An investigation into the species distribution of woodlice (Isopoda, Oniscidea) and millipedes (Diplopoda) within a disused Magnesian limestone quarry.

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by

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1.0 INTRODUCTION

1.1 Introduction and aims

Disused quarries are becoming increasingly important as sites of conservation value and ecological interest. Although most quarries are small, discrete sites they are numerous and widespread throughout Britain (Davis & Jones 1978). In particular, as limestone grasslands are becoming increasingly rare, disused limestone quarries may provide refuges for plant and animal species characteristic of these habitats.

Davis & Jones (1978) carried out a survey of ground arthropods in chalk and limestone quarries in the south of England. They suggest that some quarries can support large populations of woodlice and millipedes and that these invertebrates may be important in determining the rate of accumulation of organic matter on the ground. Davis & Jones suggest that the natural recolonization of stone quarries has received little investigation and it would appear that this situation has not improved, published studies of invertebrate ecology in limestone quarries still being scarce.

Woodlice (Isopoda, Oniscidea) and millipedes (Diplopoda) are conspicuous detrivores of grasslands and deciduous woodlands. They do not posses a waterproof layer in the cuticle as do spiders and insects and consequently they tend to avoid dry places and spend most of the time in a moist environment from which they emerge only at night when the temperature drops and relative humidity of the air increases (Cloudsley-Thompson 1977).

The basic ecology of millipedes and woodlice and their role in the soil is given in Wallwork (1976). Millipedes, as a group, are essentially animals of the woodland floor, but certain species occur commonly in grasslands and other open formation types. These include members of the Julida whose calcified integument may account for as much as one half of the weight of the body. It is to be expected, therefore, that this group of animals will be better represented on base rich soils than on base deficient areas.

The geographical distribution of the British millipede species, as well as information on taxonomy and microhabitat preferences is given by Blower (1985). Other works discussing their distribution and population ecology include Blower (1955, 1974, 1979), Camatini (1979) and Miller (1974).

The physiology and behavioural responses of woodlice to the physical aspects of the environment have for some time been the subject of considerable investigation (see Edney 1954, Sutton 1972, Cloudsley-Thompson 1977 and Wieser 1984 for reviews). In his 1954 review of woodlouse behaviour and physiology Edney called for more precise measurements of microclimate together with field observations of behaviour for comparison with the body of data collected from laboratory studies. There have been many publications since Edney's paper regarding the distribution and population ecology of woodlice (see Harding 1990) but Cloudsley-Thompson (1977) suggested that there were still few ecological studies carried out on woodlice, especially in terms of local distributions and the influence of microclimate.

More recently the situation has improved. The distribution of the British woodlice on a geographic scale together with information on preferred habitat types being comprehensively reviewed by Harding & Sutton (1985). This in turn led to a biogeographical study of the British and Irish species by Hopkin (1987).

The symposium volume based on terrestrial isopod biology (Sutton & Holdich 1984) contained valuable papers on woodlouse ecology such as those by Warburg *et al* (1984), who discussed the effects of climate on distribution and abundance of isopods, and Wieser (1984) who reviewed the ecophysical adaptions of woodlice in terms of the microclimatic factors they tend to encounter in the field.

Davis, Hassall & Sutton (1977) and Davis & Sutton (1977) investigated the spatial distribution and niche separation of woodlice and millipedes in a dune grassland. They suggested that as both groups are considered "primary decomposers" which show little resource partitioning in their food preferences it might be expected that they would show some spatial separation and concentrate feeding to one area. Davis & Sutton (1977) found that although some separation of the groups was found regarding their vertical distribution in the soil no spatial separation could be found in the horizontal distribution of the two groups.

The aims of this study were to investigate the distribution of woodlice and millipede species within a disused Magnesian limestone quarry. Although small in area the site contains a range of habitats from bare cliff faces to mature woodland. Emphasis has been placed on the preferred habitat types of the species, the environmental factors which characterize these sites and how the microclimatic elements can combine to influence species distribution. By investigating distributions of individual species, differences in the distribution of the two major taxa could be examined and the possibilities of niche separation analysed.

Different methods of sampling have been used to examine the advantages and disadvantages of each technique in the study of woodlice and millipedes and to see whether results regarding species distribution and relative abundances are dependent on the sampling method used.

1.2 Bishop Middleham Quarry Reserve

The study was carried out at Bishop Middleham Quarry Reserve (NZ332327) which is situated to the north of Bishop Middleham village, County Durham. The site is owned by the Church Commissioners and leased to the Durham County Wildlife Trust as a nature reserve. It has been notified as a Site of Special Scientific Interest by the Nature Conservancy Council.

The reserve lies at an altitude of 120m on the Magnesian Limestone escarpment which runs roughly from Sunderland south-westwards. The reserve is bordered to the north, east and west by agricultural land and on the south side by an active limestone quarry.

Quarrying in the reserve itself practically ceased in 1934 but it was reopened briefly in the early 1950's when a few hundred tons of limestone were taken from the north end. It was worked originally to win limestone for building materials and agricultural purposes. Later, due to the high proportion of the mineral dolomite found in the limestone, it was quarried to provide a raw material for the chemical industry and a high quality flux for the increased iron production of the area (Dunn 1980).

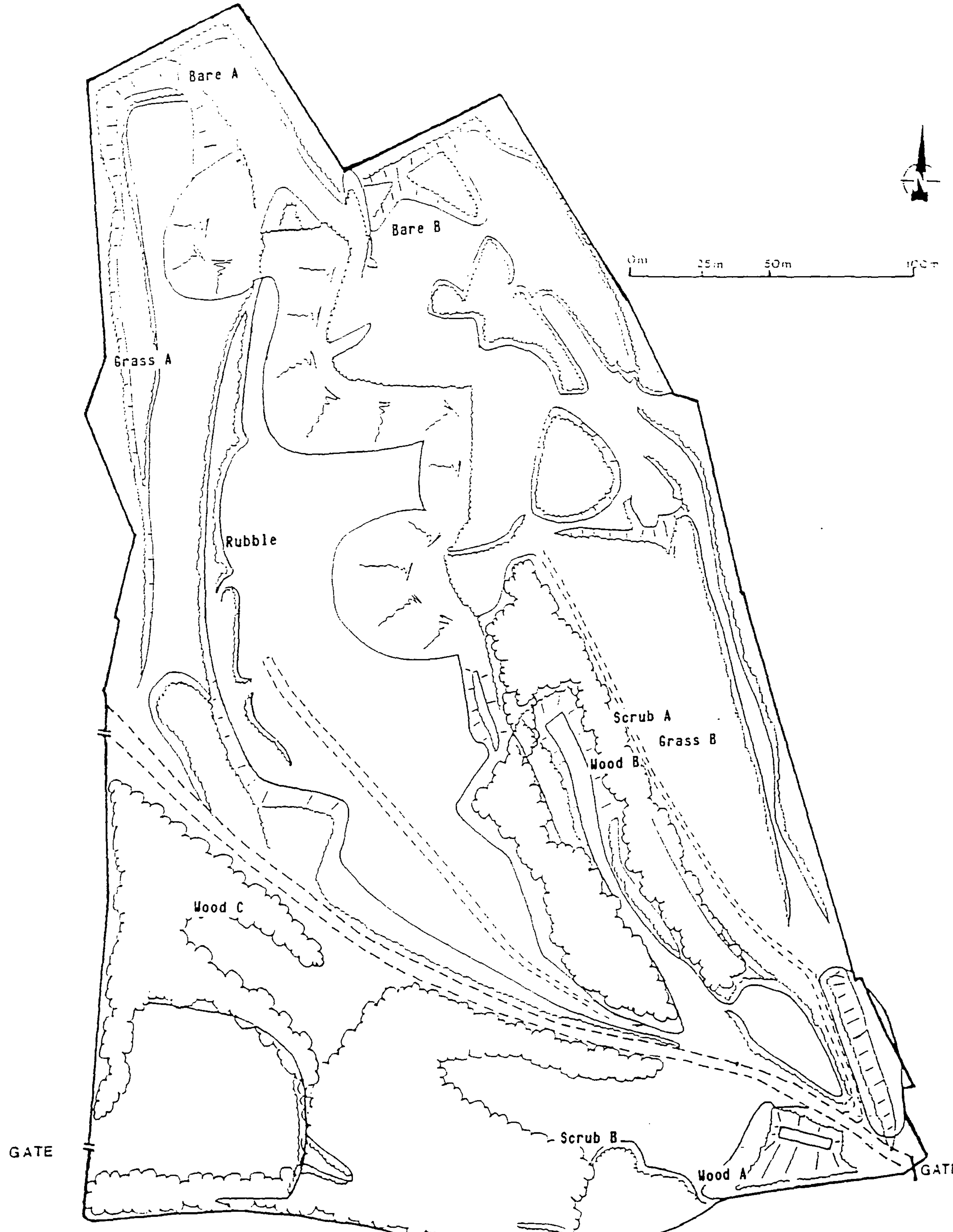
Quarrying produces flat areas of exposed rock at the quarry floor and on some of the wider terraces, large and small heaps of spoil material and extensive vertical cliff faces. All these features occur at Bishop Middleham and help to increase the diversity of habitat types present in the reserve.

Due to the relatively recent cessation of quarrying activity the soils in the reserve are largely skeletal and still in early stages of development. Soils are becoming richer in areas which are now occupied by scrubland or woods. Being on a limestone base the soils are well drained and there tends to be little or no surface water.

When quarrying ceased the disused quarry provided suitable habitats, free from competition, for colonisation by the plant species in the unique semi-natural grasslands nearby. In the north-east *Sesleria* grasslands which have developed on soils derived from the Magnesian Limestone form an important and unique grassland type. The spoil heaps and softer rocks are the first to support incoming flowering plants while on harder material the first colonists tend to be bryophytes. Early colonists at Bishop Middleham include *Fragaria vesca, Hieracium pilosella, Lotus corniculatus* and *Thymus serpyllum*.

The reserve is approximately 24 acres in extent and contains a wide range of habitat types ranging from bare rock through to well developed ash and sycamore woodland. Its importance as a reserve lies in the diversity of plant and animal species it contains which are characteristic of limestone soils. Of particular note is the colony of dark red helleborine (*Epipactis atrorubens*) which is one of only five known colonies in County Durham (Dunn 1980).

Figure 1 - Bishop Middleham Quarry Reserve (NZ332327)



2.0 MATERIALS AND METHODS.

Sampling was carried out between April and July 1991 at Bishop Middleham Quarry Reserve, County Durham (NZ 332327).

Ten sites were selected within the boundaries of the reserve which were thought to be fully representative of the range of habitats present. Two sites each were selected of bare ground (Bare A & B), grassland (Grass A & B), scrub (Scrub A & B) and woodland (Wood A & B)(Figure 1). A further two sites, one a talus of rocks at the base of a cliff (Rubble) and the remains of demolished brick buildings now overgrown with scrub and woodland (Wood C) were also investigated.

2.1 Site Descriptions.

Rubble (Rub)

The rubble site consisted of a talus located on a shelf of rock about 2m from the quarry floor. The rocks were only loosely compacted and could not easily withstand the weight of a man without some subsidence occurring. There was little vegetation present on the slope of the talus but a few species occurred at the point were it met the vertical cliff face. Specimens of *Taraxacum* sp and hawks beard (*Crepis* sp) were quite frequent and bramble bushes (*Rubus fruticosus*) were growing over the rubble. There was very little plant litter present and that which did occur was very dry and brittle.

Bare A (BA)

This site was located in the extreme north-west of the quarry. There was only scanty vegetation cover with extensive patches of bare ground and exposed limestone. There were many loose rocks and boulders. The soil was thin and of a sandy, skeletal nature. The vegetation was low consisting mainly of the colonizing *Thymus serpyllum* and the blue moor grass, *Sesleria albicans* which formed numerous tussocks. Other common plants included salad burnet *(Sanguisorba minor)*, rest harrow *(Ononis repens)* and mouse eared hawkweed *(Hieracium pilosella)*, species which tend to occur on dry grassy places, often on lime.

Bare B (BB)

Similar to Bare A this site had a thin skeletal soil and large patches of bare ground with loose rocks and boulders. The grass *Sesleria* was not so abundant as in Bare A and seemed to be replaced by

Agrostis capillaris and *Deschampsia flexuosa.* In terms of plant species this site was more species rich than Bare A. *Hieracium* spp was abundant and low lying herbs such as *Thymus, Ononis repens* and *Trifolium pratense* were responsible for much of the cover. Flowering plants such as cowslips (*Primula veris*), ox-eye daisy (*Leucanthemum vulgare*) and the wild strawberry (*Fragaria vesca*), which is often found on dry limestone grassland in northern Britain, were widespread. The common-spotted orchid (*Dactylorhiza fuchsii*) was common. The northern border of the site consisted of a large mound of dead branches which had been stacked during scrub clearance work and there appeared to be considerably more litter than at both the Rubble and Bare A sites.

Grass A (GA)

This site, situated on a ledge on the west side of the quarry, was primary grassland consisting mainly of the blue moor grass, *Sesleria*, and a number of low lying herbs such as *Thymus serpyllum, Sanguisorba minor* and *Ononis repens*. The rock rose (*Helianthumum nummularium*), characteristic of grassy and rocky places on lime, was also conspicuous. There were a few loose boulders and some small patches of bare sand. The soil still had a sandy texture but was a darker colour than in sites Bare A and B.

Grass B (GB)

This site was very different from the Grass A site both in species composition and in physical structure. This was a secondary grassland where the dominant grass species was *Dactylis glomerata.* Together with other grasses such as *Agrostis capilaris, Holcus* sp and *Festuca ovina* a dense sward was created about half a meter in height. Flowering species such as speedwell (*Veronica persica*), herb robert (*Geranium robertianum*) and cowslips (*Primula veris*) were present among the grasses. The soil was deeper than in the previous site and of a darker colour and a much richer consistency. There was little bare earth as much of the ground surface was covered by a layer of mosses. There was much litter present, consisting mainly of loose grass stems.

Scrub A (SA)

This was a species poor scrub grassland site situated about 15m from Grass B. The site consisted of hawthorn (*Cretaegus monogyna*) scrub with trailing bramble stems producing quite a dense thicket structure. Ash (*Fraxinus excelsior*) seedlings were also present. The grasses *Brachypodium sylvaticum, Festuca* sp and *Dactylis glomerata* were present in tussocks and, together with some taller flowering plants such as hogweed (*Heracleum sphondylium*), cow parsley (*Anthriscus* *sylvestris*) and yarrow (*Achillea millefolium*), created a diverse vegetation architecture. The soil was similar to that in the Grass B site and in some areas the surface was again covered with mosses. Grass and leaf litter was present in noticable amounts.

Scrub B (SB)

This area of scrub was situated in a clearing surrounded by more mature ash and sycamore (*Acer pseudoplatanus*) woodland. The shrub layer again consisted of hawthorn and bramble with taller ash cover. The soil on this site was sandy and shallow, on average about 10cm deep. The ground surface of this site was covered by a very thick layer of moss which appeared dehydrated and dead in parts. There appeared to be a very distinct layer of bedrock underneath the moss, sometimes with no apparent soil layer between the two. The grasses *Holcus* sp and *Festuca* sp were present in quite large patches and created a dense stem structure near the ground surface. *Heracleum sphondylium*, the hard head (*Centaurea scabiosa*), *Potentilla*, and birds foot trefoil (*Lotus corniculatus*) were the main herbaceous plants present and due to the range of heights and structure of these plants the site had a high foliage height diversity.

Wood A (WA)

This site was in the south-east corner of the reserve, on a steep slope bordering the active quarry to the south. The canopy consisted mainly of ash, sycamore and elder (*Sambucus nigra*) with a sub canopy of hawthorn shrubs. The canopy cover was extensive and created extensive shading and a marked drop in temperature. The herb layer vegetation consisted of herb bennet (*Geum urbanum*) and herb robert plants characteristic of shady places and more fertile soils. Also present was common cleavers (*Galium aparine*) and woundwort (*Stachys sylvatica*), which covered a large area to the side of the investigation area. Moss cover was also conspicuous in patches but there were also large areas of bare earth. The soil was much richer than in the other sites with much more clay and a darker hue. There were few boulders or stones but there was much litter present, consisting mainly of dead twigs and bark. There were also larger rotting logs and branches present.

Wood B (WB)

This site was within 10m of the Scrub A site. The canopy again consisted of sycamore, elder and ash with a hawthorn shrub layer. The herb layer was dominated by cover from violets (*Viola odoratum* and *V.riviniana*). Other herbaceous species included herb robert, cow slips and sanicle (*Sanicula europaea*), the latter two of which are often found in woodlands on lime. The extensive shading created by the canopy made this site markedly cooler than the nearby Scrub A and Grass B sites. There were large tussocks of the grass *Brachypodium sylvaticum* and other grasses such as *Festuca* sp were present. Moss cover was present in patches but there were again quite large areas of bare earth. The soil was rich and deep but possibly with less clay than in Wood A. There were no loose boulders or stones but there were pockets of litter, mainly twigs and dried leaves, formed in hollows in the ground surface.

Wood C (WC)

This site was very different from the other woodland sites. The tree species present were ash, sycamore, willow (*Salix caprea*) and hawthorn. The ground vegetation was different from the other sites in that it consisted of a dense sward of *Heracleum sphondylium, Geranium robertianum* and the white dead nettle (*Lamium album*). At places these plants were over 2m in height and thus created a very structurally diverse site providing much cover for the ground surface. There was much litter in between the plant stems, consisting largely of undecomposed nettle leaves and stems and twigs. The litter was conspicuous on the ground surface forming a light, crumbly layer of leaf fragments, bark and twigs.

The other aspect to this site was that it contained the remains of old buildings, consisting of piles of limestone building blocks and mortar. This loose building material essentially created an elongated pile of rubble so adding an extra dimension to this woodland site.

2.2 Sampling of woodlice and millipedes.

Four sampling methods were employed;

2.2.1 Soil cores.

Five soil turfs 15cm x 21cm were removed from each site using a plastic container and sharp knife. The area of the turfs ($0.0315m^2$) exceeded the 1/50th m^2 minimum value expressed by Sutton (1972) for the useful collection of woodlice. The turfs were shaken over a white tray and the specimens dislodged were hand sorted. Hand sorting rather than funnel extraction was used due to the need to replace the turfs as quickly as possible so as to minimize damage to the vegetation of the reserve.

