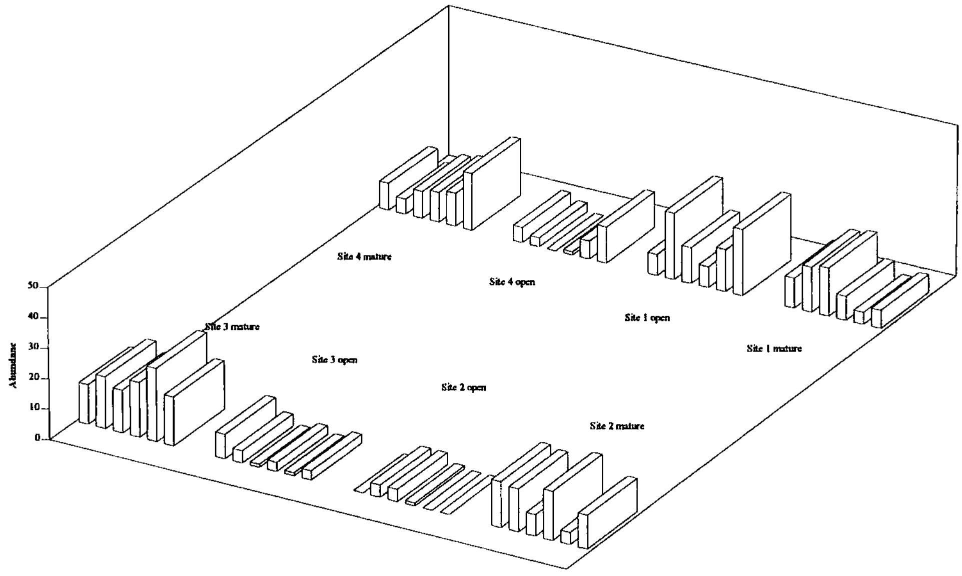
5.1.3. Coleoptera: Silphidae.

There were 98 silphidae caught in pitfall traps during the study, contributing approximately 4% of the catch and were the third most abundant beetle family trapped. The silphidae beetles caught were all members of the genus Nicrophorus, or Sexton beetles, which bury the carcasses of small vertebrates. They were found in large numbers in only 8 of the sites, and apart from one trap in mature plantation all were found in the open clearfell site. This was due to the presence of shrews (*Sorex sp.*) in the pitfall traps, and as such the distribution of this family is related more to the distribution of the 'prey' population of shrews than the habitat type *per se*.

Graph 1; Showing the number of Beetle families in each pitfall trap, for both open clearfell and Mature plantation, n=48



Graph 2; Showing spatial distribution of the abundance of Staphylinid beetle pooled for time in pitfall traps in mature plantation and open clearfell sites. n=48. Note that the x and y axis are not to scale.



5.1.4. Coleoptera: Coccinelidae.

There were 45 coccinelids, or ladybirds, trapped in the pitfall traps, this family was the fourth most abundant family trapped, accounting for approximately 2% of the catch. All the coccinelids trapped were individuals of the seven spot ladybird (*Coccinella septempunctata* L.). There were only two found in the mature plantation, with 43 found in the open clear fell (95%) 35 of the 43 were found in sites 3 and 4 (77%), that is, the eastern most side of the open clearfell, with 8 (17%) trapped at sites 1 and 2. This species was at very high number on the open habitat during the course of the study (pers obs.) with extremely visible individuals easy to notice, and at such a level that the number caught in the pitfall traps is a poor reflection of the number actually present at the site.

5.1.5. Coleoptera: Endomychidae.

There were 31 endomychidae trapped in pitfall traps, and were the fourth most abundant beetle family collected, accounting for approximately 1% of the total number of beetles caught in pitfall traps. No endomychidae beetles were trapped in the open habitat, in the mature plantation there were 7 trapped in the western plantation (site 1, 3, site 2, 4, 22.6%), and 24 trapped in the eastern plantation (site 3, 16, site 4, 8, 67.24%).

5.2. Coleoptera: Carabidae.

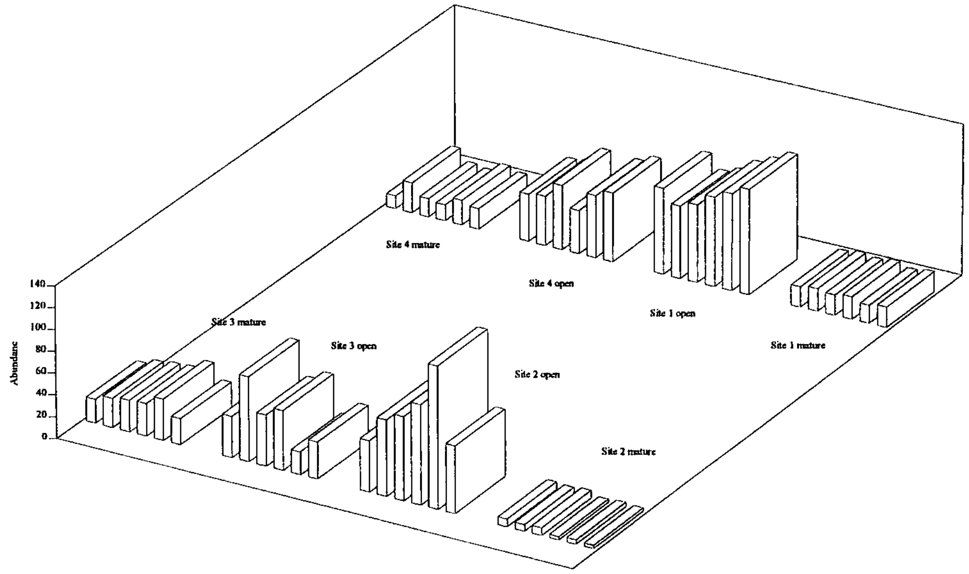
The carabids were the most abundant family collected, with 2022 carabids collected in the pitfall traps, contributing approximately 80% of the catch (76.19%). The data obtained from the pitfall traps were not normal but normalised successfully following section 2.3. Graph 3 , page 43, shows the spatial distribution of carabids of pooled pitfall abundances in the open and mature habitats, although the x and y axes are not to scale the traps are in the correct spatial orientation with respect to each other. As a family the carabids were significantly more abundant in the open habitat (t test t=-8.798, df 32, n=48, p=0.000) with a mean±1s.e. per pitfall trap of 14.09±1.16 in the mature habitat and 63.63±1.08 in the mature habitat.