2.2.2 Hand searches.

One ten minute hand search was carried out in each of the sites over an area of approximately $2m^2$ over the course of a day. This procedure was repeated a further five times so giving a total of six hand searches from each site. Ten minutes was considered sufficient time to search the area without the collector's concentration waning.

2.2.3 Cryptozoa boards.

Ceramic tiles, 15cm x 15cm, were employed as cryptozoa boards. A row of nine were placed 1m apart in each site, in a row parallel to the pitfall traps. The ground was scraped with the edge of the tile in order to bare some of the soil surface and the tile was then wedged firmly into place. An attempt to camouflage each tile was made by covering the tile with soil and loose vegetation. The tiles were checked during daylight once a week and the individuals sheltering under each tile were recorded by quickly turning the tile up onto one edge and counting all of the animals visible both on the ground surface and adhering to the under surface of the board. After making the count the board was quickly replaced into its original position. Cole (1946) found that the fauna was no more than temporarily effected by raising the boards to count the animals.

After two weeks half of the tiles were baited using raw carrot in an attempt to increase sample sizes. As this proved successful the remaining traps were baited after a further four weeks, ie six weeks after the start of the study.

In order to examine the fidelity of individuals to shelter sites a series of mark and recapture procedures were carried out. Animals found under ceramic tiles were marked using green HUMBROL paint or TIPP-EX liquid eraser. The tile was examined the following day and the number of marked individuals recorded. A search of other tiles in the series and hand searches under rocks and stones in the immediate area was used to see if individuals had deviated only slightly from the previous days shelter site.

2.2.4 Pitfall traps.

A row of nine pitfall traps of 6cm diameter were laid out approximately 1m apart in each site (apart from Rubble). 80% ethylene glycol was used as a killing agent and preservative. The traps were emptied approximately once a week for five weeks and the samples sorted in the laboratory.

2.3 Environmental factors

2.3.1 Measurement of soil depth.

Soil depth was assessed by passing a metal rod as far down into the soil as it would go, in the ground between each pitfall and tile pair. This was repeated three times and the median value taken. The soil depth was categorized using the following three classes for use in subsequent analysis;

1 0 - 5.5 cm
2 5.6 - 13.0 cm
3 > 13.0 cm

2.3.2 Soil pH.

Soil pH of each site was estimated using five 10g samples of untreated soil and mixing each with 20ml of distilled water. The samples were mixed thoroughly and then allowed to settle overnight in a refrigerator. The samples were agitated before being tested with an ELECTRONICS INSTRUMENTS LIMITED pH METER 7020. The actual reading was taken after one minute so giving the meter time to reach an equilibrium.

2.3.3 Plant species composition and ground cover.

In each habitat nine 25cm quadrats were placed at random on the ground surface between each pitfall/cryptozoa pair. With the exception of some grasses, sedges and rushes which where clumped to make up one taxa each plant present was identified to species and its percentage cover estimated. This involves some error as often many levels of vegetation were present. Therefore, percentage totals of cover may exceed 100%. The quantitative data of vegetation species composition was not used in the investigation into invertebrate species distribution but only as an aid in describing the study sites. However, tables of percentage species cover are given in Appendix 1.

2.3.4 Vegetation structure.

As a measure of the vegetation structure a meter long rod was carefully placed through the vegetation between each pitfall and tile couplet at an angle of 45^{o} and the position of all contacts between the rod and the plants recorded. The number of contacts in each 10cm section of the rod was recorded.

Foliage height diversity was calculated using the Shannon-Weiner index.

$$FHD = H' = \sum p_i \log_e p_i$$

where p_i is the proportion of the total number of contacts that occur in the *i*th stratum. This method was used by Murdoch *et al* (1972) to measure FHD in fields in an attempt to measure structural diversity of the vegetation.

The density of plant stems near to ground surface between each tile/pitfall pair was also estimated by using the number of stem touches in the first 10cm section of the rod.

2.3.5 Temperature and humidity.

The relative humidity and temperature at the soil surface was measured using a digital hygro-thermometer. Measurements were taken seventeen times in each site between 9.00am and 7.00pm over the course of two weeks. Measurements were carried out at random between the study sites but to avoid differences in humidity and temperature occurring due to measurements being taken at different times of the day there were no instances of the first and last sites being measured over an hour apart.

To assess the effects of tile cover on temperature the temperature was measured next to and then beneath a tile, allowing 3 minutes each time for the thermometer to settle. The results were compared using a paired t-test.

2.4 Multivariate analysis

In order to assess similarities between species distributions and give an objective categorisation of each habitat site based on relative species abundances several methods of multivariate analysis have been employed. Three types of multivariate methods were used. These were; i) detrended correspondence analysis (DCA), ii) canonical correspondence analysis (CCA) and iii) two-way indicator species analysis (TWINSPAN).

2.4.1 Detrended correspondence analysis (DCA) is an eigenvector ordination technique based on reciprocal averaging but correcting the faults of arch distortion and compression of the first axis ends found in principle components analysis (Gauch 1982). DCA results in the production of an ordination diagram in which similar species or samples are near each other and dissimilar entities are far apart. Gauch (1982) states that "DCA results are at least as good as, and usually superior to, other ordination techniques." For analysis of community data, DCA ordinates samples and species simultaneously, objectively, efficiently and effectively. Gauch (1982) goes on to say that "DCA appears to be most appropriate to the Gaussian community model and most successful in applications to community analysis."

For more technical details of the DCA process and a review of its usefulness see Hill & Gauch (1980)

2.4.2 Canonical correspondence analysis (CCA) is a direct gradient analysis technique which attempts to explain the species responses by ordination axes that are constrained to be linear combinations of supplied environmental variables (Ter Braak 1988). CCA provides an integrated description of species-environment relationships by assuming a response model that is common to all species, and the existence of a single set of underlying environmental gradients to which all the species respond. CCA has the advantage over other techniques in that it focuses on the relations between species and measured environmental variables and so provides an automated interpretation of the ordination axes.(Ter Braak 1986)

The solution of CCA can be displayed in an ordination diagram with sites and species represented by points and environmental variables represented by arrows.

CCA can be used in combination with DCA to assess the importance of the environmental variables used in the analysis. When the solutions do not differ much, we infer that the measured environmental variables can account for the main variation in the species data. When the solutions differ considerably, it can be inferred that the environmental variables account for less conspicuous directions of variation in the species data or, if the correlations are small,that they cannot account for any of the variation. (Ter Braak 1986)

The computer program used for DCA and CCA was CANOCO (Canonical Community Ordination) formulated by Cajo J.F. Ter Braak (1988).

2.4.3 Two-way indicator species analysis, TWINSPAN, is a polythetic divisive technique. The data are first ordinated by reciprocal averaging then those species that characterize the reciprocal averaging axis extremes are emphasized in order to polarize the samples. The samples are then divided into clusters by breaking the ordination near its middle. The division process is then repeated on the two sample subsets to give further clusters. A corresponding species classification is also produced. The results of both classification procedures are usually expressed as a dendrogram. (Gauch 1982)

The advantages of TWINSPAN are that it uses actual sample-by-species data and is not dependent upon the previous calculation of a similarity matrix. Also the most similar entities are placed next to each other so making dendrograms more lucid (Gauch 1982). Used in conjunction with DCA, TWINSPAN can be used to emphasize clusters and determine their mutual relationships.

3.0 RESULTS.

3.1 Environmental variables

The results of the environmental variables are summarized in Tables 1, 2, 3 and 4.

Table 1 - Mean values of measurements of soil and vegetation structure.

Site	Soil; Depth	% Bare	% Litter	pH	Vegetation; Stems/m	Height (cm)	FHD
Rubble	1	63	0	8.22	12.44	12	0.46
Bare A	1	34	2	7.96	29.78	5	0.14
Bare B	1	34	10	8.14	31.22	6	0.26
Grass A	1	7	3	7.82	55.11	7	0.19
Grass B	2	0	40	7.48	130.33	1	1.59
Scrub A	3	0	13	7.51	56.56	4	1.52
Scrub B	2	0	8	7.65	144.44	28	1.15
Wood A	3	21	7	7.65	26.44	26	1.12
Wood B	3	23	9	7.54	39.11	16	0.88
Wood C	3	11	13	7.61	55.00	37	1.58

3.1.1 Soil depth.

From Table 1 it can be seen that soil depth increased with the successional stage of the site, being shallower in those sites which were less developed than in the later stages.

3.1.2 Soil pH.

The pH of the soil ranged from 7.48 in the Grass B site to 8.22 in amongst the Rubble. All the soils were of a basic nature which is as expected on a limestone escarpment. There was a tendency for the barer areas to have higher pH values than the more vegetationally developed sites which is probably a reflection of the higher mineral content present in the more skeletal soils. (Table 1)

3.1.3 Vegetation species composition.

The details of species percentage cover are given in Appendix 1.

The mean percentage area of bare ground (Table 1) was greatest in the Rubble and Bare A and B sites where there was much exposed limestone and patches of bare chalky ground. Those sites with dense vegetation, such as the scrub and grassland sites had very little or no exposed ground.

The woodland sites had intermediate amounts of bare ground. It was, however, very different to the bare ground found in the more exposed sites, being bare soil rather than bare rock.

The mean percentage area cover by dead plant material and litter is given in Table 1. The barer sites (Rubble, Bare A, Bare B and Grass A) had significantly less litter cover than the more developed sites ($t = 4.56$, $P < 0.0001$ fo 74 dof) but Bare B did have plant litter in amounts comparable to those of the scrub and woodland sites. Grass B had by far the largest amount of dead plant material present, consisting mainly of loose grass stems.

3.1.4 Vegetation structure.

The stem density was greatest in those sites with large areas of dense grassy tussocks such as Grass B and Scrub B (Table 1). There was no linear trend of increasing stem density with stage of succession, the woodland sites, Wood A and B having stem densities similar to those of Bare A and B. This reflects the large patches of bare ground found within both these habitat types.

There is a distinct division between the sites regarding foliage height with Bare A, Bare B and Grass A all having very low lying vegetation in comparison to the other sites ($t = 11.46$, $P < 0.0001$ for 88 dof). (Table 1)

The foliage height diversity index appears to be largely a reflection of the vegetation height rather than the density of plant stems. The correlation coefficient, r, for FHD against vegetation height equals 0.869 ($P < 0.001$ for 88 dof) whereas r for FHD against stem density was only 0.351. This point can be illustrated by looking at the values recorded for the Scrub B and Wood A sites which have very similar height and FHD indices but very different stem densities (Table 1).

It was noted that the Rubble site had a comparably high FHD when taking into account its paucity of vegetation. This was caused by those plant specimens which were present growing vertically on the sloping rubble which in essence was analogous to the plants growing at approximately 45^{o} to the ground surface.

3.1.5 Temperature and humidity at the ground surface.

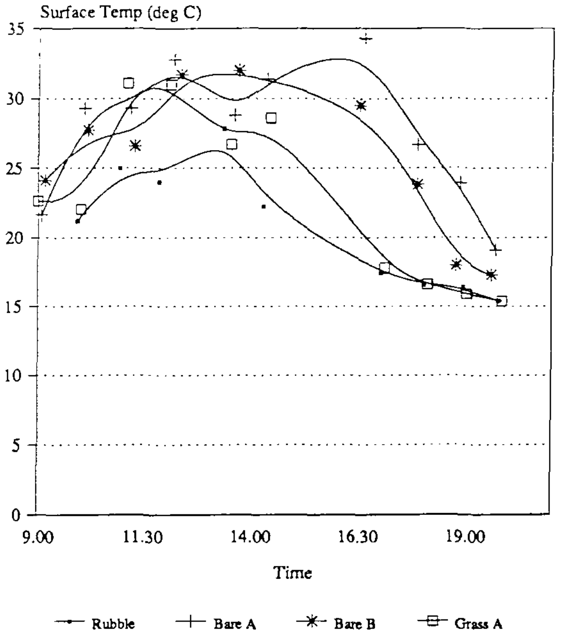
Table 2 - Temperature measurements (°C).

Site	Mean	S.D.	Max T	Min T
Rubble	21.1	6.0	33.5	15.0
Bare A	24.6	5.6	34.3	13.0
Bare B	23.3	5.4	32.0	14.2
Grass A	22.2	5.5	31.1	15.2
Grass B	20.6	5.3	30.4	13.6
Scrub A	19.5	4.4	31.3	13.2
Scrub B	22.3	4.9	30.6	16.2
Wood A	16.0	2.4	19.5	11.5
Wood B	16.2	2.2	19.0	12.7
Wood C	17.0	2.5	20.4	13.2

The temperature was affected greatly by the amount of shading caused by tree and shrub cover (Table 2). The woodland sites, therefore, tended to have the lowest mean temperatures during the day due to reflection of light from the vegetation surface. The more sparsely covered sites were warmed up during the daylight hours and on sunny days in particular the ground surface became very hot, approaching 40°C in some cases. This may have been caused by reflection of light from the surrounding cliff faces but is more probably due to the lack of vegetation cover, therefore allowing direct incidence of light onto the ground surface.

The standard deviation of the temperature was highest in the more exposed sites and it was these sites which showed the greatest fluctuations in temperature during the daytime (Fig 2) These results are unfortunately incomplete in showing only the daytime temperature changes but it can be postulated that the sites which vary most during the day may do so again at night. The standard deviation in temperature is highly positively correlated with mean temp ($r = 0.909$, $P < 0.001$ for 8 dof) so it would appear that the high standard deviation seen in the bare sites is due to their reaching higher extremes which increases both the mean temperature and the variation around it.

Figure 3 and Table 3 show the differences in temperature created by the ceramic tiles. It can be seen that the temperature under the tiles is always cooler than on the nearby ground surface and that this difference is significant in all but one of the sites examined. This difference was most highly marked in the exposed areas with a mean difference of 4.75°C in Bare A and 5.8°C in Bare B. These values can be compared to mean differences of 1.4°C in Wood A, 1.1°C in Wood B and 1.6°C in Wood C.



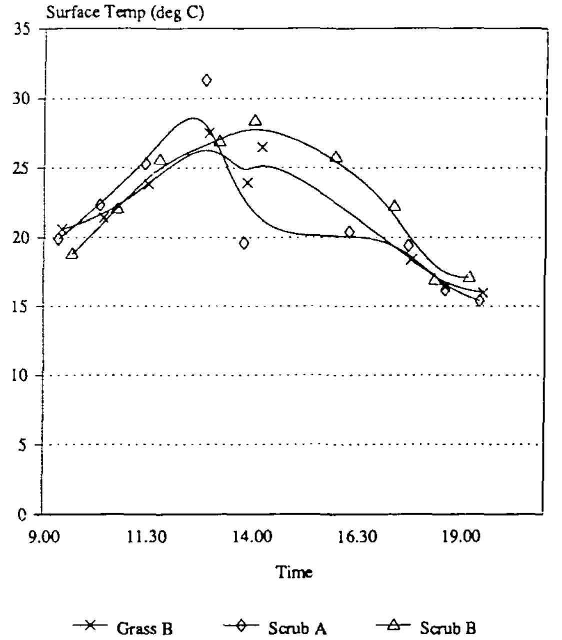


Figure 2 - Trends in surface temperature
in ten sample sites during daytime

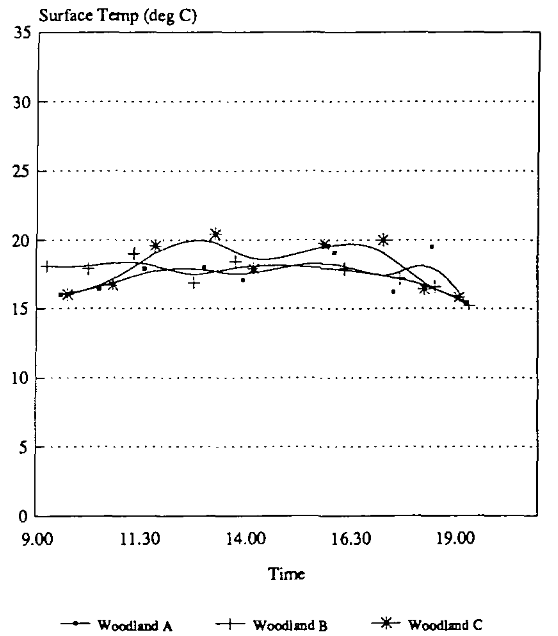


Table 3 - Mean difference between temperature on ground surface and beneath ceramic tiles.

Site	Mean Difference (^{o}C)	t	dof	P
Rubble	3.9	5.42	3	<0.02
Bare A	4.6	6.59	3	<0.01
Bare B	5.8	3.53	3	<0.05
Grass B	2.0	8.71	2	<0.02
Scrub B	3.1	2.06	3	>0.05
Wood A	1.4	5.95	3	<0.01
Wood B	1.1	10.18	3	<0.001
Wood C	1.6	8.41	3	<0.01

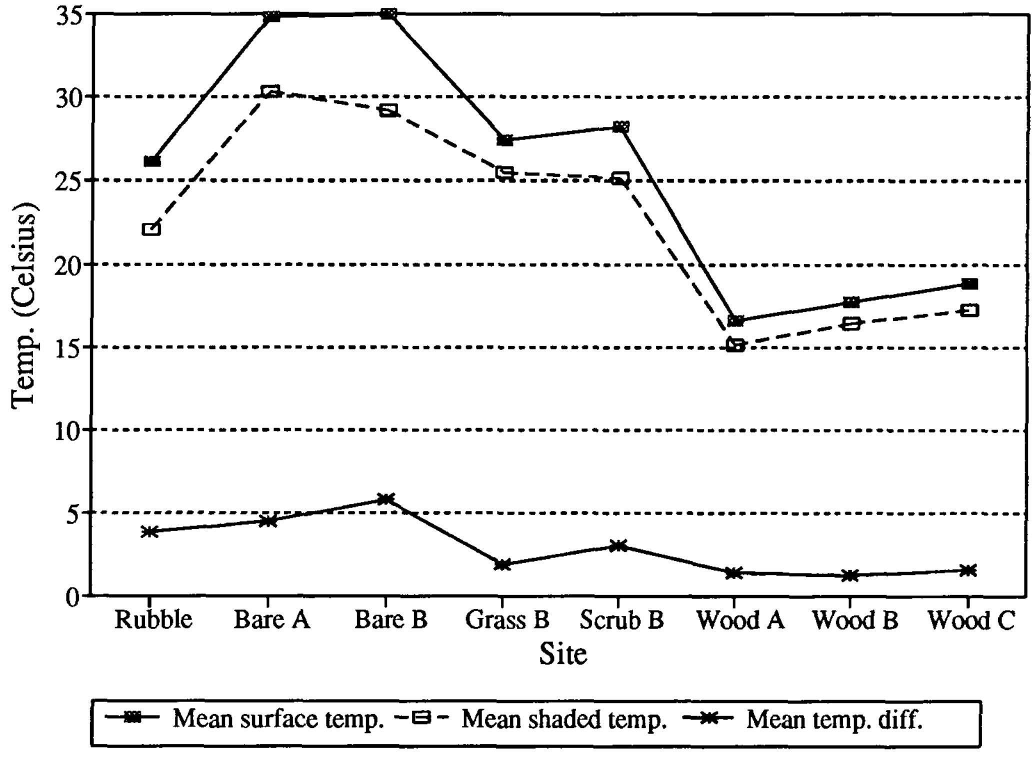
Table 4 - Humidity measurements (R.H.).

Site	Mean	S.D.	Max Hum	Min Hum
Rubble	62.3	11.7	92	41
Bare A	65.4	11.3	79.5	37
Bare B	66.8	9.9	81	45
Grass A	66.7	5.2	79	59.5
Grass B	75.2	7.6	88	62
Scrub A	71.9	7.6	85.5	58
Scrub B	80.3	7.8	96	63.5
Wood A	67.8	9.9	87	48
Wood B	62.0	8.1	79.5	47
Wood C	69.6	8.2	84	53.5

There was a low correlation between mean humidity (Table 4) and mean temperature (Table 2) ($r = 0.142$). There was, however, a high correlation between mean humidity and mean stem density ($r = 0.906$, $P < 0.001$ for 8 dof) suggesting that those sites with dense surface vegetation have increased humidity at the ground surface, possibly by preventing forced evaporation of water from the surface and also due to increased transpiration of the plants. Therefore, the most humid conditions were found in those areas with high stem densities such as Grass B and the scrubland sites. These three sites were significantly more humid than the other seven sites during the daytime ($t = 6.91$, $P < 0.0001$, for 108 dof).

The woodland sites were found to be not significantly more humid than the more exposed sites, a comparison of the means of all humidity readings taken in sites Rubble, Bare A. Bare B and Grass A and those taken in the woodland sites gave a value of $t = 0.531$ which is not significant

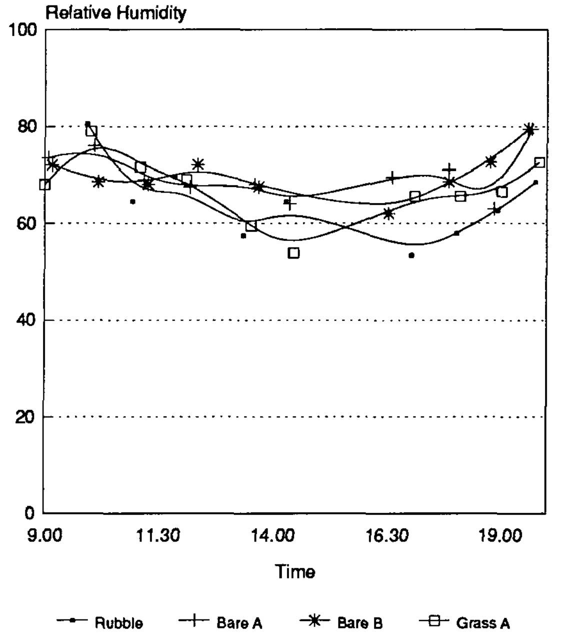
Figure 3 - Difference in average temperature due to tile cover



for 113 dof. This may be a reflection of the large areas of bare ground present in both these site types, allowing rapid evaporation from the soil surface.

The largest variation in humidity was found in those sites with the greatest areas of bare rock or soil ($r = 0.82$, $P < 0.01$ for 8 dof) such as the Rubble, Bare A and B and Wood A and B. This large variation would appear to be due to drying out of the soil surface and lack of ability to retain moisture near to the ground surface due to lack of vegetation. This is supported by a significant negative correlation with the proportion of bare ground and the minimum humidity measurement recorded on the site ($r = -0.87$, $P < 0.01$ for 8 dof). There is no mutual correlation with bare ground and maximum humidity recorded at the site.

Figure 4 shows changes in relative humidity over the course of a day. The general trend is for the surface humidity to drop to a minimum around 12.00 - 14.00 hours and then rise again around dusk. Although no obvious differences are shown it would appear that the graphs for the Bare areas and the woodland sites are similar, which is a reflection of these sites having similar mean humidities. The graphs of Grass B and Scrub A & B tend not to reach such low humidities during mid afternoon and hence have what appear to be higher, more stable, relative humidities. This is supported by these sites having high mean relative humidities with a low standard deviation (see Table 4).



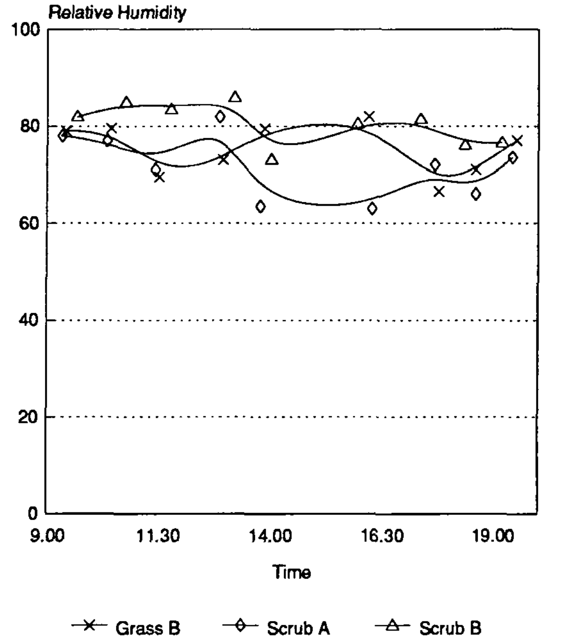
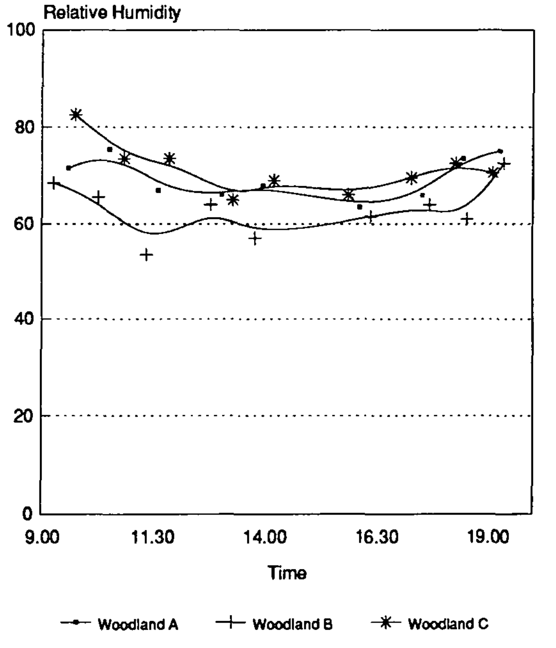


Figure 4 - Trends in relative humidity at ground surface in ten study sites during daytime



3.2 Sampling of woodlice and millipede populations in different sites.

In all, six species of woodlice were found; *Philoscia muscorum* (Scopoli), *Oniscus asellus* Linnaeus, *Porcellio scaber* Latreille, *P.spinicornis* Say, *Armadillidium vulgare* (Latreille) and *Trichoniscus pusillus* Brandt.

Five species of millipede were collected; *Ommatoiulus sabulosus* (Linne), *Tachypodoiulus niger* (Leach), *Cylindroiulus punctatus* (Leach), *Julus scandinavius* Latzel and *Polydesmus angustus* Latzel.

In general, millipedes were more commonly found in the sites with deeper, more developed soils and the woodlice were relatively more abundant on the Rubble, Bare A, Bare B and Grass A sites ie those sites with a poorly developed soil structure. This separation between the major invertebrate groups was significant for the results obtained by hand searches, ceramic cryptozoa boards and pitfall trapping. Chi-squared tests were performed on contingency tables of the numbers of millipedes and woodlice found in the rubble and bare sites, the grassland sites and the scrub and woodland sites (Table 5). (These site groupings were obtained using the results of the DECORANA analysis to be described later (see 3.3). In the case of pitfall trapping there were no results from the Rubble site and the site groupings were slightly different; Wood C being partnered by Scrub A and Grass B was placed with the remaining scrub and woodland sites (see Figure 6b).)

Table 5 - Chi-square values obtained from contingency tables of woodlice and millipedes versus groups of sites given by DECORANA analysis.

Sampling method	Chi-Square	dof	P
Hand searches	78.5	2	<0.001
Ceramic tiles	434.6	2	<0.001
Pitfall trapping	2541.0	2	<0.001

3.2.1 Soil cores.

The numbers of individuals obtained with soil cores was very low (Table 6) and only six species were recorded. Some general trends are still apparent, however. The absence of millipedes from the 'barer' areas (Bare A, Bare B and Grass A) and the high numbers of *Philoscia muscorum* in the tussocks present in Woodland B are consistent with results found by other sampling methods. The low sample size prevents any solid conclusions being drawn from these results, however.

Soil cores do nevertheless provide the only definite results where population densities can be compared. Densities of *O.asellus* in the Rubble site have a mean of around $19/m^2$ whereas densities for *T.niger* and *J.scandinavius* are only $6/m^2$. These are comparable with 7 and 9 per square meter respectively found by Blower (1979) in British limestone woodland.

P.muscorum was found in the highest densities, $70/m^2$ in site Wood B which is low compared to that of $115\text{-}265m^{-2}$ found by Sutton (1968) and $240\text{-}1040m^{-2}$ found by Sunderland on dune grassland.

Table 6 - Sampling results obtained from five $0.03\ m^2$ soil cores.

	Rub	BA	BB	GA	GB	SA	SB	WA	WB	WC	Total
P.muscorum	-	-	-	-	2	3	-	-	11	-	16
O.asellus	3	-	-	-	-	-	-	-	-	-	3
A.vulgare	-	-	1	1	-	-	2	-	-	-	4
O.sabulosus	-	-	-	-	-	2	-	1	-	-	3
T.niger	-	-	-	-	-	-	1	1	-	-	2
J.scandin.	-	-	-	-	-	1	1	-	-	1	3
Total	3	-	1	1	2	6	4	2	11	1	31
No. of species	1	0	1	1	1	3	3	2	1	1	6

3.2.2 Hand searches.

The results obtained from the timed hand searches are given in Table 7. It can be seen that *Armadillidium vulgare* is widespread throughout the reserve occurring in high densities on the barer grassland areas (Bare A & B and Grass A). This species was usually found sheltering under rocks and loose stones but was often seen wandering in the open during hot spells.

P.muscorum was another widespread species tending to occur under rocks and deep inside grass tussocks and amongst dense vegetation. It was found to be most abundant in those areas were these tussocks were present, such as Wood B.

Oniscus asellus was found in relatively high densities in sites which contained piles of loose rocks such as the talus at the bottom of cliff faces (Rubble) and Wood C which contained a large heap of old building material.

Trichoniscus pusillus was found most commonly in Woodland C where it occurred under the thick layer of loose, decomposing vegetable matter.

Of the millipedes only *Tachypodoiulus niger* was collected in any great numbers. This species would appear to prefer those areas with deeper soil and thicker vegetation although large numbers were collected amongst the loose rocks of the Rubble site.

Table 7 - Sampling results obtained from six ten minute hand searches.

	Rub	BA	BB	GA	GB	SA	SB	WA	WB	WC	Total
P.muscorum	2	24	20	18	18	31	1	-	47	7	168
O.asellus	25	3	-	-	-	1	-	-	-	27	56
P.spinicorn.	1	-	1	-	-	-	-	-	-	-	2
P.scaber	2	4	28	1	2	-	-	-	1	4	42
A.vulgare	8	87	67	75	1	1	4	2	-	1	246
T.pusillus	2	-	-	-	-	3	2	-	-	27	34
O.sabulosus	-	-	-	-	1	-	-	-	-	-	1
T.niger	18	-	1	3	9	23	3	11	4	16	88
C.punctatus	1	-	-	-	-	1	-	5	-	1	8
J.scand.	1	-	-	-	-	1	-	-	-	1	3
P.angustus	1	-	-	1	-	-	-	1	-	2	5
Total	61	118	11	98	31	61	10	19	52	86	653
No of spec.	10	4	5	5	5	7	4	4	3	9	11

3.2.3 Cryptozoa boards.

The results from the ceramic cryptozoa boards are shown in Table 8. Differing numbers of tiles were baited throughout the sample sites so total numbers of animals collected could not be given. The values in Table 8 are mean numbers of individuals per baited tile, multiplied by nine (as there were nine tiles in each site) to give values closer to the actual number of individuals collected in each area.

Baiting the tiles with raw carrot increased the numbers of individuals found under the tiles in all of the species examined except *J.scandinaveous*, where two individuals were collected under both baited and non baited tiles. The result was found to be significant at the $P < 0.05$ level using a standard Student's t-test on untransformed data for six of the remaining species (Table 9). A $\log(x + 1)$ transformation was carried out on the data in an attempt to reduce skewness and decrease the variation around the mean but the results were found to be still not significant for *T.pusillus, O.sabulosus* and *P.angustus*. For the latter two species this lack of significance may have been caused by the sample size being too small. For *T.pusillus*, although the animals do show a preference for the baited tiles (74% of the individuals counted were found under baited tiles) the difference is not significant due to the high aggregation of the individuals which creates large variances. This large variance in turn reduces the value of t.

Table 8 - Sampling results obtained from ceramic tiles.*

	Rub	BA	BB	GA	GB	SA	SB	WA	WB	WC	Total
P.muscorum	2	9	14	22	27	11	4	-	7	4	100
O.asellus	94	2	2	-	-	9	2	-	-	-	109
P.scaber	4	14	16	11	-	2	-	-	-	-	47
A.vulgare	218	250	182	148	9	-	4	-	-	-	811
T.pusillus	-	-	-	-	2	2	7	2	2	70	85
O.sabulosus	-	-	2	-	4	2	-	2	5	2	17
T.niger	25	-	-	4	9	18	22	2	4	65	149
C.puntatus	-	2	-	-	-	5	2	-	4	5	18
J.scandin.	-	-	-	-	-	-	-	-	-	4	4
P.angustus	-	-	-	4	-	2	4	-	-	2	12
Total	343	277	216	189	51	51	45	6	22	152	1352
No of spec.	5	5	5	5	5	8	7	3	5	7	10

(* - see Text for details of values given.)

From the data collected from the ceramic tiles some obvious trends are apparent in species distribution between sites.

A.vulgare shows an obvious preference for the more open, stoney grassland areas (Rubble, Bare A & B and Grass A). *P.scaber* had a similar distribution but did not occur in such large numbers.

T.pusillus, a species which mainly occurs under the soil surface, was found only in those areas with deeper, more developed soils such as scrub and woodland sites. It was found at its highest numbers in the Wood C site.

P.muscorum was again ubiquitous throughout the reserve being recorded in all but one of the sites. This species was most numerous in the grassland sites.

O.asellus occurred in relatively high densities at the Rubble site where it lived amongst the loose rocks. It was not found under tiles in the Wood C site where the hand searches and pitfall results suggested it did actually occur. This was thought to be indicative of individuals not selecting the tiles as refuges, preferring to shelter instead amongst the old building material found in this site.

Table 9 - comparison of numbers of individuals found under baited and non-baited tiles.

Species	Baited	Non-baited	t	P
P.muscorum	53	27	2.08	< 0.05
O.asellus	50	7	2.07	< 0.05
P.scaber	23	4	2.58	< 0.02
A.vulgare	390	80	3.65	< 0.001
T.pusillus	46	16	1.38	> 0.05
O.sabulosus	9	4	1.38	> 0.05
T.niger	77	11	3.44	< 0.01
C.puntatus	10	2	2.14	< 0.02
J.scand.	2	2	0.00	1
P.angustus	6	1	1.73	> 0.05

T.niger was the most widespread species of millipede and was also found in the largest numbers. It was not recorded in the thin soiled areas, Bare A and B.

The remaining millipede species were not present in any great numbers but in general it can be seen that they tended to occur in those sites with deeper soils and tended to be absent from the more exposed, shallow soiled sites.

The results of the mark and recapture experiments were not easy to interpret as very few marked individuals were recaptured. It appeared that the animals did not have habitual retreats although in the rubble site 14 individuals of *A.vulgare* were found under the same ceramic tile out of 48 marked the previous day.

3.2.4 Pitfall traps.

The results obtained from pitfall trapping are given in Table 10. In terms of numbers pitfalling was the most successful sampling technique, with eleven species and 5929 individuals collected. Many species were collected in sites where they had not been recorded by any of the other three sampling methods, suggesting that they are more eclectic in the places that they are active than their choice of sheltering site.

Because of this the separation of woodlice and millipedes between the sites is not so distinct as suggested by the results obtained from the ceramic tiles (see Table 8). This may also be a reflection of the pitfalls measuring cumulative amounts of surface activity of the species over an extended time period whereas the ceramic tiles give, in essence, a snapshot of the distribution of the animals at any one time.

Gauche (1982) suggests that mobility of animals can make the community more diffuse and therefore the community as ordered by pitfalling, which measures activity, may not be as clear cut as that found by ceramic tiles.

Table 10 - Sampling results obtained from pitfall trapping.

	BA	BB	GA	GB	SA	SB	WA	WB	WC	Total
P.muscorum	605	143	479	156	57	90	3	239	9	1781
O.asellus	4	2	5	-	7	1	2	-	12	33
P.spinicornis	-	1	2	-	-	-	1	-	-	4
P.scaber	62	48	6	2	-	-	2	1	-	121
A.vulgare	912	358	1452	9	14	167	41	24	6	2983
T.pusillus	-	-	2	-	-	-	-	-	-	2
O.sabulosus	2	-	-	44	18	1	1	48	-	114
T.niger	12	23	22	144	98	100	110	46	134	689
C.puntatus	-	-	-	1	6	1	2	2	8	20
J.scandin.	4	-	9	10	26	10	1	6	20	86
P.angustus	1	-	6	6	44	18	6	1	14	96
Total	1602	575	1983	372	270	388	169	367	203	5929
No of spec.	8	6	9	8	8	8	10	8	7	11

A.vulgare was again found to be widespread throughout the reserve and was one of three species collected in every site. Large numbers were trapped on the exposed, low grassland areas (Bare A & B and Grass A).