The carabids were identified to species to allow community analysis at the most specific level. There were 19 species identified in total, with the total number caught and percentage of the catch of each species shown in table 22.

Table 22; Total abundance and percentage abundance of Coleoptera: Carabidae species in pitfall traps, of untransformed data pooled for habitat and time., n=48.

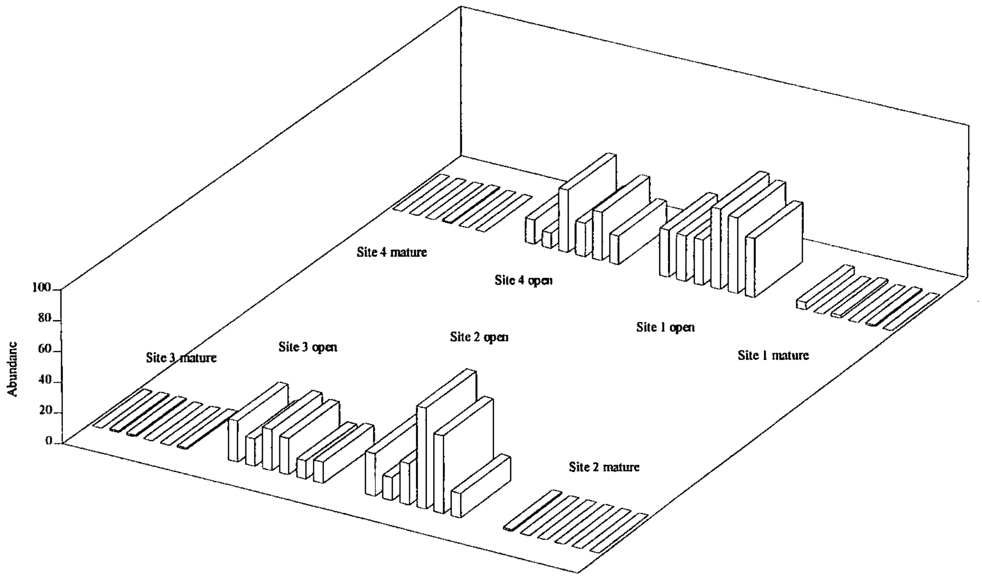
Species	Abundance	Percentage abundance
Carabus problematicus	446	22.06
Agonum assimile	5	0.25
Loricera pilicornis	4	0.20
Elaphrus cupreus	3	0.15
Trechus obtusus	143	7.07
Trechus quadristriatus	7	0.35
Calathus micropterus	178	8.80
Amara similata	10	0.49
Notiophilus biguttatus	55	2.72
Pterostichus adstrictus	711	35.16
Pterostichus diligens	10	0.49
Pterostichus niger	189	9.35
Pterostichus nigrita	4	0.20
Pterostichus strenuus	5	0.25
Pterostichus madidus	8	0.40
Leistus rufescens	27	1.34
Nebria salina	214	10.58
Cychrus caraboides	3	0.15
total	2022	

Graph 3; Showing the spatial distribution of abundances of Carabid beetles in pitfall traps in Open clearfell and Mature plantation habitats. n=48, Note that the x and y axis are not to scale.



There were two species which accounted for approximately half of the total number of carabid species trapped (*Pterostichus adstrictus*, 35.16%, *Carabus problematicus*, 22.06%) with 10 of the 19 species contributing less than 1% of the catch (*Agonum assimile*, 0.25%, *Loricera pilicornis*, 0.20%, *Elaphrus cupreus*, 0.15%, *Trechus quadristriatus*, 0.35%, *Amara similata*, 0.49%, *Pterostichus nigrita*, 0.20%, *Pterostichus strenuus*, 0.25%, *Pterostichus madidus*, 0.40%, *Cychrus caraboides*, 0.15%).

Graph 4; Showing the spatial distribution of abundances of *Pterostichus adstrictus* in pitfall traps for mature plantation and open clearfell habitat., n=48, Note that the x and y axis are not to scale



5.2.1. *Pterostichus adstrictus.*

Pterostichus adstrictus was the most abundant carabid species of trapped in pitfall traps, with 711 individuals collected, or approximately 35% of the total number of carabids in the pitfall catch (35.16%). This species was trapped in pitfall in both the mature plantation and open clearfell habitats with individuals found in 32 of the 48 pitfall trap sites (66%) but all 24 of the open clearfell sites, *i.e.* this species was found in only 8 of the mature sites. There were only 13 of the 711 individuals trapped in the mature plantation (1.8%), and the difference in the abundance of individuals caught in the four open sites was not significant (One way ANOVA, F=2.160, df 3, n=24, p=0.079).

5.2.2. *Carabus problematicus.*

Carabus problematicus was the second most abundant carabid species trapped, with 446 individuals trapped, or approximately 22% of the total number of carabids collected. This species was trapped in pitfall in both the mature plantation and open clearfell habitats with individuals found in 46 of the 48 pitfall trap, approximately 95% of the traps (95.83%). The data was not normally distributed but normalised following section 2.3. There was significantly more individuals in the open clearfell than in the mature plantations (t test, t=5.2994, df 46, n=48, p=.0000) with mean±1s.e. of 13.62±0.53 individuals per pitfall trap in the open clearfell, and a mean±1s.e. of 5.25±0.54 individuals per pitfall trap in the mature habitat.

5.2.3. *Nebria salina.*

Nebria salina was the third most abundant species, with 214 individuals trapped contributing approximately 10% of the total number of carabids in the pitfall catch. This species was found in 29 of the 48 pitfall traps (60.42%) with individuals trapped in 23 of the 24 open clearfell pitfall traps (95.83%) compared to 5 of the 24 pitfall traps in the mature plantation (20.83%). Only 8 individuals were trapped in the mature plantation habitat. There were significantly more individuals trapped in the open clearfell sites 1 and 2, than sites 3 and 4 (one way ANOVA, F=11.4531, df 3, n=24, p=.0002) with means±1s.e. of 16.5±4.18 and 12±1.64 for sites 1 and 2, and means±1s.e. of 3.5±1.81 and 2.33±0.93 for sites 3 and 4 respectively.