P.scaber, like *A.vulgare* was found to be most abundant in the bare, stoney areas, Bare A and B.

P.muscorum was another species collected in all the sites examined. It was most abundant in the Bare A, Grass A and Wood B sites.

O.asellus was found to be more widespread in its patterns of activity than in its choice of sheltering sites being collected by pitfalls in all but two of the sites examined.

Only two specimens of *T.pusillus* were recorded in five weeks of sampling. This result is thought to be due to the inadequacy of pitfall trapping in collecting this species rather than any real scarcity of occurrence. Due to its small size it may regain balance on the lip of the pitfall and then escape. Also, this species tends to move through the litter layer rather than on the ground surface.

The millipedes tended not to occur on the drier soiled, exposed limestone sites being found mainly on the sites with deeper, richer soils. *T.niger* was recorded in all the sites examined and was by far the most common millipede found in the reserve. However, this species was still found in relatively lower numbers on the shallow soiled sites.

O.sabulosus was found mainly in one geographical area of the quarry, the three sites Grass B, Scrub A and Wood B which were all within 30m of each other (Fig. 1). These sites also contained dense grassy tussocks which is a preferred sheltering place of these species.

3.2.5 The species richness of the sites as shown by different techniques.

The number of species of millipedes and woodlice obtained by the different sampling methods is summarized in Table 11. It can be seen that the species richness obtained by the soil cores is very low in comparison to the number of species collected by other methods. This is largely a result of the small number of individuals collected by this method, many of the rarer species and those which tend to occur under rocks and in crevices such as *P.scaber*, being neglected.

For the remaining three sampling methods similar values for the total species richness of millipedes and woodlice in the reserve were obtained, the only difference being that *P.spinicornis* was not found under the ceramic tiles. With only 11 species being recorded in total there appears to be little variation in species richness between the sites but some interesting points can be raised.

Table 11 - Species richness of sites obtained by different sampling methods.

	Rub	BA	BB	GA	GB	SA	SB	WA	WB	WC	Total	Mean
Soil cores	1	0	1	1	1	3	3	2	1	1	6	1.4
Hand searches	10	4	5	5	5	7	4	4	3	9	11	5.6
Cryptozoa tiles	5	5	5	5	5	8	7	3	5	7	10	5.5
Pitfalls	-	8	6	9	8	8	8	10	8	7	11	8.0

The mean number of species recorded per site is higher in the data collected by pitfall trapping than by handsearching ($t = 2.92$, $P < 0.02$ for 14 dof) and cryptozoa boards ($t = 4.26$, $P < 0.001$ for 17 dof). The mean species richness per site obtained from hand searches and Cryptozoa boards were not significantly different (t = 0.12, P = 0.91 for 15 dof). The greater number of species recorded by pitfall trapping may simply reflect the greater sample sizes obtained by this collecting technique but it also indicates that a wider range of species are active in the sites than shelter there by day.

The hand searches and cryptozoa boards give consistent estimates of species richness in the bare and grassland areas but this similarity in the numbers of species recorded is not so obvious in the scrub and woodland sites.

The hand searches indicate relatively high numbers of species present in the Wood C and Rubble sites, which is not corroborated by the other sampling methods. These sites both contained piles of loose rocks and building materials and this may suggest that hand searching may be the best method of sampling this type of habitat in order to establish whether a species is present or not.

Relatively few individuals were collected by all the sampling methods in site Wood A. This site was given a low species richness by handsearches and ceramic tiles but a relatively large number of species were collected by pitfall trapping. This suggests that this site may be unsuitable as a location for daytime sheltering but provides a suitable feeding ground for a wide number of species.

3.3 Multivariate Analysis

3.3.1 Ordination and classification of study sites.

a. Twoway Indicator Species Analysis.

A TWINSPAN procedure was carried out in order to group sites with similar species composition. The TWINSPAN was performed on the totals of the species data collected using the ceramic tiles or the pitfall traps separately.

i. Tile data

Figure 5a shows the dendrogram produced by such a procedure performed on the ceramic tile data. The species given are the indicator species for each division and the number below each branching point is the eigenvalue for that division which gives an indication of the biological significance of separation. The clusters of sites produced by the analysis were relatively predictable. The first division of the sites is due to the relative abundance of *A.vulgare* in the bare areas and grassland sites which are thus separated from the scrub and woodland sites.

The presence of *O.asellus* separates the Rubble and Bare sites from the grassland sites. The Rubble site is further distinguished due to the large numbers of the millipede *T.niger* which occurred there.

Wood C, the site with rubble and remains of old buildings, is split from the second major group due to the presence of *Julus scandinavius* in this site.

ii. Pitfall data.

Figure 5b shows the corresponding dendrogram produced by a TWINSPAN procedure based on pitfall data. The Rubble site is not included in this diagram due to no pitfalls being set in this site. The only difference at the first division is that Grass B is placed with the woodland and scrub sites as opposed to the bare and Grass A sites. Also the eigenvalues obtained are very low compared to those produced by the TWINSPAN procedure on the tile data. This is possibly due to the divisions between the sites being less pronounced when taking into account activity patterns of the animals than when considering shelter sites.

The Bare A & B and Grass A are grouped together on the basis of low numbers of *T.niger* and relative abundance of *P.scaber* and *P.muscorum.* The relatively higher numbers of *P.scaber* then split off Bare A & B from Grass A.

Figure 5a - dendrogram of sites based on TWINSPAN classification of tile data.

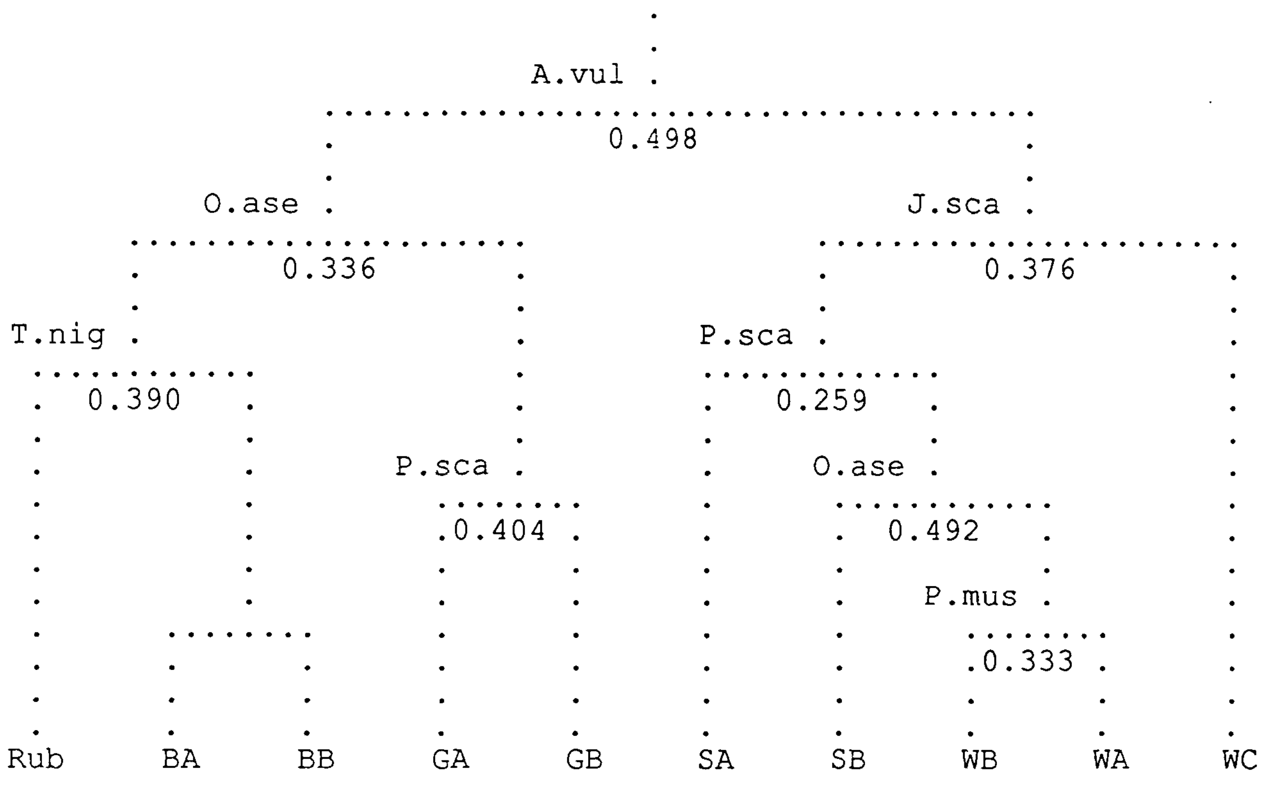
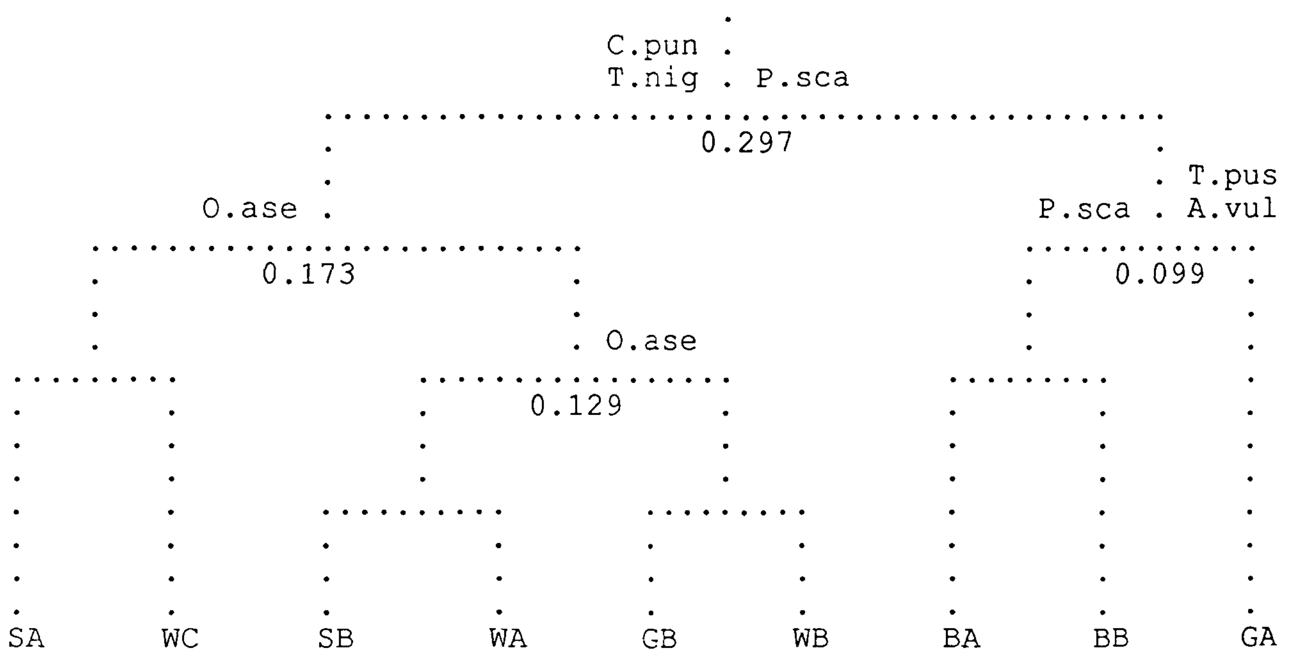


Figure 5b - dendrogram of sites based on TWINSPAN classification of pitfall data.



Three pairs of sites are formed from the other major division. These are Scrub A and Wood C due to their relatively high numbers of *O.asellus*; Grass B and Wood B due to their relatively high numbers of *O.sabulosus*; Scrub B and Wood A due to their lack of the these two indicator species.

b. Detrended Correspondence Analysis.

Figures 6a and 6b shows ordinations of the sample sites based on detrended correspondence analysis of the totals of data obtained by ceramic tiles and pitfalling. This procedure gives each of the sites an axes scores on the basis of their respective species compositions. The eigenvalues (E.v.) for each axis are given in brackets after each axis title.

i. Tile data.

Figure 6a shows the plot of sites based on data from the ceramic tiles. The fist ordination axis has an eigenvalue of 0.74 suggesting that 74% of the variation in species composition between the sites is "explained" by the scores for this axis. Sites Bare A & B and Grass A are clearly grouped and the Rubble site also has a similar first axis score to this group but is distanced from it on the second axis. This separation of the Rubble site is likely to be due to the presence of *T.niger* at this site, as indicated by the TWINSPAN procedure.

The two scrubland sites have similar scores on both axes suggesting that their species compositions are relatively similar.

The remaining four sites do not form a tight cluster. It can be seen, however, that the woodland sites are all distanced from the barer sites on the first axis, suggesting differences do occur in the species compositions of these dissimilar site types. By comparing the groups found using DECORANA with those obtained by TWINSPAN it would appear that those sites with low first axis scores ie towards the left of the ordination diagram have high numbers of *A.vulgare*. Indeed a correlation of the numbers of *A.vulgare* found in a particular site and its respective first axis score was found to be significant ($r = 0.903$, $P < 0.001$ for 9 dof).

Figure 6a - Ordination of sites based on DECORANA of tile data.

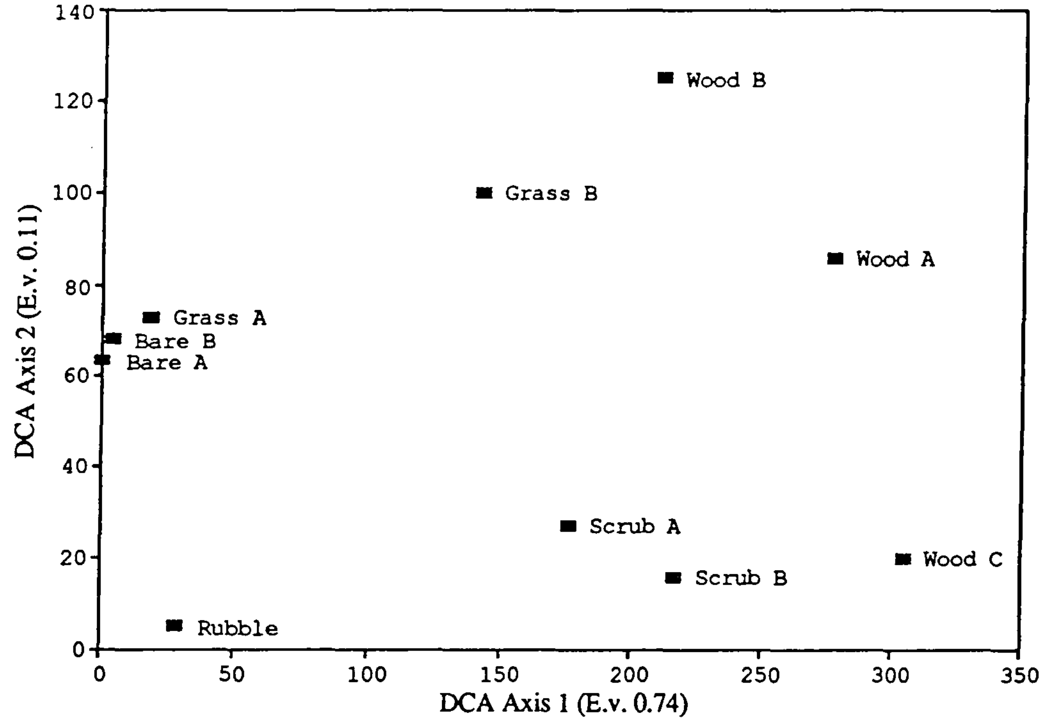
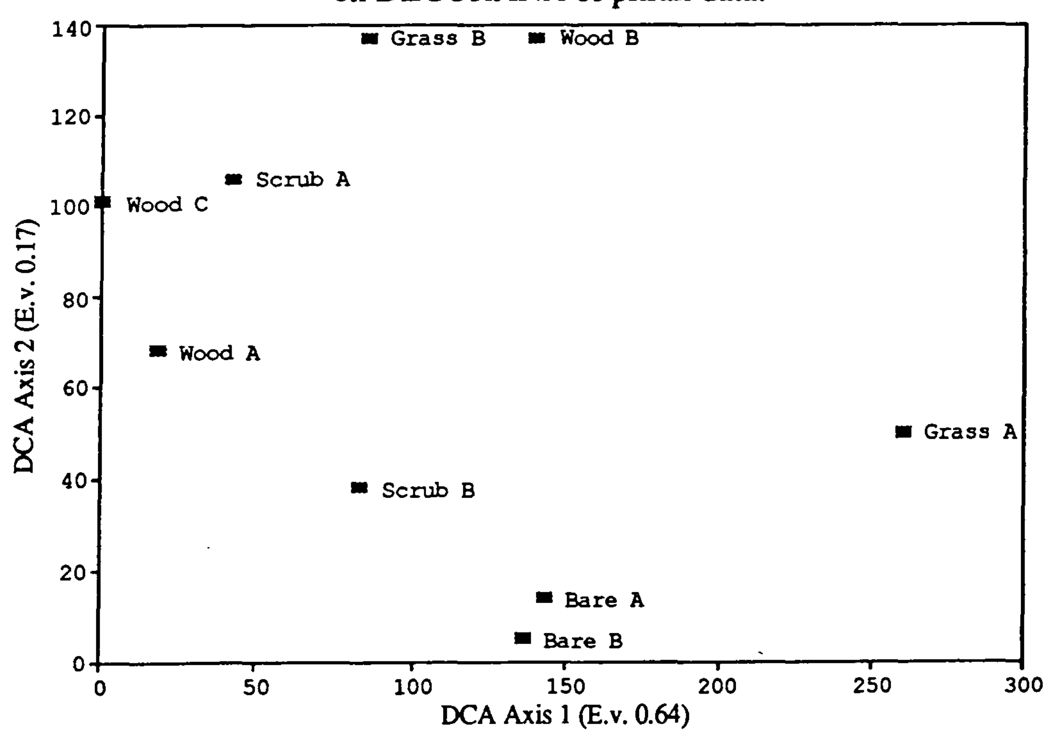


Figure 6b - Ordination of sites based on DECORANA of pitfall data.



ii. Pitfall data.

Figure 6b shows a similar plot based on data collected from pitfall trapping. As with the TWINSPAN result for pitfalling this plot is less easy to explain than the ordination diagram based on data obtained from the ceramic tiles and the eigenvalue of the first principle axis is lower (0.64). This is likely to be due to species being more widespread over the range of sites when active than when selecting suitable sheltering sites during the daytime.

The bare sites again form a distinct group having similar scores on both the first and second axes. The remaining sites are relatively spread out over the plot. By using the information obtained from the TWINSPAN procedure some groupings can be shown. Grass B and Wood B form a pair, probably on the grounds of having high scores of *O.sabulosus*. Wood C and Scrub A form another pair, probably on the basis of having relatively large numbers of *O.asellus*.

3.3.2 Ordination and classification of species.

a. Twoway Indicator Species Analysis.

Figures 7a and 7b show the results of TWINSPAN procedures carried out using each ceramic tile or pitfall as an individual sampling unit.

i. Tile data.

Figure 7a shows the dendrogram obtained using the data collected from the ceramic cryptozoa boards. On the whole, the first division produces groups which are essentially woodlice species and millipede species, with one exception in each group. It can be seen that four obvious groups are formed. *P.muscorum* and *O.sabulosus* are paired. This is likely to be due to these species occurring in high numbers in those sites with dense grassy tussocks, such as Wood B and Grass B.

O.asellus, P.scaber and *A.vulgare* are clustered together. These three species of woodlice tended to occur in those sites with loose rocks and high proportion of bare ground such as the Rubble site and Bare A and B.

T.pusillus, T.niger, C.punctatus and *J.scandinavius* are all species which prefer deeper, richer soils found in the more developed sites, such as the scrub and woodland sites.

Figure 7a - dendrogram of species based on TWINSPAN classification of tile data.

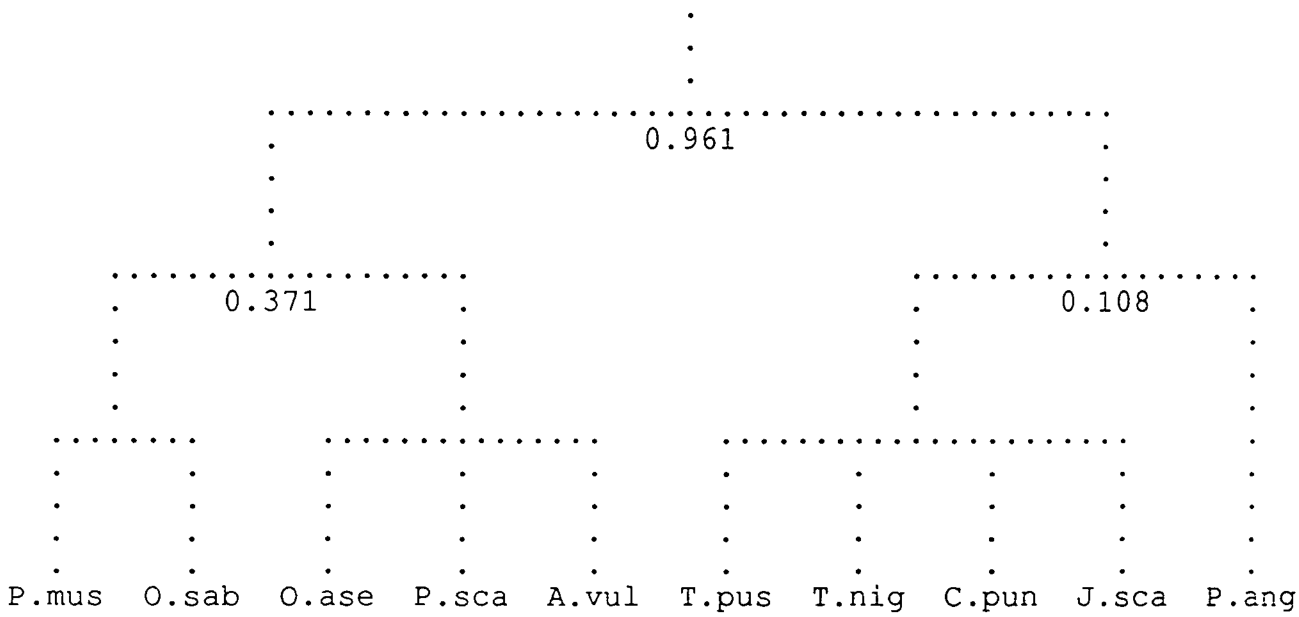
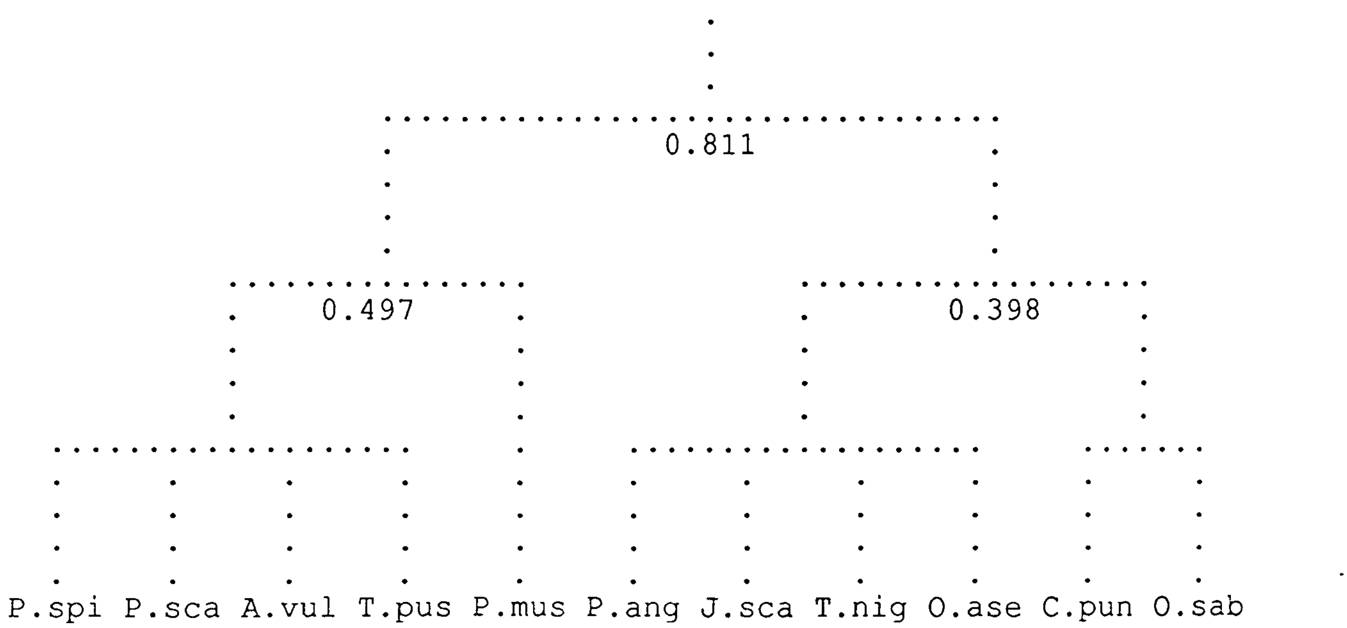


Figure 7b - dendrogram of species based on TWINSPAN classification of pitfall data.



P.angustus is isolated from the other species of its group. This may be due to this millipede being taxonomically isolated, being a "flat-back" millipede whose mode of life and ecological tolerances differ from those of the Julid millipedes.

ii. Pitfall data.

Figure 7b shows the dendrogram obtained from the pitfall data. The first division with an eigenvalue of 0.811, splits the species into two groups on the basis of their areas of activity. The woodlice species *P.spinicornis* (which was not found under the ceramic tiles), *P.scaber, A.vulgare, T.pusillus* and *P.muscorum* were all found in larger numbers on the barer, more skeletal soil types, with loose rocks and stones. *T.pusillus*, which is usually thought of as a species of deeper woodland soils, is placed in this group almost on default as this species does not lend itself to pitfall trapping and only two individuals were captured in total, these being in the Grass A site.

The second group consists of the millipedes species plus *the woodlouse O.asellus*. The millipedes tend to avoid the barer areas and occur mainly in the deeper soiled areas. *O.asellus* is placed in this group due the high count in the Wood C site. No pitfalls were set in the Rubble site, where *O.asellus* occurred at high densities according to the other sampling methods, so its association with species occurring in the "bare site" group is not taken into account.

P.muscorum is separated from the other species in its major group. This is likely to be due to its occurrence in relatively high numbers in the Wood B site whereas the other members of the group were found in low quantities in this site.

C.punctatus and *O.sabulosus* form a pair from the second major group. The reason for this is not obvious but it may be due to these species both being absent from the Bare A and Bare B sites.

b. Detrended Correspondence Analysis.

The corresponding ordination plots of species produced by a DECORANA procedure carried out on individual ceramic tiles and pitfalls are given in Figure 8.

i. Tile data.

For ceramic tiles (Figure 8a), those species found in bare, shallow soil areas with low vegetation are given low scores on the first axis. *A.vulgare* and *P.scaber* are placed close together due to their cooccurrence in the Bare A and B sites in high numbers. *O.asellus* is also grouped with this pair due to its high occurrence in the Rubble site.

Figure 8a - Ordination of species based on DECORANA of tile data.

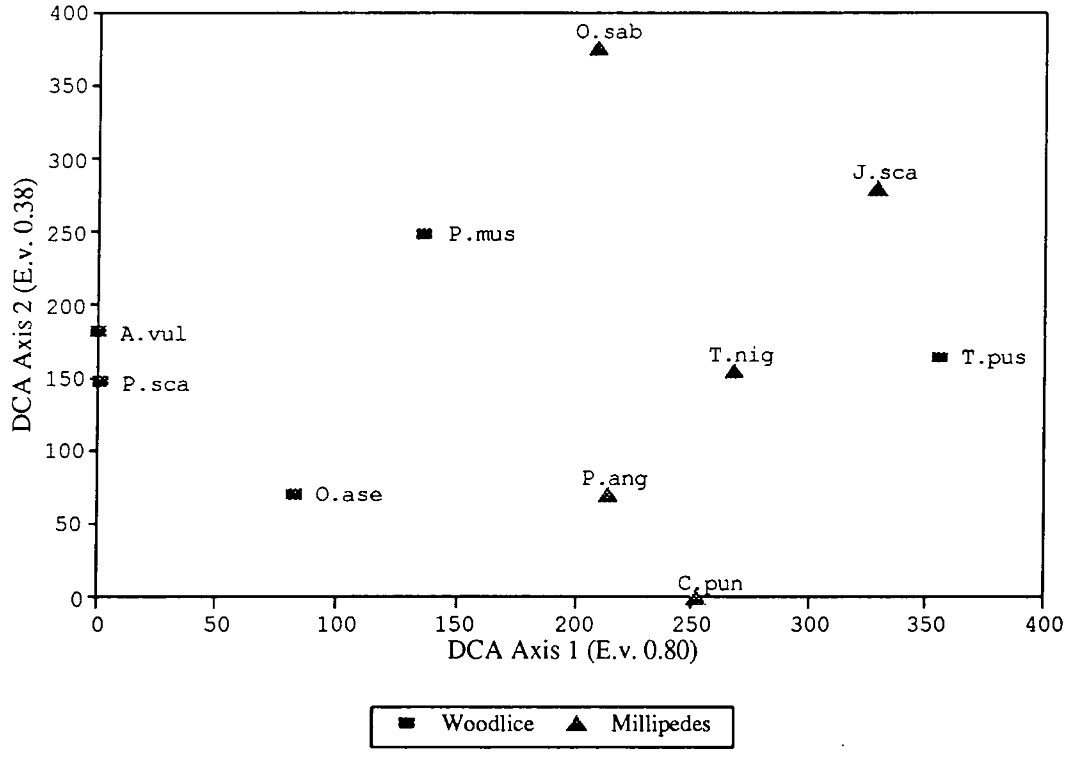
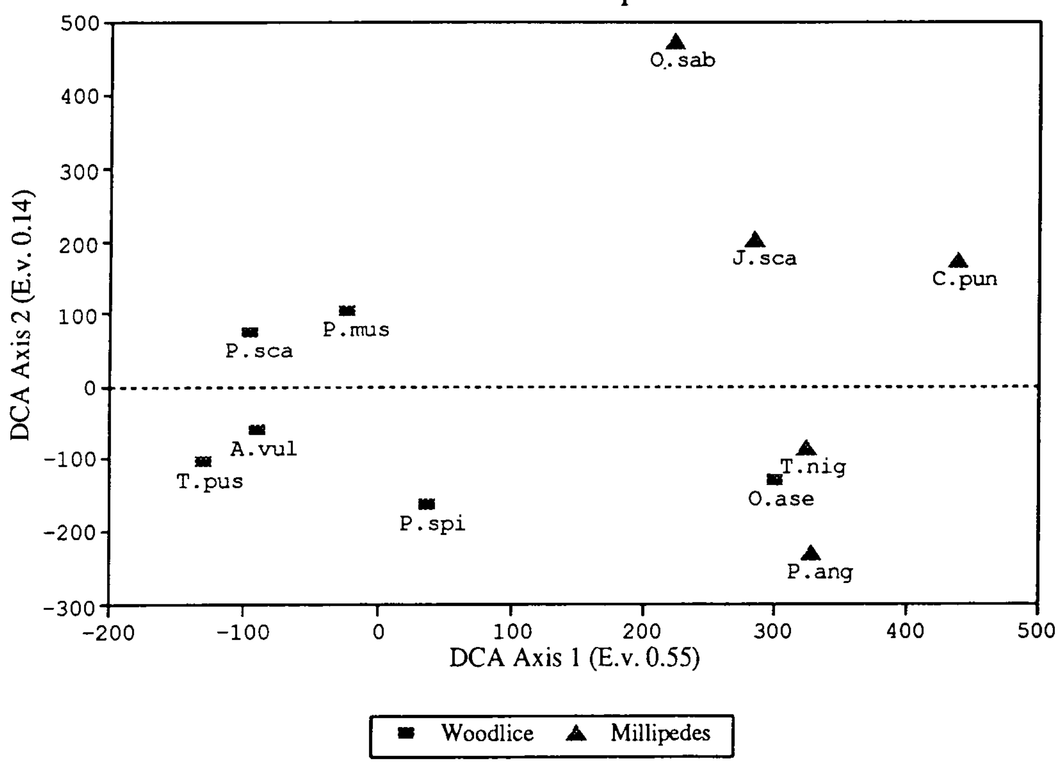


Figure 8b - Ordination of species based on DECORANA of pitfall data.



The remaining seven species are not closely grouped so the clusters produced by the TWINSPAN on this data were used to aid identification of species groups. *O.sabulosus* and *P.muscorum* can be paired due to these species occurring in Grass B and Wood B in high numbers.

T.pusillus is placed with the millipedes as it tends to occur with these species in the richer, deeper soiled areas such as the scrubland and woods.

ii. Pitfall data.

Figure 8b shows the ordination diagram of species based on pitfall data. Again the first axis divides the species on their occurrence in the bare, shallow soiled sites. Regarding the placement of *T.pusillus* with *A.vulgare* and *P.scaber*, this is due to the lack of data and is probably best ignored. *O.asellus* is placed with *T.niger* and *P.angustus* as it was found in relatively large numbers in site Wood C, where it sheltered amongst the disused building blocks. As no data was collected from the Rubble site using pitfalls the association of *O.asellus* with *P.scaber* and *A.vulgare* which occurs at this site is not taken into consideration in the analysis.

3.3.3 Canonical correspondence analysis of species and environmental variables.

Initial CCA procedures were carried out to establish which of the environmental variables measured were having the greatest influence on species distributions ie those environmental factors which were most highly correlated with the first and second principle axes. CCA was then performed on data from the individual pitfalls and individual tiles, omitting those environmental variables which were shown to be relatively unimportant in influencing the ordination of the species. The environmental variables which were used in the final ordinations were; soil pH (pH), mean surface temperature (Temp), standard deviation of surface temperature (Temp SD), mean surface humidity (Humidity), percentage cover of bare ground (Bare), stem density (Density), soil depth (Depth) and vegetation height (Ht)

Figures 9a and 9b show the ordination plots of species and environmental factors produced by CCA using this reduced environmental data set.

i. Tile data.

Figure 9a shows the CCA ordination diagram produced by data from individual ceramic tiles. It can be seen that the five species of millipede are tightly grouped. Together with the woodlouse *Trichoniscus pusillus* the millipede species have high scores on the first principle axis. This is highly

Figure 9a - CCA ordination of species and env. factors (Tile data).