5.2.4. *Pterostichus niger.*

There were 189 *Pterostichus niger* individuals trapped during the course of the study, accounting for approximately 10% (9.35%), of the total number of carabids caught in pitfall traps, and were the fourth most abundant carbid beetle trapped. Individuals were collected in 29 of the 48 pitfall traps (60.42%) but only 6 of the 24 (25%) of the pitfall traps in the mature plantation habitat with individuals collected in 23 of the 24 (95.83%) pitfall traps in the open clearfell pitfall traps. Only 10 of the 189 individuals trapped were collected in the mature plantation, and were all trapped in the same plantation block, (sites 3 and 4), there were not significant differences in the number of *Pterostichus niger* individuals trapped in the different open clearfell sites (one way ANOVA, F=2.7158, df 3, n=24, p=0.07).

5.2.5. *Calathus micropterus.*

Calathus micropterus was the fifth most abundant carabid beetle trapped in pitfall, with 178 trapped, accounting for approximately 8% of the total number of carabid beetles trapped (8.80%). Individuals were collected from 39 of the 48 pitfall traps (81.25%) with individuals collected in 16 of the 24 pitfall traps in the open habitat (66%) and 23 of the 34 pitfall traps in the mature plantation habitat (95.83%). There were significantly more individuals trapped in the mature plantation (t test, t=4.900, df 30, n=48, p=0.000) with a mean±1s.e. of 6±0.93 trapped per pitfall trap in the mature plantation, and a mean±1s.e. of 1.38±0.36 individuals trapped in the open habitat.

5.2.6. *Trechus obtusus.*

There were 143 *Trechus obtusus* individuals trapped, accounting for approximately 7% of the total number of carabids collected in pitfall traps, and were the sixth most abundant carabid collected in pitfall traps. Individuals were collected in 37 of the 48 pitfall traps (77%) with individuals collected in 20 of the 24 (83.33%) pitfall traps in the mature plantation habitat, and 17 of the 24 pitfall traps in the open clearfell habitat (70.83%). There were significantly more individuals trapped in the pitfalls in the open clearfell habitat (t test, t=-2.2689, df 27, n=48, p=0.0314) with a mean±1s.e. of 4.00±0.09 individuals per pitfall trap in the open clearfell habitat, and a mean±1s.e. of 1.95±0.27 individuals per pitfall trap in the mature plantation habitat. There were not significant differences in the number of individuals trapped in the different plantation sites (one way ANOVA, F=0.8615, df 3, n=24, p=0.477) although site 1 in the open had significantly more individuals collected than sites 2, 3 and 4 (one way ANOVA, F=4.6352, df 3, n=24, p=0.0128) with a mean±1s.e. individuals per pitfall trap of 8.50±2.42 in site 1, and 1.83±1.49, 3.16±1.65, 2.5±1.08, in sites 2, 3 and 4 respectively.

5.2.7. Rare species of Carabid.

12 species of carabid collected contributed less than 7 percent of the catch, with a total of 141 individuals. Less than 10 individuals were trapped for most of these species, with *Notiophilus biguttatus* and *Leistus rufescens*, the exceptions with 55 and 27 trapped respectively. *P.strenuus*, and *L.pilicornis* were found exclusively in the open habitats, as were *P.diligens*, *P.madidus*, *T.quadristriatus*. *P.nigrita* and *A.assimile* were found manly in the mature habitats, with only one individual of each species found in the open habitat. *Cychrus caraboides* was the only species found only in the mature plantation, with only three individuals trapped.

5.3. Discussion

Until recently little was known about the upland beetle fauna (Ratcliffe and Thompson 1988, Butterfield and Coulson 1983). The work which had been carried out was mainly of species responses to altitudinal gradients (*e.g.* Pearson and White 1964). The study by Butterfield and Coulson (1983) identified five main peatland carabid communities, and species from each of those communities were recorded in this study.

The more detailed examination of the two habitat types in this study at the beetle family and species level revealed large differences in the surface active component, that is those caught in pitfall traps, but not such a difference in those extracted from the soil cores. Only seven families of beetles were extracted from the soil cores, with one family, the rove beetles (Staphylinidae), accounting for the bulk of the catch. The number of rove beetles extracted from the soil cores was not different in the two habitats, suggesting that an underlying characteristic, such as soil type, may account for this families distribution. The rove beetles were the second most abundant family caught in the pitfall traps, with a more caught in the mature plantation than in the open clearfell. In fact from the surface active component of this family a mean twice as large as the one from the open clearfell was obtained in the mature plantations. The rove beetle family is the largest in Britain, with over 2,000 species, most are predators, though there is a large proportion that are fungivorous. It is probable that these species were fungivores, although this would require further examination, as there was a strong fungivore guild sampled, with the Endomychidae, Leiodidae, Erotylidae, families trapped in the pitfalls, and the Cryptophagidae from the soil cores, all fungivores. These were found in the mature plantation habitat, suggesting a high fungus populations, compared to the open clearfell. However as the Rhizophagidae are predators, there may be a proportion of the rove beetles predatory.

As there were no more families caught in the open clearfell than in the mature plantation, the higher abundances in the open clearfell suggests that there is a larger resource base in the open habitat. The large difference between the two habitats is manly due to the abundances of Carabids in the open clear habitat, with the Carabidae accounted for over 75% of the Coleopteran catch in the pitfall traps, and 30% of the soil fauna.

Although 20 species of carabids were identified in total from this area of Hamsterley forest, one species dominated the number caught. *Pterostichus adstrictus* was by far the most abundant species caught, with almost twice as many found as the next common species, *Carabus problematicus*. However this difference is more astonishing as *Pterostichus adstrictus* was only found in just over half the traps, whereas *Carabus problematicus* was found in nearly all the traps. This difference in distribution is as a result of *Pterostichus adstrictus* being found almost exclusively in the open clearfell sites, with less than 2% caught in the mature habitat. A mean of almost three times as many *Carabus problematicus* were found in the open clearfell site than in the mature plantation site, so although this species is found almost through the sampling area there are very different abundances in the open clearfell and plantation habitat. This would suggest that the plantation habitats are of low utilizable value to *Carabus problematicus* as this species is a generalist predator (Forsythe 1987), or that as the plantations abut the open habitats the individuals trapped are from the periphery of the core open clearfell population (*sensu* Krebs 1985). No other species were as dominant as the two discussed above, and the remanining species will be discussed in relation to the community composition.

Chapter 6

Results:

Multivariate analysis

6.1. Multivariate analysis of invertebrate orders.

The abundances of the taxa from each sample were analysed simultaneously using the multivariate analysis techniques outlined in section 2.3. Illustrated in the analysis of individual orders, chapter 4, there was significant differences between the time periods, which may mask the real differences in the invertebrate communities between the two habitats, for this reason the samples for each pitfall in the 5 time periods were pooled, to generate 48 rather than 240 replicates, and the soil cores were pooled further, as these were not samples from the exact same spatial location, to generate 8 replicates from the 240.