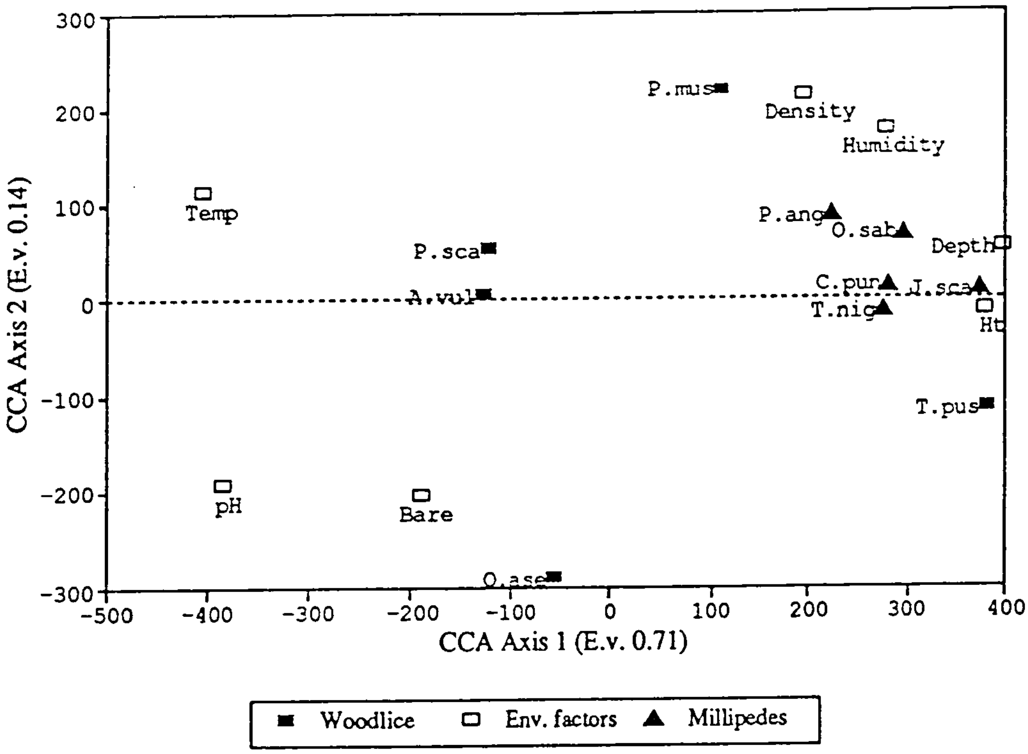
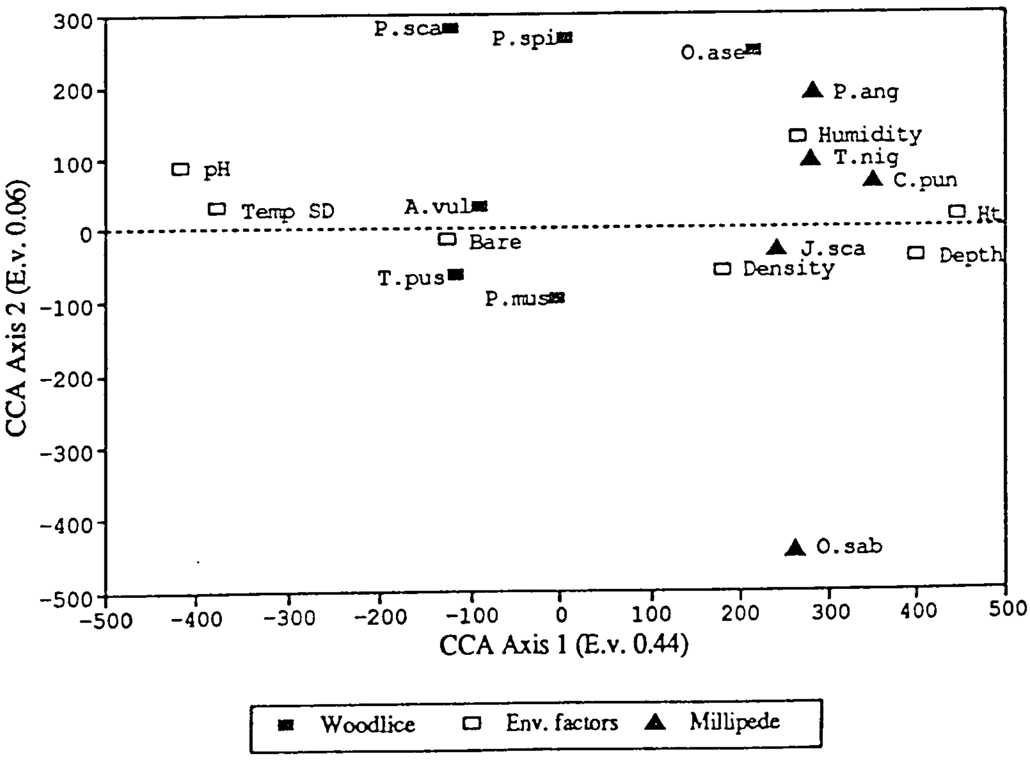


Figure 9b - CCA ordination of species and env. factors (Pitfall data).



correlated with increased soil depth and high relative humidity. The avoidance of high temperatures by these species is also apparent on this plot.

P.muscorum occurs in situations with high stem density and high relative humidity and tend to avoid bare ground. This is realistic as this species is characteristic of grasslands and tends to form aggregations in dense grassy tussocks.

P.scaber, A.vulgare and *O.asellus* are found to occupy sites of lower relative humidity and higher temperatures. These species tend to occupy sites with a high proportion of bare ground and sites with high pH values which is indicative of poorly developed, skeletal soils. It is known that heavily armoured species such as *A.vulgare* and *P.scaber* require large quantities of calcium carbonate to strengthen the exoskeleton so these species may be expected to occur in sites where there is a ready supply of limestone.

O.asellus is shown to be especially associated with the amount of bare ground present in an area. This is a result of this species occurring in relatively high numbers in the Rubble site.

The clusters of species produced by CCA on the tile data are very similar to those formed by detrended correspondence analysis (Figure 8a) suggesting that, for the distribution of species as indicated by the cryptozoa boards, the environmental factors used in the CCA procedure do explain a large proportion of the variation in the sample-species data.

ii. Pitfall data.

Figure 9b shows the CCA ordination plot based on results from pitfall trapping. As pitfall catches are a result of surface activity which, in woodlice and millipedes, occurs mainly at night it seemed unrealistic to use daytime temperatures as an environmental factor influencing the distribution of species activity. For this reason, temperature was replaced by the standard deviation in temperature, as this factor is assumed to have similar relative values between sites at night as during the daytime.

The millipede species again have high first axis scores, relating these species to high vegetation density, high humidity and increased soil depth. The millipede species tend to avoid soils with a high pH but this is thought to be a reflection of the deeper soils becoming relatively neutral as opposed to the millipedes showing preferences towards acidic conditions.

O.asellus is placed in the proximity of the millipede species and it would appear that *Oniscus* avoids bare areas and tends towards increased vegetation density and high relative humidity.

However, this is known not to be the case and this classification is likely to be a reflection of the fact that no data was collected by pitfalls from the rubble site, where *Oniscus* did occur in relatively high numbers in a habitat that had high proportions of bare ground and had a relatively dry and hot microclimate.

P.scaber, P.spinicornis and *A.vulgare* are shown to occur in situations with lower relative humidity and greater variation in temperature. These sites also tend to have increased bare ground and shallower, more basic, skeletal soils.

T.pusillus is placed near to the above group to the lack of data obtained on this species by pitfalling.

P.muscorum is placed near to the vector point representing bare ground in this ordination as opposed to showing strong associations with stem density, as indicated in the CCA ordination based on ceramic tiles. This could represent increased activity of *Philoscia* over areas of bare ground due to its unsuitability as a habitat type. The situation may also be caused by pitfall catches of this species being negatively affected by dense vegetation, which limits horizontal movement of individuals and so gives diminished trap returns.

Again, the major groupings of this plot are similar to those found by DCA (Figure 8b) although the placement of some species relative to others is slightly different. However, it still suggests that variation in species distribution has been explained to a large extent by the environmental variables used in the analysis.

4.0 DISCUSSION.

4.1 Assessment of sampling techniques.

4.1.1 Soil cores.

Most quantitative sampling of ground invertebrates is carried out by taking soil cores or turfs followed by a mechanical extraction procedure (see Sutton 1972 p109). These extraction devices are usually similar to, or based on, Tullgren funnel apparatus which use lights to produce heat which causes the animals to evacuate the soil or litter and drop into a collecting vessel (Sutton 1972).

This type of procedure has been used in a number of works on woodlice and millipede population ecology such as Banerjee (1967), Blower (1970), Sutton (1969), Davis (1984), Sunderland *et Al* (1976) and Paris (1963).

In this current study 0.0315 m^2 soil cores were used in conjunction with hand sorting in the field. There is an obvious danger with handsorting that smaller individuals may be missed but for the more conspicuous animals hand sorting would appear to be adequate. Blower (1970) suggests that careful handsorting may be as efficient as using extraction funnels in the recovery of adult millipedes.

It was found that sample sizes from the soil cores were very low, only 31 individuals being obtained from 50 soil cores. In some areas this may have been caused by the shallowness and coarse skeletal nature of the soil which could exclude many subterranean species. Also animals in the barer, more exposed sites, were often found in crevices in rocks and under large boulders where it was difficult to remove a soil turf. It appeared that catches were higher in sites with deeper soils, such as the scrub and woodland sites.

Each core took around 20 minutes to be carefully sorted, before the turf was replaced, and it was concluded that this method was too time consuming in terms of the sample sizes obtained. Far more individuals in almost twice as many species were collected during the hand searches which were carried out on a similar time scale (*cf* Tables 6 and 8).

It is likely that greater sample sizes would have been obtained if larger turfs had been used but whether any higher population densities would have been obtained remains to be seen. Also the removal of large turfs in this study was undesirable due to the botanical importance of the site.

The densities obtained in this study tend to be low compared to published data (see section 3.2) but it is interesting to note that some of the estimated densities are greater or at least on a similar order of magnitude to those obtained by the timed hand searches in this study. For example, *T.niger* had an average density of just $2m^{-2}$ in the woodland sites based on soil core results but on average less than 1 individual per square meter was found by hand searches. *P. muscorum* which was found in large aggregations in the Wood B site had a density of 70^{m-2} based on soil cores but a density of only $4m^{-2}$ based on hand searches.

Soil cores undoubtedly provide the most accurate estimates of population densities but their use may be confined to deeper soil situations and, due to the time taken in obtaining results, are probably best suited to long term studies.

4.1.2 Hand searches.

The timed hand searches were the simplest method of collecting used and could be performed in almost any locality. Hand searches give an idea of what species are present and in what relative proportions. Obviously there are some biases towards species which are larger and more conspicuous. Smaller, more cryptic species may overlooked and Miller (1974) suggests that hand sampling rarely yields millipedes of early stadia since these are not easily seen. However, a greater area can be covered than is feasible with soil cores and Tullgren extraction thus adults, which occur at low density, can be obtained in large numbers.

Lawlor (1976) too concedes that soil sampling gives a more accurate representation of the density and size distribution [of *A.vulgare* populations] but only hand sampling provides the number of adults required for further analysis.

Some sites provide obvious aggregation sites for cryptozoic animals, such as rocks and rotting logs, whereas other sites will prove more difficult to search, such as dense grassy tussocks or antagonistic vegetation types, such as thorny scrub and stinging nettles. Therefore the sample size produced by handsearching will be affected to some extent by the habitat type.

Catches will also depend on the experience of the collector, both in the actual capture of individuals in and recognition of suitable habitat types. It is likely also that the capture of an individual of a common species will be forfeited in an attempt to gain an individual of a rarer species, possibly leading to a disproportionate number of individuals of rarer species in the final results.

Hand searches, then, have many faults and biases but their employment still seems of use in preliminary survey work and some quantitative information can be gained. Dominant species can be identified and relative species richness of different habitats can be estimated.

4.1.3 Cryptozoa boards.

The ceramic tiles used as cryptozoa boards could be used in all of the habitat types investigated and, once settled, gave comparable quantitative results based on a standard sample area. Absolute values of population density cannot be derived from the results, however, as animals tended to aggregate beneath them. It is possible that using tiles of a greater size may have improved results but the ceramic tiles used (15cm x 15cm) were of a similar size to many of the loose rocks found in the quarry under which woodlice and millipedes were found. The use of ceramic tiles as opposed to seasoned, untreated wood, as suggested by Sutton (1972) was justified in this case as they appeared not out of place on a quarry surface strewn with loose rocks and stones but with little wood or litter present.

The tiles may not be so effective in areas where there are few loose rocks or logs as the presence of the tiles may provide a new niche to the site and thus promote the presence of species in sites where they would not naturally occur. Also species living in such a site may prefer not to shelter under the tiles, selecting more natural shelter sites. This appears to be the case with *P.muscorum* in the Wood B site, which largely consisted of dense grassy tussocks situated amongst a more loose cover of violets and other herb species. Pitfalls and handsearching suggest that this species is quite abundant in this site yet few individuals were found beneath the ceramic tiles. It seems that, if given the option, *Philoscia* prefers to shelter amongst the vegetation rather than under the ceramic tiles. Where dense vegetation did not occur, such as Bare A and B sites, *Philoscia* was found using the tiles as a shelter site.

Baiting the tiles significantly increases the size of samples but may also introduce further species bias as baits may be more or less attractive to various species. It may even be the case that the bait itself, raw carrot, was not responsible for the increased numbers of individuals found beneath tiles due to its food potential but rather due to the increased humidity under the tile due to the presence of the carrot.

During the counting of individuals beneath the tiles predation of woodlice, especially of juvenile *A.vulgare* by staphylinids and centipedes, was often observed, a situation previously studied by Sunderland & Sutton (1980). Whether this predation had significant effects on the results was not investigated but it seems unlikely that predation was occurring to any greater or lesser extent than in the natural situation.

Studies using cryptozoa boards were found not to be common. Sutton (1972) suggests that they can provide steady supplies of animals and can be used to investigate rates of dispersal of animals. Cole (1946) used solid oak cryptozoa boards of $0.4m^2$ in a quantitative study of cryptozoic animals in an Illinois woodland. The boards proved successful in the recording of both woodlice and millipedes and were used in an investigation of aggregation phenomenon in these groups.

Cryptozoa boards, although not giving "real" population densities do give good estimates of the relative frequencies of animals present in each habitat. Other advantages include the fact that killing the animals found is unnecessary as species soon become recognizable and animals can be counted alive. This means that overtrapping an area does not become a problem.

Mark and recapture experiments have not proved useful regarding woodlice. Cloudsley-Thompson (1958,1959) in a series of papers describing the effects of wind and other climatic factors on the nocturnal emergence of woodlice attempted many mark and recapture experiments and found that very few of the marked animals were seen again. These experiments were carried out at night when the animals were active whereas this study attempted to show if woodlice used an habitual refuge and it was supposed that a higher proportion of woodlice would be recaptured. This was the case but, as only the animals under one tile were counted, the initial sample sizes were low, usually less than 10, so that often no marked individuals were seen the next day.

Collinge (1942, quoted in Edney 1954) found that woodlice did not use the same retreat to shelter under day after day. This agrees with what was found in this work although, again, very few marked animals were recaptured so conclusions are unclear. It appeared that around quarter of the individuals of *A.vulgare* in the Rubble site were found under the same tile next day and it was supposed that these individuals, rather than leave the tile to forage and return, had spent the night under the tile as the bait present provided a good food source in a site that was largely devoid of plant litter.

4.1.4 Pitfall trapping.

Much has been written about the use of pitfalls as a comparative sampling technique of surface active invertebrates (Sutton 1972, Greenslade 1964, Uetz & Unzicker 1976). Catches depend both on the density of the populations and activity of the individuals within it. Species which are diurnal and less mobile would be expected to be caught in pitfall traps in fewer numbers than nocturnal species which are highly surface active. Also subterranean species would be thought to be poorly represented in pitfall catches.

Small animals may recover balance on the rim of the pitfall and then make their escape. In this study, *Trichoniscus pusillus* appears to have behaved in this way as only two individuals were collected. Catches would also be reduced due to the tendency of *T.pusillus* to live amongst the litter rather on the soil surface. Heavy, bumbling, surface active species such as *A.vulgare* tend to be caught readily in pitfalls due to their lack of agility.

To illustrate the point of species differences in pitfall catches Sutton (1972, p106) gives an example of pitfalls grossly under estimating the numbers of *T.pusillus* while at the same time over estimating those of *A.vulgare*, therefore giving a totally wrong picture of the species composition of the area.

Habitat structure will influence surface activity of individuals. Dense vegetation will tend to impede surface activity and thus decrease pitfall catches. Open areas may allow more fluent movement over the surface and may even encourage it as animals seek a more sheltered position. If this is so we may expect pitfall catches to be higher in areas of bare ground and negatively effected in sites which have a more complex vegetation structure.

For species such as *P.scaber* and *A.vulgare* where catches are greater in areas of low resistance to surface activity (Bare A & B) some doubt may be expressed when making conclusions about their distribution of these species. It is in these instances where comparison of results from other sampling techniques is of value.

However, it must be taken into consideration that these bare areas are more exposed and prone to high degrees of air movement over the ground surface than areas where the vegetation is tall and dense. It has been shown that increased wind speed can decrease surface activity of woodlice (Cloudsley-Thompson 1958, 1959, 1973) so this factor might have a detrimental effect on pitfall catches.

Pitfalls have previously been used in quantitative analysis of millipedes and woodlice. Al-Dabbagh & Block (1981) used pitfalling in association with soil cores in a population study of

A.vulgare. As only one species was being investigated and the work was concerned with comparing two similar habitat types (Breckland heath) there appears no reason why activity of individuals should differ in the two sites. Therefore pitfall catches should give a valid result of relative abundances.

Blower (1970) again used pitfalls in conjunction with soil cores in his study of millipedes in a Cheshire woodland. He suggests that the advantage of pitfalls is that they provide adult millipedes in large numbers. No estimates of density were made from the pitfall data but they provided valuable information on age structure.

Davis & Jones (1978) used pitfalling in their survey of ground arthropods in chalk and limestone quarries and, after admitting to the limitations of the method, suggest that for large-scale survey purposes continuous trapping produces more surface-active invertebrates than any other sampling method.

It seems that the complexity of environmental factors which may influence surface activity of invertebrates, especially of woodlice and millipedes, is great and it is probably best to concede that they occur and treat the results obtained from pitfalling with due caution.

It is obvious, therefore, that pitfalls must be used with discretion and should not be used in determining absolutes. However, it is equally obvious that they do provide a very useful survey apparatus and can be used to glean information of relative abundances and comparisons in species distributions between sites. Used in conjunction with other sampling techniques they can be used to illuminate differences between shelter sites and areas of surface activity.

Greenslade (1964) suggests that pitfalls, when used in conjunction with other sampling methods such as hand searches, can be employed for the qualitative assessment of different habitats, especially when many species are restricted to one habitat type and can also yield some information on the frequency of the species.

In this study once the initial problems of sinking pitfalls in sites with very shallow soils had been overcome, the pitfalls proved easy to maintain and provided large numbers of individuals. The species distributions found by pitfalling, with the exception of *T.pusillus*, were reasonably consistent with those found by the other techniques. However, the pitfalls could not be sunk in the Rubble site as they were split and tipped over by the loose stones. Also, sorting the desired species from the countless others which were caught could become tedious and time consuming as so much material was often collected.

4.1.5 Summary of the uses of the sampling techniques.

Using more than one sampling method can provide a useful source of cross reference and help assess the validity of conclusions. Problems can still occur, however, when all the methods used could be showing the same bias. For example, *A.vulgare*, due to its large size, slow bumbling movements and tendency to occur on the ground surface, would be expected to occur in relatively high numbers in pitfalls, handsearches and beneath ceramic cryptozoa boards. Other species such as the burrowing millipede *Polydesmus angustus*, would not be expected to occur too frequently in pitfalls and would be overlooked during handsearches.

Also certain habitat types may contain biases consistent throughout all the sampling methods employed. For example, in dense lush vegetation pitfall catches of ground invertebrates have been shown to be lower (Greenslade 1964), hand searching is not as easy as in bare areas and species living in such habitats may prefer to shelter amongst the vegetation rather than under ceramic tiles, which may seem quite alien in such an environment.

When taking into account the drawbacks and biases of all the methods used, and the lack of a cross reference where negative factors overlap, the derivation of valid conclusions appears to be impossible. However, provided the method used to acquire the information is always stated, for example "the results as shown by hand searches" or "relative frequencies found by pitfalling", the reader is left to appreciate the intricacies of the technique and grasp the full implications of the statement.

Gauche (1982) suggests that exchanging and comparing methods and results are important in identifying the most effective methods and approaches towards finding the structure of a guild or community and discovering methods which are complimentary.

4.1.6 Differences in species richness as revealed by different sampling methods.

The number of species found by soil cores over all the sites examined was very low compared to the other techniques which is probably a result of relatively few individuals being collected by this method.

In Section 3.2.5 it was shown that there are significant differences between the mean species richness per site found by pitfalls and the other collecting methods. This may be a result of the sample sizes being much larger when using pitfalls so it would be expected that representatives of rarer species would be collected. Alternatively it may indicate that more species are active in each site at night when conditions are more equable than shelter there during the day.

Although differences were shown in the mean values of species richness per site it was found that the total number of species found in the reserve was very similar using the three more successful collecting methods, only the absence of *P.spinicornis* separating the results from the cryptozoa boards from the other two methods. This suggests that the reserve as a whole may have been surveyed comprehensively by these techniques and that any one of these methods may be considered an adequate survey procedure.

There was very little consistency between patterns of species richness between the sites indicated by the different techniques although the results obtained from handsearches and ceramic tiles were comparable and very similar values were obtained in the bare and grass sites. This gives a more meaningful picture of the communities of species in the different sites clustered by the ordination techniques.

4.2 Multivariate analysis.

The ordinations produced by DECORANA and CCA (Figure 6, 8 & 9) although largely similar in their major groupings did have slight differences depending on whether they were performed on pitfall data or ceramic tile data.

This may have been expected as any two data sets are unlikely to produce identical plots and what should be remembered is that the clusters produced on the grounds of the first and second axis using either the pitfall data or tile data are comparable. Only when data is sparse, such as for *T.pusillus* and *O.asellus* in the pitfall data, do spurious groupings seem to occur.

It would appear, therefore, that providing sufficient data is available for species present in a site, both pitfall trapping and cryptozoa boards provide ordinations in which the obvious trends and varying similarities of sites, or species, can be seen.

4.2.1 Multivariate analysis of sites.

The classification by TWINSPAN and ordination by DCA of the study sites are largely a reflection of their gross physical and vegetational structure (Figures 5,6). This is particularly clear with analyses based on data from the ceramic tiles (Figures 5a,6a) which shows sites clustered in a similar manner to their initial subjective classification.

On both DCA ordinations of sites (Figure 6) Grass B is placed close to Wood B, although this is more pronounced with the pitfall data. The similarity in species composition in these two sites may be a result of both these sites containing tussocks of cocksfoot (*Dactylis glomerata*) grass or simply due to geographical proximity.

The replication of habitat types proved interesting as it shows that the bare sites are very similar to each other and these in turn are grouped near Grass A site which had a similar structure and vegetation types. The Grass B site, being secondary grassland as opposed to primary *Sesleria* grassland as was Grass A, was positioned closer to the scrub and woodland sites on the ordination diagrams. It can be seen that, although both sites are obviously grassland, their species compositions are different, reflecting the differences in structure and microclimate of the two areas.

The woodland sites are not tightly grouped on the DCA ordination (Figure 6) suggesting that although there are similarities in the species composition of the sites (see Figure 5 for clusters produced by TWINSPAN) they are not as alike as the bare sites, which are tightly grouped.

4.2.2 Multivariate analysis of species.

With the TWINSPAN and DCA (Figures 7 & 8) it was found that on the whole the first major division separates the millipede species from the woodlice suggesting that there are differences in the distributions of the two major invertebrate groups within the quarry. Although there were some species, such as *T.pusillus* which, due to their habitat preferences or lack of data were placed with the "wrong" group, this division was similar for both pitfall and ceramic tile data.

The CCA analysis (Figure 9) clarifies the division of the two groups in terms of the environmental factors which influence the distribution of each constituent species. The ordination diagrams produced by canonical correspondence analysis (Figure 9) indicate that the five millipede species are similarly influenced by the physical factors of the habitat, being positively associated with deeper soils, high humidity, low temperature and tall, dense vegetation. Abiotic factors do not always operate in isolation from each other and it is likely that the structure of the soil and vegetation have a considerable influence on the microclimate (Wallwork 1976) therefore creating a complex of factors which co-occur.

The factors seen to influence the distribution of woodlice within the quarry are a positive association with areas of bare ground, high pH and warmer temperatures. They have a negative association with places which have high humidities, lush vegetation and deeper soils.

It is those environmental factors listed above, which, from the CCA, appear to be the more important causal agents in the distribution of woodlice and millipedes that are discussed further.

4.3 Niche separation in woodlice and millipedes.

Davis & Jones (1978) suggest that some quarries can support large populations of woodlice and millipedes and these invertebrates may be an important factor in determining the rates of accumulation of organic matter in the ground, and thus the development of soil and the rate of vegetation development.

Woodlice and millipedes are generally considered "primary decomposers" and find a wide range of food types acceptable. As a result of this they show little resource partitioning as far as food is concerned (Davis & Sutton 1977) although Sutton (1972) warned that, due to the need of "softening up" of some litter types by micro organisms and the need for other litter types to be leached of tannin before they become palatable, assumptions that food is in abundance for these animals are not always correct. It might be expected, therefore, that species would show some spatial distribution and concentrate on an area of foraging so as to avoid interspecific competition.

Previous studies by Davis, Hassall & Sutton (1977) and Davis & Sutton (1977) have examined the spatial distribution of diplopods and isopods within a dune grassland system. They found that differences in vertical distribution between woodlice (*P.muscorum, A.vulgare, P.scaber*) and a species of millipede (*C.latestriatus*) did occur with the millipede burrowing deeper down into the soil than the woodlice species, which are mainly litter inhabitants. However, no evidence of spatial isolation of the groups was shown regarding their horizontal distribution within this habitat.

In the current study, however, a significant disassociation of woodlice and millipedes was shown by the numbers collected by hand searching, ceramic tiles and pitfall trapping (Table 5) with millipedes being more abundant on the scrub and woodland sites and woodlice more common on the Rubble and more exposed grassland sites. This indicates that there is a difference in distribution between the groups in both daytime shelter sites and areas of feeding activity after dark. This difference in distribution maybe caused either by competition between the groups for food and shelter sites or due to differences in microhabitat preferences and physiological tolerances.

4.3.1 Distribution of millipede species.

Millipedes are essentially animals of the forest floor (Blower 1955) often occurring at the interface of the soil and litter layer on which many of them feed (Blower 1985). They are often found in greater numbers and with a greater species richness in areas with calcareous soils (Blower 1955) but there appear to be few instances of species being confined to such soils.

Most millipedes are detrivores, eating dead vegetation such as woodland leaf litter and dead wood, preferably leaves and wood which have been on the ground for some time and have undergone some microbial decomposition (Blower 1985). Some millipedes, however, such as *Tachypodoiulus niger* and *Ommatoiulus sabulosus* do feed on living material.

The cuticle of millipedes is covered by a surface film of lipoid which is produced continually by gland cells in the epidermis and this film renders the surface impermeable and hydrofuge to varying degrees according to the species . This lipoid layer has been shown to be more effective in Julid millipedes than in the "flat-backed" millipedes such as *Polydesmus* (Blower 1955). Nevertheless millipedes are very susceptible to desiccation and are consequently to be found only in places where they are assured of humid and moist conditions.

Tachypodoiulus niger was the most numerous and widespread species of millipedes found within the quarry. It is a common millipede which is often associated with base rich limestone. It spends more time above ground than other millipedes and undertakes considerable horizontal migrations (Blower 1955). This fact tends to increase numbers of this millipede collected by hand searching and gives good returns in pitfall traps. The species also shelters under rocks and logs so cryptozoa boards make obvious sheltering sites for this species.

T.niger tended to be found sheltering more commonly in the scrub and woodland sites, especially Scrub A and Wood C, where conditions were cooler and more humid and the soil was deeper and more developed. It was also found sheltering by day in the numbers amongst the loose stones of the Rubble site. Pitfall catches indicate that this species did pass through the barer areas in relatively low numbers.

Ommatoiulus sabulosus is another wandering species, often characteristic of duneland and associated with sandy soils (Blower 1955). In the reserve this species was not often found by hand searching but was recorded sheltering under cryptozoa boards and collected in greater numbers by pitfalling. Like the other millipede species found in the quarry they tend to avoid the barer, shallower soiled sites. The species was found most often in scrub and woodland sites, especially those which had dense grassy tussocks, such as Grass B and Wood B.

The mode of action of millipede species also affects their distribution. Julids have slow powerful gaits and tend to push their way through a substrate. "Flat-back" millipedes tend to act as a wedge and push their way into "cracks" in the soil which then "split" along a plane (Blower 1955). Therefore, polydesmids tend to be active in layers of leaf litter, parting them as they progress through.

Polydesmids, therefore, due to their susceptibility to wetting and dehydration through their cuticle and their mode of action tend to be found in the layers of damp, semi decayed leaves found on woodland floors. This litter will tend not to become as waterlogged as the soil itself yet still retain moisture in the lower layers to prevent the animals dehydrating.

In the current study *Polydesmus angustus* was found not to shelter in the bare ground sites (as indicated by hand searches and cryptozoa boards) but was present in those sites which had higher humidities and denser vegetation. Pitfall trapping suggested the species was more active in scrubland sites and the Woodland C site, which had a particularly rich, deep litter layer.

Julids, with their greater tolerances of drier conditions and lower vulnerability to soil waterlogging may be expected to have a wider habitat range than *Polydesmus*. In the case of *Julus scandinavius* this appears not to be the case as it too appears to be most numerous in the scrubland and woodland sites. This species is most often found in mixed woodlands with reasonable litter cover.

Cylindroiulus punctatus is a common millipede often associated with bark and dead wood can extend its range into quite acid conditions and often found in slowly decomposing deciduous leaf litter and in the humus beneath. It is, therefore, an animal of richer soils and within the reserve this species tended to be found mainly in the scrub and woodland sites.

4.3.2 Distribution of woodlice species.

Of the six species of woodlice found within the quarry only *Porcellio spinicornis* is thought not to be common or widespread in the British Isles.

All the species found were also recorded by Davis & Jones (1978) in their study of ground invertebrates in disused quarries in Kent, Derbyshire and Lincolnshire, although no one quarry they studied contained more than five species of woodlice.

Although most of the *A.vulgare* and *P.scaber* collected were of the usual slate grey colour many animals were found that had some yellow mottling or even regular patches of yellow on the dorsal side of the integument. This mottling may be of some benefit to individuals as it increases crypsis in the sandy coloured skeletal soils found in the bare quarry sites. Although not investigated in this study it would be interesting to discover if the frequency of these mottled individuals is higher in a quarry situation than in an area of woodland or grassland, where the increased fitness of mottled individuals may not be so apparent.

Woodlice are often considered to be more common on calcareous soils (Sutton 1972) and Ong (1979) showed that in *A.vulgare, O.asellus, P.scaber* and *P.muscorum* peak population densities occurred when soil pH was between 7-8, although whether this be due to a requirement for lime, the effect of pH on soil structure or its indirect effects on vegetation was not indicated.

The distribution of the woodlice species within the quarry is largely a reflection of their known micro habitat preferences.

T.pusillus is ubiquitous throughout the British Isles and very common, being found in wide range of habitat types (Harding & Sutton 1985). It is susceptible to desiccation and survives drought periods by vertical migration into the soil (Sutton 1972). This susceptibility to desiccation cannot be attributed solely to its small size as juveniles of other species are of a similar size to adult *Trichoniscus* and can live in much drier habitats. (Sutton 1968).

Trichoniscus pusillus was found to shelter under cryptozoa boards only in those sites which had more humid conditions together with a complex vegetation structure and richer, deeper soils

(Table 7). It was most abundant in the Wood C site which had a rich litter layer of partially decomposed leaves.

Oniscus asellus is probably the most commonly seen woodlouse in Britain and is well adapted to northern conditions. It often tends towards moist conditions and is strongly associated with the underside of dead wood and stones (Harding & Sutton 1985).

O.asellus was found by pitfalls to be active over a wide range of habitat types within the quarry. It appeared to shelter more frequently on those sites which had loose stones and rocks, such as Rubble, where it was found in high numbers under the ceramic tiles and Wood C, where it was often found adhering to the undersurface of stones.

Philoscia muscorum is one of Britains most widespread woodlice occurring all over the British Isles. It has been the subject of many detailed studies, including those of Davis, Hassall & Sutton (1977), Sutton (1968) and Davis (1984).

It is characteristic of hedgerows and can reach high densities in ungrazed calcareous grassland (Sutton 1972). It is also found in some woodlands where it occurs under the leaf litter, but it is designed for quick movement over the ground surface and not built for efficient burrowing (Walwork, 1976). It can tolerate surprisingly dry conditions and is abundant in dune grassland (Sutton 1972).

This species was the second most numerous species of woodlice found and it was distributed widely through the quarry, being collected by pitfall trapping in all of the sites. It was not common in the Rubble site but was found to be numerous in the bare areas, where it was collected in large numbers by pitfall trapping.

Aggregations of *P.muscorum* were found in the dense grassy tussocks found in the Grass B and Wood B sites. Sutton (1972) suggested that their aggregation in tussocks of *Dactylis glomerata* was because of the protection against predators provided by the close set stems, although no doubt the increased stability of micro climate and higher relative humidity do increase the attractiveness of the tussock as a habitat.

Porcellio scaber is the second most abundant and widespread British species after *O.asellus*. It is found in a wide range of habitats and often thought to be characteristic of drier conditions, although this was not born out in micro habitat data given by Harding & Sutton (1985).

P.scaber was not common in the scrubland and woodland areas, being more numerous in the barer, more exposed sites where it was found sheltering under stones and in crevices.

Porcellio spinicornis is most often found on limestone walls, quarry faces and cliffs in opens areas. It is also found on old ruins and buildings where mortar or limestone has been used (Sutton 1972).

It is widespread on the northern Pennines and much of Northumberland and would appear to have an "anti-Atlantic" north eastern distribution in the British Isles (Harding & Sutton 1985).

This species was not common in the quarry and was only found six times, five of which were on the exposed limestone areas where suitable cliffs, loose rocks and crevices were present.

Armadillidium vulgare, although common and widespread in the south and east becomes rarer in the north and west, where it is said to become increasingly coastal (Harding & Sutton 1985). Its preferred habitat is stony turf on chalk or limestone and it is much more common on calcareous soils (Sutton 1972, Hopkin 1987).

Armadillidium vulgare was found to be the most numerous woodlice in the quarry. It was relatively more abundant in the Rubble, Bare A, Bare B and Grass A sites. These sites were relatively warm and dry with sparse, low standing vegetation. There were many loose boulders and rocks under which aggregations of *A.vulgare* were often found.

Hand searches and cryptozoa boards suggested that relatively low numbers shelter in the scrub and woodland sites and pitfalls indicated that the species was relatively inactive in these areas.

It is apparent that the water relations of woodlice are of major importance in determining their local distribution. Different species are capable of withstanding dry air and high temperatures to varying extents and the assumption is that the humidity requirements of each species determines its distribution to a large extent (Edney 1954).

It has long been known that various species of woodlice differ with regard to the length of time they can survive in dry air (Cloudsley-Thompson 1977). Edney (1954) suggested that relative rates of transpiration between species were;

P.muscorum > *O.asellus* > *P.scaber* > *A.vulgare*

and Miller (1938, quoted in Edney 1954) listed the "moistness" of genera micro habitats as;

Philoscia > *Porcellio* = *Armadillidium*

Armadillidium shows a greater general fitness for dry conditions than most other genera. *A.vulgare* occurs in extreme conditions in Arizona (Warburg 1984) and Californian arid grassland (Paris 1963). This species is capable of tolerating the driest conditions, so far as the British species are concerned (Edney 1954) but it can be seen that even hot, dry conditions as experienced in the exposed limestone areas of the reserve may be thought of as intermediate when considering the world wide distribution of this species.

It has been shown that in *A.vulgare* and *P.scaber* rather more water is lost from the ventral surface than from the dorsal, about 13% more in *A.vulgare* (Edney 1954). This water loss is minimized by *A.vulgare* by rolling into a ball, so decreasing the area of exposed ventral surface. Rolling into a ball may also help to avoid the drying out of the respiratory surfaces which causes death by preventing respiration to occur.

P.scaber, with *A.vulgare* can tolerate relatively dry conditions and has a number of morphological adaptions which increase this tolerance. These include the development of a more advanced respiratory system in the form of pseudotracheae which are more efficient at gas exchange and cut down on water loss. Woodlice with pseudotracheae have been shown to be more efficient in oxygen uptake in dry air than those without (Sutton 1972).

The distribution of species throughout the range of habitat types examined in the reserve can be explained, therefore, largely by their varying ability to resist desiccation and survive in drier situations.

The physiological and morphological adaptions to drier, more exposed, habitats would indicate that *A.vulgare*, *P.spinicornis* and *P.scaber* are suited to, and can tolerate, the exposed, relatively dry conditions found in the Bare A and Bare B sites in which they were found to be relatively numerous. Such species are often found in situations where there is a good supply of calcium as this is needed to reinforce the cuticle against desiccation.

Species such as *Philoscia muscorum* are less well adapted to dry conditions and showed a tendency to occur in the more humid sites such as the Grass B and the scrub sites. This species, although showing a preference for more humid conditions, is known to have a relatively high tolerance of dry conditions (Sutton 1972) and it was found in some numbers in the barer sites.