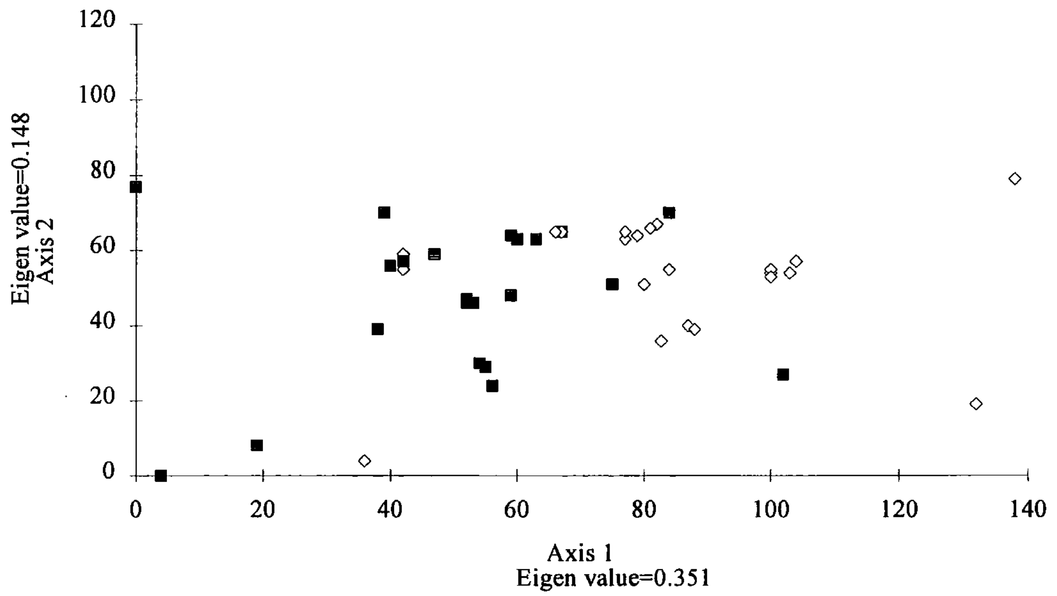
The order data from the pitfall traps and Berlese extraction were analysed using DECORANA, using the a log series transformation. The resulting eigen values for each axis in the analysis can be seen in table 23, for both the pitfall and the Berlese data.

Table 23; Eigen values for the first four axes obtained from Detrended Correspondance analysis of the pooled abundance data of orders collected from Berlese extraction and in pitfall traps.

Axis	Pitfall traps	Berlese extraction
1	0.351	0.047
2	0.148	0.010
3	0.036	0.001
4	0.018	0.000

There was no complete separation between the habitats from the pitfalls data, there is however a gradation along axis 1, for habitat types, with the mature plantation habitat having mainly high eigen scores, and the open clearfell having mainly low eigen scores, see graph 5. There was a larger spread of Eigen scores for the open habitat for axis 2, suggesting that differences in the open clearfell habitat sites are much stronger than the differences in the mature plantation habitat sites. As the eigen values obtained for axes 3 and 4 are much lower than those for 1 and 2 they were not be considered. There was little separation of the habitats with the Berlese extraction data with neither the sites nor habitats forming groups along axis 1, or 2.

Graph 5; Showing two dimensional plot of the first two axes of Detrended Correspondance analysis scores for the pooled order abundances pitfall traps samples, n=48. Open habitat pitfalls are represented by squares, Mature plantation habitats are represented by diamonds.



The results of Twinspan analysis, see table 24, broadly agree with that of the Detrended Correspondance Analysis, where the first division was between a group of 9 of the 24 mature plantation sites, and 1 open clearfell site, and the rest of the sites. At the second division four groups are present, with two almost exclusively mature plantation sites, one group exclusively open clearfell sites, from sites 1 and 4, and one group a mixture of open clearfell mature plantation sites. It is not until the next

Table 24; Showing results of Two Way Indicator species analysis of pooled pitfall order abundances, n=48, pitfalls from the open sites are shown by an o, pitfalls from the mature sites are shown by an m

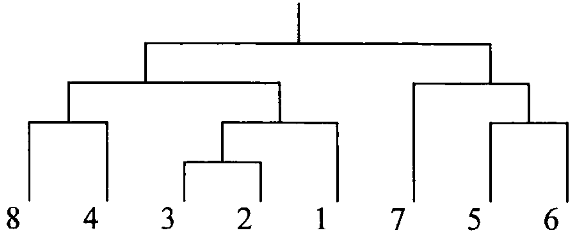
```
                        ooooooooooooooooooommmmommmmmmoommommmmmmmmmmomm
                         421214441 241223332223334433341231111    2 1
                        8841223570904913674567089021256393458623568771
  7 Dermaptera          ------222-------------------------------------  0000
  5 Lithobiomorpha      22----------2---------------------------------  0001
  8 Hemiptera           2222222222222222223222----22222--22---------22  001
  6 Collembola          2-----2-2222---222-22222222-2-2222223322333333  0100
 12 Hymenoptera         3232222222332333333333333332222222233232222322  01010
  3 Opiliones           3333222223332222233333333333222233232222223332  0101100
 11 Diptera             4343433333343443343443344443333433444433333344  0101101
 13 Coleoptera          4333333334443433333333333333333333333333233333  0101110
  2 Araneae             4343434333333333333333333333333333333333333333  0101111
 10 Lepidoptera         222222222-22----22-----------------222-----2--  011
 14 Pulmonata           2-22-22--2-----------------------2222222222222  100
  4 Acari               ---------2---------------------------------2--  101
  1 Pseudoscorpionidae  -------------------------------------------2-2  110
  9 Thysanoptera         ---------------------------------------------2  111
                        0000000000000000000000000000000000011111111111
                        0000000001111111111111111111111111100000000011
                        0000111110001111111111111111111111100000000101
                        0111011110110000000000000001111111100011111
                         011 0011 010000001111111110000001101100111
                          01 0101   01111101111111100001101 0101001
```

division in the classification that this groups separates more distinctly into the two habitat types. TWINSPAN analysis of the Berlese data showed broadly similar patterns to that of the detrended correspondence analysis, with the first TWINSPAN division separating all the open clearfell sites and one mature plantation site, table 25, from three mature plantation sites. At the second division the samples from site 4 actually separated together, numbers 4 and 8 in fig. 2. The other mature plantations sites, numbers 7, 5 and 6 in fig 2, and open clearfell sites, numbers 1, 2, and 3 in fig. 2, formed separate groups.

Table 25; Showing results of TWINSPAN analysis of the pooled Berlese extraction data for order abundances, n=8, soil cores from open sites are shown by o, those form mature sites by a m

```
                    moooommm
                    84321756
Diptera             22222333  000
Hemiptera           32222333  00100
Thysanoptera        222-2222  00101
Opilione            2222-32-  0011
Acari               44555454  01000
Diptera adults      33333344  01000
Hymenoptera         22222332  010010
Coleoptera adults   33333333  010010
Coleoptera larvae   22333333  010010
Collembola          45554544  010011
Araneae             33434333  01010
Lepidoptera         2222222-  010110
Pseudoscorpionidae  32333322  010111
Oligochaetae        --224332  011
Diptera larvae      --22-223  10
Orthoptera          ------2-  110
Polydesmida         -----2--  111
                    00000111
                    00111011
                    01001 01
                     01
```

Fig 2; Dendrogram drawn from results of the TWINSPAN analysis of pooled Berlese order data, showing the hierarchical classification of sites, n=8, sites 1-4 are open clearfell, sites 5-8 are mature plantation



6.2. Multivariate analysis of beetle families.

The first division of the analysis of the beetle families pitfall data with TWINSPAN, table 26, separated the samples into a group of 24 mainly mature plantation sites and 24 mainly open clearfell sites. Only two samples from each habitat type actually were classified in the 'wrong' group, samples 15 and 41, from sites 2 and 4 in the mature plantation, and samples 20 and 8, from sites 1 and 2 in the open clearfell habitat. The first division in the TWINSPAN analysis was due to the abundance of carabids in the open samples, coupled with presence of the Silphidae and Coccinelidae, and absence of the Endomychidae, in the open sites. The psuedospecies cut level for staphylinid of 3 was used for the first division, which is why samples 14 and 41 are misclassified, as these samples had low numbers of this family. Samples 20 and 8 both had weevils, Curculionidae, present, which is why they have been classified with the mature plantations.

Table 26; Showing results of TWINSPAN analysis for Coleoptera Families. N=48., pitfall traps from the open habitat are shown by o, and pitfall traps from the mature habitat are shown by m

```
              omommmmmmmmmmmmmmmmmmmmmmooomooooooooooooomoooooo
              2  222311 443 1231123    111343144242233344423 1
              068789974402718503668523712518206445233451371699
Curculionidae 2222222-------------------------2---------------  1111
Erotylidae    ---2--------------------------------------------  1110
Endomychidae  ---22222222222222-------------------------------  110
Staphlynidae -233333232223333333332333322232322--22222222222-  101
Carabidae     324333333233323333333222333333333333333333333333  1001
Leiodidae     -------22-------------------------------------2-  1000
Psephenidae   --2-----------------------------------------2222  011
Coccinelidae ------------2-----------22------22-22222222222--  010
Silphidae     ---2-------------------------223333----------2--  00
              000000000000000000000000111111111111111111111111
              000000011111111111111111000000000001111111111111
              000111100000111111111111000000011110000000000111
              001011100111000001111111001111100110000000001001
              01     01011011110000111  000110101011111111 01
                        0111    011     01
```

Detrended correspondence analysis also revealed a similar pattern with a split along the first axis of habitat (Eigen value=0.501) however the gradient on the second axis was to be related more to differences in the open clearfell sites (Eigen value=0.173) as the highest and lowest points on this axis were from open clearfell sites.

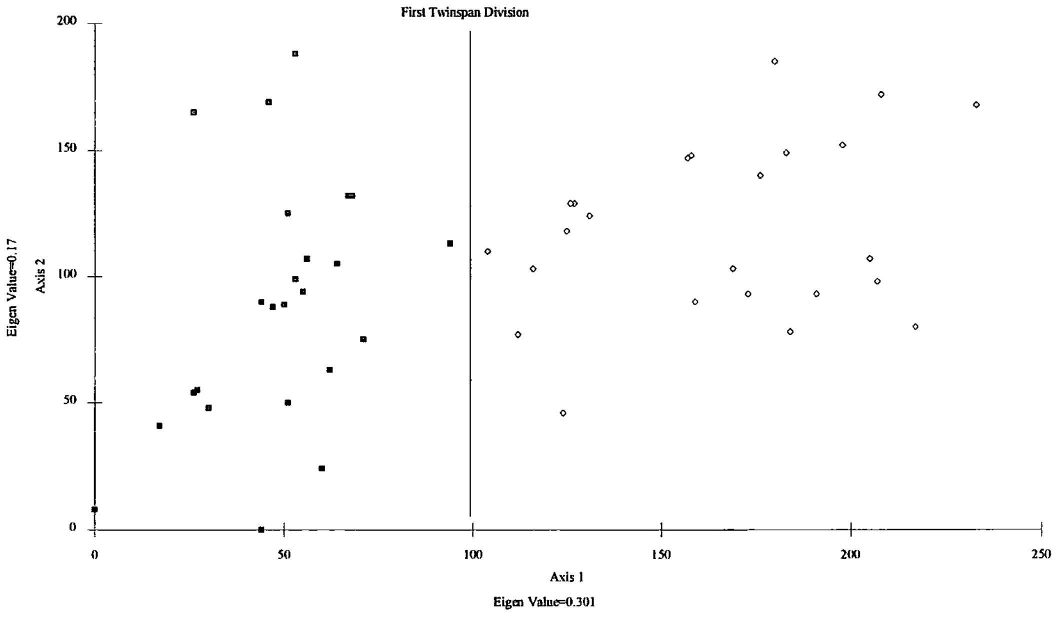
6.3. Multivariate analysis of Carabid species.

A TWINSPAN was carried out on the pooled pitfall abundance data, with a log transformation carried out for the pseudospecies cut levels. The results can seen in table 27, all of the mature plantation sites are split from all of the open clearfell sites at the first division. The indicator species for the first division was the abundance of *P. adstrictus* at psuedospecies level 3 in the open clearfell site, that is samples with more than 10 individuals. Preferential species are those which are at least twice as likely to be found on one side of a division than the other (Hill 1979a). The preferential species for the open clearfell site were *Amara similata, P. diligens, P. niger, and N. salina*, with the preferential species for the mature plantation being *N. biguttatus, and L. rufescens.* Non preferential are species who are as likely to be found on one side rather than the other (Hill 1979a), for the first division there were three non preferential species, *Carabus problematicus*, *T. obtusus*, and *Calathus micropterus*. Further examination of the analysis yielded two further groups, one composed of *P.strenuus*, *P.madidus*, and *Agonum assimile*, and another composed of *E. cupreus*, *L.pilicornis*, *P. diligens*, and *T. quadristriatus*.