T.pusillus is known to be poorly adapted to resisting desiccation and this species was rarely found in the drier sites being more numerous in the woodland sites where it shelters amongst the damp layers of leaf litter present.

O.asellus also tends towards moister conditions as it too is prone to desiccation. In the quarry it was associated with piles of loose Rubble in which the microclimate in the deeper parts of the pile is likely to be cool and humid.

4.3.3 Factors influencing the complementary distributions of woodlice and millipedes

The ordination diagrams produced by canonical correspondence analysis (Figure 9) indicate that the five millipede species are similarly influenced by the physical factors of the habitat, tending to prefer habitats with deeper soils, relatively low temperatures and high humidity.

The conditions preferred by millipedes were found to occur in woodland and scrub sites, where there is tall, relatively lush vegetation which keeps the local micro climate cool and humid and also helps create a rich soil with deep litter layer. The deep litter layer provides a damp microhabitat and also ensures a moist food supply. This may be an important factor in influencing the distribution of this group as millipedes will not usually eat dry litter (Miller 1974.) such as the rather dehydrated, mainly monocot litter, found in the more exposed areas of the quarry.

It is possible that some of these millipede species, especially the more robust Julids, may have been able to tolerate the conditions found in the more exposed areas but the lack of suitable food material present may have given them no reason to wander into these sites. It is equally likely that the shallow, coarse textured soil, with its very low humus content also prevents the more subterranean species from moving efficiently through these sites.

It would appear that the relative exclusion of millipedes from the barer more exposed sites is not due to direct competition with woodlice but rather is promoted by the unsuitable physical characteristics of these habitats.

From the CCA ordinations the woodlice species, with the exception of *T.pusillus*, show a preference for habitats with relatively lower humidity and higher surface temperatures. These sites, such as Bare A & B and Grass A, also tended to have low vegetation cover, shallow soil with patches of bare soil or exposed limestone and usually had very little in the way of dead plant material and litter.

Although woodlice are often thought of as denizens of the woodland floor and litter layer only *T.pusillus* occupies this habitat. The other woodlice are often found to be abundant in dry grasslands and sand dune systems (eg Sunderland *et al* 1976) and so, unlike the millipede species, are likely to readily consume the types of vegetation litter which occur in these barer sites. It is known that when woodlice eat low quality food and nutritional deficiency occurs the animals can revert to coprophagy in order to increase the efficiency of the overall digestion of the plant material. This may partially explain their ability to occupy the more exposed, vegetationally sparse, sites of the quarry.

Although the distribution of the woodlice species within the quarry can be explained in terms of their known habitat preferences there is still an anomaly between their microclimate selection in the field and their behavioural responses towards physical factors such as temperature and humidity in the laboratory. It has been shown that all species show a continuous loss of water at relative humidities of 95%. Therefore woodlice must try and shelter in situations which approach saturation to avoid excessive water loss.

Aggregative behaviour is thought to increase the relative humidity experienced by any one individual so minimizing losses by transpiration (Edney 1954). Also Miller (1938, in Edney 1954) showed that the optimum humidity for survival of all the species of woodlouse investigated was 100% RH and that 81.8% of *A.vulgare* aggregated in saturated air. Edney (1954) suggests that these humidities may occur in shelters in which the animals spend the day and that advantage is then taken of the higher humidity by night to emerge for feeding.

What appears to be the anomalous situation of woodlice selecting sites with dry conditions such as the bare sites and Grass A rather than the woodland sites, which is against their behavioural responses in the laboratory, is explained partially in that there was in fact no significant difference between the relative humidities at the ground surface in the bare areas and the woodland sites (see Table 4, section 3.1.5) and rather it was the sites with dense vegetation such as Grass B, which had the highest mean humidities with the lowest variation.

Even though it was found that the woodland sites were no more humid than the bare areas this still does not explain why fewer woodlice occurred in the woodland than in the more open sites. Differences in woodlice numbers between the woodland and bare areas would appear not to be caused by preferences to a particular humidity regime.

In their experiment on the physiology and behaviour of woodlice Barlow & Keunen (1957, in Cloudsley-Thompson 1977) concluded that the woodlice *O.asellus, P.scaber* and *A.vulgare* preferred the cooler temperatures offered in a temperature gradient and that the avoidance of high temperatures was more pronounced than the avoidance of cold. Also Warburg (1964) found that given a number of temperature ranges *O.asellus* and *A.vulgare* animals were found more frequently and for longer periods at the lowest temperature available.

Again the distribution of the woodlice appears anomalous with their known physiology and behaviour. As indicated by the CCA ordinations woodlice species tended to prefer relatively warmer sites in the reserve, with high variation in temperature over the course of a day.

Although temperatures under rocks and stones are lower than those which occur on the surrounding ground surface, temperatures under tiles in the warmer sites, such as Bare A and Bare B, where woodlice were found to be relatively abundant, were still much higher than those on the ground surface of the woodland (Figure 3).

This apparent preference for higher temperatures may be to minimize the risks of another problem which affects woodlice, that of waterlogging. It is known that woodlice tend to behave as if they were trying to shed water after periods in very damp or waterlogged conditions (Sutton 1972) and that many small animals are found to drown in deep litter accumulations after periods of rain (Standen, pers comm). Woodlice, therefore, may be selecting areas with good drainage, but which are drier or warmer than is optimal, in order to reduce the risk of drowning and to aid drying if a temporary water overlaid should occur.

A second reason for the tolerance of higher temperature shelter sites may be linked with nitrogenous excretion which in woodlice is in the form of ammonia. Ammonia is lost when the animals are at rest but excretion of ammonia is suppressed when the animals are active (Wieser 1984). Increased temperature is known to have a dramatic effect on the rate of ammonia production in some woodlice species (Wieser 1984) so selecting relatively warm refuges may aid excretion of ammonia and prevent the build up of nitrogenous wastes.

It is unlikely that the distribution of the woodlice is limited by only one factor and it can be seen that the woodlice tend towards situations of high pH, indicative of a high proportion of limestone in the soil. Species with a heavily calcified integument, such as *A.vulgare* and to a lesser extent *P.scaber* will require large amounts of calcium for the maintenance of their cuticle. The sites which have areas of exposed limestone and skeletal soils also happen to be those with the highest surface temperatures so these species may be forced to tolerate high temperatures, to which they are relatively well adapted, in order to be near a ready supply of calcium in the form of limestone.

Microhabitat selection in isopods appears, then, to be based on a complex interaction of factors. The mineral requirements, especially of calcium, of the species, their susceptibility to water logging, the effect of temperature on diffusion of ammonia through the cuticle, presence of preferred shelter type and their ability to make use of higher humidity at night to feed or disperse are all superimposed on the basic tolerances of the animals regarding humidity and temperature. These elements may combine to make what would at first appear to be an attractive, more typical, habitat for woodlice on the basis of its physical and environmental features, such as a woodland floor, actually relatively unsuitable in terms of the physiological needs of the animals.

Finally, some reference should be made to the role of competition in influencing the distribution of the two groups. The large variability and abundance of food that is palatable and suitable to woodlice and millipedes is unlikely to bring them into direct competition and therefore competition for food is not considered an important factor in influencing the species distribution within the quarry. The distributions of the groups shown by pitfalls indicate that representatives of both groups are feeding throughout the whole range of quarry habitats. Indeed the presence of *Trichoniscus* in those sites characterized by high millipede numbers suggests that this species at least is not significantly affected by competition from diplopods.

The apparent abundance of shelter sites suitable for cryptozoic animals such as woodlice and millipedes present in the quarry suggests that competition for refuges is not likely to occur.

It is thought that the complimentary distributions of the two groups are more a result of the autecology of the species present and their microhabitat preferences than an attempt to minimize the effects of interspecific competition. Spatial separation of millipedes and woodlice occurs due to the wide range of niche types present within the reserve, allowing each group to select a habitat most suited to its requirements.

5 SUMMARY

i) The distributions of woodlice and millipedes within a disused Magnesian limestone quarry were investigated.

ii) A number of habitat types, ranging from bare rubble at the bottom of a cliff face to mature mixed woodland, were examined.

iii) A number of environmental, physical and botanical measurements were taken in order to classify each site.

iv) Four sampling techniques were employed (soil turfs, hand searches, cryptozoa boards, pitfalls) to assess their relative usefulness and to establish whether results regarding species distributions were dependent upon the sampling method used.

v) It was discovered that soil cores did not prove useful in providing information on species distribution. The other methods used gave comparable results regarding dominant species, species richness and species distributions. The advantages and disadvantages of each method were discussed further.

vi) Sampling showed that on the whole millipedes demonstrated a preference for the woodland sites within the quarry, whereas woodlice were found to be relatively more abundant in the exposed, barer sites.

vii) Multivariate methods (TWINSPAN & DCA) were used to group sites on the grounds of their species composition. It was found that the bare areas and primary grassland were grouped and had dissimilar woodlice and millipede communities to the scrub and woodland sites.

viii) Canonical correspondence analysis was used to show which environmental factors were influencing the distribution of woodlice and millipedes. Millipedes showed a positive association with high humidity, low temperature, lush vegetation and deep soil. These conditions were typical of the woodland sites found within the quarry.

ix) Woodlice were shown by CCA to occur in situations with relatively high temperature, low humidity, high proportions of bare ground with sparse vegetation cover and shallow, basic soils.

x) The distributions of the woodlice and millipede species throughout the range of habitats found in the quarry was explained in terms of their known habitat preferences and autecology.

xi) The spatial separation of the woodlice and millipedes was thought to be a result of a difference in habitat selection of the constituent species rather than the result of interspecific competition.

xii) An attempt was made to explain the apparently anomalous habitat preferences of woodlice with regards to their physiological and behavioural responses often observed in the laboratory. Reasons have been suggested why woodlice, often thought of as animals of the woodland floor, were found to be relatively scarce in this habitat type.

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8.0 APPENDIX

Vegetation structure and species percentage cover.

The percentage cover of each plant species and the measurements of vegetation structure in the area between each pitfall and tile (1-9) are summarized below.

Rubble

	1	2	3	4	5	6	7	8	9
Seslaria albicans	50		5						
Grasses				15					10
Salix sp								5	
Crepis sp	40	50			30			10	
Rubus fruticosus		25		10	20		10	5	
Taraxacum sp	25					20			
Bare earth/rock	15	25	75	75	50	80	90	70	90
Stem density /m	28	14	0	14	14	14	14	14	0
Height (cm)	18	8	19	5	18	3	14	24	0
FHD	1.1	0.7	0	0	0.7	0	0.7	1.0	0

Bare A

	1	2	3	4	5	6	7	8	9
Sesleria albicans	10	60	15	10	20		10		5
Agrostis capillaris							5		30
Briza media	1								
Sanguisorba minor						5			
Ononis repens			5	1			1	1	
Medicago sp							1		
Trifolium pratense							10		
Helianthemum nummularium			1						
Thymus serpyllum	10	1	40	20		10	15	5	
Hieracium pilosella	5	10	5	10	10		10	35	10
Dactylorhiza fuchsii							5		
Moss	1	20	5	1				10	75
Litter	1	1	1	1	5		5	5	
Bare earth/rock	70	5	15	40	60	40	75		5
Stem density /m	42	14	42	28	14	0	57	57	14
Height (cm)	5	14	4	11	1	0	3	3	1
FHD	0	0.6	0	0.7	0	0	0	0	0

Bare B

	1	2	3	4	5	6	7	8	9
Sesleria albicans	25		5						
Agrostis capillaris		35	30		10	40	20	15	
Deschampsia sp									5
Carex nigra								20	
Potentilla sp	1				1				
Ononis repens		15	5						
Medicago sp						5			
Trifolium pratense			5						
Linum sp							1		
Epilobium angustifolium		10	10	15					
Thymus serpyllum	20			15		5		5	
Mycelis muralis						5			
Leucanthemum vulgare	5								1
Hieracium pilosella	20	5		10	5	10	1		15
Crepis sp	5	40							
Moss	10	30	10		5	15	10	15	
Litter	10	1	1	30	20	15	5	5	5
Bare earth/rock	10	15		30	60	10	70	40	75
Stem density /m	42	42	42	14	0	42	14	57	28
Height (cm)	3	6	8	4	0	4	1	7	20
FHD	0	0	0.7	0.6	0	0	0	0	1.0

Grass A

	1	2	3	4	5	6	7	8	9
Lolium sp	1								
Sesleria albicans	30	80	50	95	50	40	70	70	40
Sanguisorba minor					15	5	5	20	
Ononis repens	60	1	25		5		5	5	5
Helianthemum nummularium	10		5	5	15	20	1		10
Thymus serpyllum		20	2		5				
Hieracium pilosella			3		5	10	5	10	1
Dactylorhiza fuchsii	1								
Moss	5			1	20	5	5		
Litter	5	7	7		1	5			1
Bare earth/rock		10			5	10	10	25	
Stem density /m	42	42	57	57	71	71	71	57	28
Height (cm)	13	8	6	7	8	8	4	5	3
FHD	0.7	0.6	0	0	0	0.5	0	0	0

Grass B

	1	2	3	4	5	6	7	8	9
Dactylis glomerata	80	90	70	30	60	40			50
Agrostis capillaris					5	20	50	50	
Holcus	10	10		20	20			50	
Festuca sp						5			
Sanguisorba minor						1			
Rubus fruticosus	1		1			1			
Vicia sp					1				
Lotus corniculatus						1	1		
Erodium cicutarium			1	1		5	1		
Geranium robertianum	10				5				
Cruciata laevipes			10						
Galium sp		15							
Veronica persica			40	15		1	2		
Plantago lanceolata					15	5			
Cirsium sp			10						
Centaurea scabiosa					15	25			
Taraxacum sp				1		5			
Moss	40	50	50	40	40	25	30	10	70
Litter	20	15	25	30	40	40	50	70	70
Stem density /m	99	113	212	71	113	99	127	141	198
Height (cm)	45	40	45	35	38	22	65	45	33
FHD	1.9	1.5	1.5	1.6	1.7	1.9	1.1	1.6	1.4

Scrub A

	1	2	3	4	5	6	7	8	9
Dactylis glomerata			10						
Festuca sp	10		50	5	70	60	45	10	60
Brachypodium sp	5	60			10				
Fraxinus excelsior				5					
Stellaria media					1				
Rubus fruticosus		30		10	3	5	5	10	
Erodium cicutarium					1				
Epilobium angustifolium						10	20		
Anthriscus sylvestris							5	5	
Heracleum sphodylium	5		20			25			
Galium aparine	1							5	
Veronica persica		1							
Cirsium sp		5							
Centaurea scabiosa					25				
Achillea millefolium		5	20	15			10	5	
Taraxacum sp					5				
Moss	80	40					13		15
Litter	5	1	5	25	10	5	5	55	10
Bare earth/rock	5								
Stem density /m	28	28	57	57	85	113	42	42	57
Height (cm)	36	44	23	32	32	23	42	25	52
FHD	1.7	1.9	1.4	1.4	1.4	1.2	1.5	1.2	1.9

Scrub B

	1	2	3	4	5	6	7	8	9
Holcus sp	25								
Festuca sp	5	30	20		40	30	40	15	
Carex nigra	5	1	35	20					5
Rubus fruticosus	10			4		1			
Potentilla sp		2	35	4	5	5	25		
Cretaegus monogyna	25								
Lotus corniculatus	1	1	1			1			5
Trifolium pratense								5	
Heracleum sphodylium		5	1	15				50	
Veronica persica								1	
Centaurea scabiosa	2			10	20	30			40
Achillea millefolium	5				4		1	5	
Taraxacum sp							1		
Moss	80	70	90	75	80	80	20	60	35
Litter	15	10	5	5	5	5	10	10	5
Stem density /m	226	113	212	71	113	99	127	141	198
Height (cm)	28	21	21	42	20	43	24	23	32
FHD	0.9	1.1	1.0	1.4	1.0	1.5	1.1	1.2	1.0

Wood A

	1	2	3	4	5	6	7	8	9
Fine grass									20
Geum urbanum	50	50	25	70	35	25		15	
Cretaegus monogyna							15		
Geranium robertianum	10	1				5	5	10	15
Viola riviana	2								
Galium aparine	3	1		10	20	5	3		20
Veronica persica	3								
Taraxacum sp					5				
Stachys sylvatica						70	30	30	
Moss	30	1	20	5	25	15	5	5	5
Litter	5	7	5			5	10	15	15
Bare earth/rock	5	50	30	10	20	40	10	20	
Stem density /m	14	14	28	28	28	42	14	28	42
Height (cm)	23	18	32	22	30	16	34	29	30
FHD	1.1	1.0	0.6	1.0	1.3	1.0	1.0	1.3	1.6

Wood B

	1	2	3	4	5	6	7	8	9
Festuca sp		2		3				25	
Brachypodium sylvaticum	15		2					20	35
Fragia vesca			3						
Geum urbanum	1		5	15	10	15		15	25
Cretaegus monogyna		1							
Geranium robertianum			6	10	5	25			
Viola odorata	50			30	15	25	50	25	5
Viola riviana		5	2						
Sanicula europaea		15	50	1	15	15			
Primula veris					10	5			
Cruciata laevipes							15	5	
Galium aparine		5							1
Moss	15		2	50	1		15	5	60
Litter	15	25	3	5	10	10	5	5	5
Bare earth/rock	20	60	40	10	40	15	15	5	
Stem density /m	42	42	57	42	14	14	42	28	71
Height (cm)	17	11	11	11	21	12	12	18	33
FHD	1.1	0.6	0.7	0.7	1.0	0.6	0.6	1.1	1.5

Wood C

	1	2	3	4	5	6	7	8	9
Vicia sp							5		
Geranium robertianum	30	70	15	20	20	25	25	75	25
Heracleum sphodylium		10	50	30	5	40	45		
Galium aparine	1	5	5	5					5
Lamium purpureum		5	10		35	30	20	10	50
Moss	1	30	1	7			2	3	
Litter	15	10	5	35	15	5	5	10	15
Bare earth/rock	40			15	20	5	5	15	
Stem density /m	42	85	57	28	57	57	113	42	14
Height (cm)	14	30	38	46	36	39	57	26	49
FHD	1.5	1.4	1.6	1.7	1.4	1.5	1.9	1.3	1.8