Table 27; Showing results of TWINSPAN analysis using log transformed values of for Carabid pseudospecies, where 0 becomes 1, 1 becomes 2, 10 becomes 3, 100 becomes 4 and 100 becomes 5. n=48. m are mature plantation pitfall traps o are open clearfell traps.

```
                   oooooooooooooooooooooooommmmmmmmmmmmmmmmmmmmmmmm
                   3222312244 34444113 331 31344 111     1212233242
                   312412037384468509276519778211356234654586709908
E.cupreus         -------------2-22-------------------------------  0000000
L.pilicornis       --------------2-2-------------------------------  0000001
P.diligens         ------------2-222-----22------------------------  000001
T.quadristraitus   ----------2----------222------------------------  00001
P.strenuus         --------222-------------------------------------  00010
P.madidus          2-222----22-------------------------------------  00011
P.niger            -222222222323222223322322-222-----------------22  001000
P.adstrictus       33333333333333333333333222-2222-----------2-----  001001
N.salina           33322332223-22222323223322-2222-----------------  00101
A.similata         -2-2---2--222-----------------2--------------2--  00110
P.nigrita          ---22------2------------2-----------------------  00111
A.assimile         ---------2--22---------------------------------2  010
C.problematicus    233332332222333223323233223222222222--2322222232  011
T.obtusus          ----22222222222-3--222232222---222222222222-2222  100
C.micropterus      --2------22222222222222222323222 2-2222322222 3222  101
N.biguttatus         -------2-2------2---2-22222222222----2222222-322  110
L.rufescens        22----------------------2-----2---------22222222  1110
C.caraboides       -------------------------------22---------------  1111
                   000000000000000000000000111111111111111111111111
                   000000000000111111111111000000011111111111111111
                   000000001111000001111111000001100000011111111111
                   000111110111001110000011011110100111100000000011
                   00100111 001010110000101 0001  01011100000000101
                    01 01001 01    010011    001      00100011111
```

Graph 7; Two dimensional plot of Detrended Correspondance Analysis Eigen scores from the first two axis of Carabid species abundances, pitfall traps from the open habitat are shown as squares, pitfall traps from the mature habitats are shown as diamonds. The vertical line divides pitfall traps separated by the first TWINSPAN division.

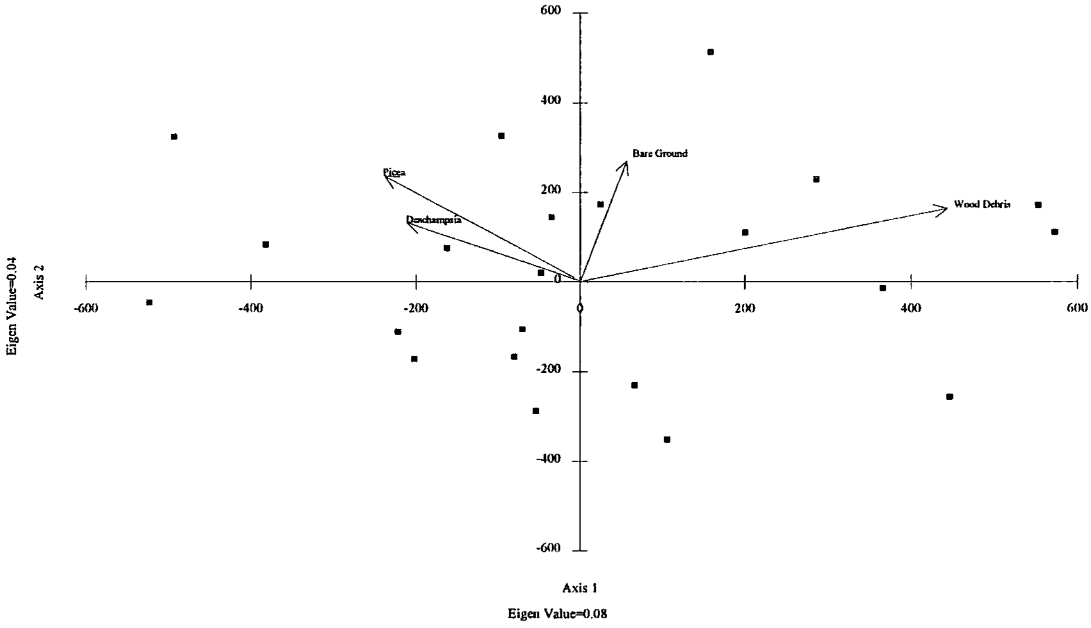


The first three of these groups, that is those identified at the first division, are the three dominant groups, with the open clearfell group highest in abundance and dominated by one species, *P. adstrictus*.

A DECORANA was carried out on the pooled pitfall abundances, with the same data transformation as for TWINSPAN, the eigen scores for axis one were less than from the DECORANA of the family data (0.301, *c.f.* section 6.2) although the second axis score was very similar (0.173, *c.f.* section 6.2). All of the mature plantation samples and open clearfell samples separate when the first two axis are plotted, see graph 7, agreeing with the first TWINSPAN division. The first axis relates to the habitat type, and again the second axis seems to relate to differences within the open clearfell community, with these samples being much more spread out in the graph than the mature plantation habitat.

To determine whether these differences could be explained in terms of the habitat variables collected canonical correspondence analysis was used, using CANOCO (ter Braak 1988). The DOMIN values of *Picea sitchensis*, *Deschampsia flexuosa*, wood Debris and bare ground, which between them are correlated with all the other environmental variables collected, see Appendix 2. The results of the preliminary analysis can be seen in graph 8, which shows the sample sites plotted as a linear combination of the environmental variables, and the environmental variable bi-plot scores. Monte Carlo analysis of the data showed that these environmental variables did not significantly explain the differences in the sample sites.

Graph 8; Showing Canonical Correlation Analysis linear combination eigen scores for open clearfell habitat carabid species abundances in terms of the environmental variables (Shown as arrows).



6.4. Discussion

A reduction in the needle litter layer following felling allows more sunlight to hit the soil surface, consequently dehydration of the soil may cause changes in the litter layer fauna, due to a deleterious effect on the microbial food resource (Hogervorst 1993). However the multivariate analysis did not separate the two habitats on the basis of the soil invertebrates present, even though the individual orders themselves showed significant differences. Virtually no quantitative data are available on predation in the decomposer web (Cousens 1974), and so determining mechanisms for changes in community structure would be difficult. Carabids were sparse as a component of the predatory soil fauna, represented in the main by one species, *Trechus obtusus*, which is a generalist predator.

Multivariate analysis separated the surface carabids into four groups. The 'generalists' (the non preferential of the first TWINSPAN division) were found in both habitats, with approximately equal abundances in the two habitats. The three species in this group *Carabus problematicus*, *Trechus obtusus*, and *Calathus micropterus*. Both

Trechus obtusus and *Calathus micropterus* are soil and litter dwellers, and predate on most of the fauna present in the soil litter and the first species TWINSPAN actually separates this group on this basis. There was one group particular to the plantations, composed of three species, *Cychrus caraboides*, *Notiophilus biguttatus* and *Leistus rufescens.* The last two of this group are specialist springtail predators, and *Cychrus caraboides* is a specialist predator of slugs and snails (Forsythe 1987). The species found abundantly in the open sites formed a group, and included *Pterostichus adstrictus*, *P.niger*, *P.nigrita*, *Nebria salina* and *Amara similata* These are polyphagous species, and serological work is required before the prey they consumed could be identified. The less common species formed three groups, one of which only contained *Agonum assimile* and was closely associated with the 'generalist' species. The two other open clearfell sub groups where composed of *P.strenuus* and *P.madidus*, in one group, and *Elaphrus cupreus*, *Loricera pilicornis*, *P.diligens* *Trechus quadristriatus* in the other. These species were associated more with the dominant open group.

The environmental variables recorded in the open clearfell habitat did not explain the differences in the carabid assemblages, shown by the CANOCO analysis. The important variables in determining carabid assemblage composition in Butterfield and Coulson (1983) were vegetation structure, soil moisture and temperature. In the current study it seems that temperature is the main cause for the differences with the other two factors, if existing at all, playing a role in determining the assemblages within the open site. A morphological point of note is that the 'generalists' as outlined above are all apterous species and can not fly, whereas all the dominant open clearfell group are macropterus and are capable of flight (Lindroth 1974, Thiele 1977, J. Butterfield pers. comm.). The composition of these groups may therefore be linked with the physiological requirements for flight, as it is known that both reduced ground level solar radiation and low temperatures reduce flight activity (Lacey *et al.* 1994), and as the percentage of species which can fly has been seen to decrease with the closure of forest canopies (Thiele 1977) it appears as these may be successional assemblages.

From the data so far discussed there were two main factors affecting the invertebrate community structure in the mature plantation and open clearfell sites. The main effect was the differences in structure of the habitats, and was probably expressed through the difference in insulation properties of the two habitat types. Underlying this main effect there was a secondary effect from the differences in the plant communities in the open clearfell. These two factors seem to apply at all the taxonomic levels with the first axis of the ordinations reflecting the two habitat types, and the second axis reflecting the differences within the open habitats. The examinations at progressively more detailed taxonomic levels only serves to emphasise these differences. Unlike the separation of upland communities described by Coulson (1988) which were most pronounced in herbivores and detritovores, but with little separation in the predatory species, such as beetles and spiders, this study has shown that the differences between the two habitats are sufficiently large to overcome the tendency for the highly mobile predators to 'spill over' into the adjacent habitat.

Chapter 7

Discussion

7.1. Validity of interpretations

The surface active invertebrate data resulting from the use of pitfall traps requires cautious interpretation as the numbers of invertebrates caught will reflect not only their abundance but also their activity (Greenslade 1964, Southwood 1971). The vegetation of a habitat may also impede the activity of invertebrates, reducing their collection (Greenslade 1964, Southwood 1971). This may affect the different taxa to varying degrees. However the four replicate sites within the mature plantation had almost identical litter layers and no vegetation, where as the open clearfell sites had vegetation of varying complexity. The general decrease in numbers caught in the mature plantations can not be attributed to impedance of the invertebrates to the pitfall traps, and reflects a real ecological difference. Comparison of Berlese extracted data from widely different soil types is not valid (Southwood 1971), as the extraction efficiency will vary in an unquantifiable manner with soil type. However the soil samples in this study were sufficiently similar between the two habitats to redress this problem. The differences between the two habitats were not reflected in the soil inhabiting invertebrates sampled, and this may indicate a higher degree of stability in the soil habitat following felling.

7.2. Biological monitoring of forestry practices

Previous studies of this system (Butterfield and Benitez Malvido 1992, Day and Carthy 1988) have shown that there are marked differences in the species of carabid in chronosequences of forest plantations. Butterfield and Benitez Malvido (1992) showed that mixed species of conifers had a significantly higher densities of invertebrates than single species, and also found that plantation blocks were dominated by *Trechus obtusus*, *Carabus problematicus*, and *Calathus micropterus*, agreeing with the current study. Day and Carthy (1988) only found *Carabus problematicus*, abundant towards the end of rotation period, which was the case with the current study. Butterfield (1992) found that there was a significant differences in the numbers of the major arthropod taxa between moorland, plantation and recently clearfelled sites, with higher abundances recorded in the clearfelled sites in some taxa. The response of the carabids was complicated by different dominant species in two types moorland class, but generally showed that the open site had a carabid assemblage which did not reflect either the plantation assemblage or the moorland assemblage, with *Pterostichus adstrictus* an important member of this assemblage. The results of this study agree with these findings, as the assemblages found on the open clearfell had little in common with the plantation assemblages, or to the assemblages listed in Butterfield and Coulson (1983). These difference were not however reflected in the soil community. This suggests that there are observable and predictable changes in the invertebrate communities during the forestry cycle. There is a potential then to use invertebrate surveying to monitor the changes at a multiple of taxonomic levels. Mechanisms to promote ecological improvement of the ground beetles diversity in conifer plantations may also serve as a model for other taxa, with ground beetles acting as useful indicators of the change induced by forestry practices.

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Appendix 1

Table A.1; DOMIN scores of the plant species, wood debris and bare ground recorded around each pitfall transect site in a 1m^2 quadrat. n=24

Site	1						2					
Quadrat	1	2	3	4	5	6	7	8	9	10	11	12
Bare ground	0	0	0	5	4	4	5	7	6	8	5	6
Wood debris	0	0	0	0	0	0	5	5	6	5	7	7
Eriophorum vaginatum	5	5	5	5	5	5	0	0	0	0	0	0
Calluna vulgaris	7	8	8	7	8	8	0	5	5	5	7	5
Chamerium angustifolium	0	0	0	0	0	0	8	5	5	0	0	4
Deschampsia flexuosa	5	4	6	5	0	4	0	0	4	0	0	0
Picea sitchensis	0	0	4	4	0	0	4	5	4	0	0	0
Erica tetralix	4	5	4	4	0	5	0	0	0	0	0	0
Vaccinium myrtilus	4	4	4	0	4	4	0	0	0	0	0	0
Site	3						4					
Quadrat	13	14	15	16	17	18	19	20	21	22	23	24
Bare ground	2	0	4	4	4	3	0	0	4	5	4	3
Wood debris	2	2	0	5	5	4	2	5	0	0	0	3
Eriophorum vaginatum	5	0	4	5	5	5	10	6	5	7	7	7
Calluna vulgaris	10	10	10	8	8	8	4	7	8	7	7	7
Chamerium angustifolium	0	0	0	5	0	5	2	4	0	0	4	4
Deschampsia flexuosa	0	0	0	0	0	0	0	0	0	0	0	4
Picea sitchensis	0	2	4	0	5	4	0	0	0	0	0	0
Erica tetralix	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium myrtilus	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2: Correlations between environmental variables recorded.

Table A.2.1; Spearman Rank Correlation Coefficients for each environmental variable measured, n=24, for significance of these values see Table A.2.2.

Env. Variable	bare ground	calluna	chame	ciorg	corg	desch	erica	erio	h20	minres	ph	picea	vacc
calluna	-0.3715	1											
chame	0.2389	-0.6237	1										
ciorg	0.6527	-0.6237	0.3721	1									
corg	0.5513	-0.6549	0.5214	0.6975	1								
desch	-0.2829	0.0678	-0.2039	-0.1087	-0.4466	1							
erica	-0.3560	0.1620	-0.3985	-0.2037	-0.6391	0.8169	1						
erio	-0.5179	0.2850	-0.2057	-0.8338	-0.4395	0.1401	0.1809	1					
h20	0.0059	-0.4057	-0.4057	-0.0806	0.1009	0.5058	0.4829	0.1339	1				
minres	-0.5569	0.6898	0.6898	0.1087	-0.9946	0.3829	0.5726	0.4466	-0.1979	1			
ph	-0.5177	0.4172	0.4172	-0.5786	-0.8805	0.6509	0.8174	0.4892	0.3823	0.8300	1		
picea	0.1999	-0.1320	0.2383	0.2052	-0.0406	0.1182	-0.0116	-0.3184	-0.3024	0.0566	-0.1147	1	
vacc	-0.4066	0.2026	0.2026	-0.2053	-0.2053	0.5984	0.7644	0.1823	0.4866	0.5771	0.8238	-0.1795	1
wood	0.4196	-0.4483	0.5564	0.6883	0.6883	-0.3714	-0.5247	-0.5874	-0.2798	-0.6433	-0.7620	0.1595	-0.5435

Table A.2.1, shows the Spearman rank statistic and **Table A.2.2**, the associated probability level. The DOMIN score for *Picea sitchensis* was not significantly correlated with any other variable, this is surprising as this site has in the main been left to reseed naturally. The DOMIN score for wavy hair grass, *Deschampsia flexuosa* was only negatively correlated with the organic carbon content of the soil, (Spearmans Rank correlation, df 22, Rs=-0.4466, p=0.0290). Between them bare ground and wood debris are significantly correlated with all the other environmental variables, and these two environmental variables along with *Picea* and *Deschampsia* DOMIN scores were chosen for use in CANOCO analysis, where a maximum ratio of 1 environmental variable to every 3 samples may be used but 1 environmental to 5 samples is preferable (I. Downie, *pers comm.*, ter Braak, 1988).

Table A.2.2; Showing the significance level of the Spearman Rank Correlation coefficients given in Table A.2.1, significant was taken at the 0.05 level, n=24

	bare ground	calluna	chame	ciorg	corg	desch	erica	erio	h20	minres	ph	picea	vacc
calluna	0.0740	.											
chame	0.2610	0.0010	.										
ciorg	0.0010	0.0010	0.0730	.									
corg	0.0050	0.0010	0.0090	0.0000	.								
desch	0.1800	0.7530	0.3390	0.6130	0.0290	.							
erica	0.0880	0.4500	0.0540	0.3400	0.0010	0.0000	.						
erio	0.0100	0.1770	0.3350	0.0000	0.0320	0.5140	0.3980	.					
h20	0.9780	0.9780	0.0490	0.7080	0.6390	0.0120	0.0170	0.5330	.				
minres	0.0050	0.0050	0.0000	0.0000	0.0000	0.0650	0.0030	0.0290	0.3540	.			
ph	0.0100	0.0100	0.0430	0.0030	0.0000	0.0010	0.0000	0.0150	0.0650	0.0000	.		
picea	0.3490	0.5390	0.2620	0.3360	0.8510	0.5820	0.9570	0.1290	0.1510	0.7930	0.5940	.	
vacc	0.0490	0.3420	0.0520	0.3360	0.0010	0.0020	0.0000	0.3940	0.0160	0.0030	0.0000	0.4010	.
wood	0.0410	0.0280	0.0050	0.0000	0.0000	0.0740	0.0080	0.0300	0.1850	0.0010	0.0000	0.4560	0.0060

Appendix 3: Scientific Nomenclature and Authorities

Coleoptera (as Lindroth 1974)

Carabus problematicus Herbst.
Leistus rufescens Fabricus.
Nebria salina Fairmore.
Notiophilus biguttatus Fabricus.
Elaphrus cupreus Duftschmid.
Loricera pilicornis Latrielle.
Trechus obtusus Erichson.
Trechus quadristriatus Schrank.
Pterostichus madidus Fabricus.
Pterostichus niger Schaller
Pterostichus nigrita Paykull
Pterostichus adstrictus Eschscholtz
Pterostichus strenuus Panzer.
Pterostichus diligens Sturm
Calathus melanocephalus Linnaeus
Calathus micropterus Duftschmid
Agonum assimile Paykull
Amara similata Gyllenhal
Cychrus caraboides Linnaeus

Plants (as Graham 1988) follow *Flora Europaea* 1964-1980,