Carabid beetle communities of Northern heath: their response to management practices

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CARABID BEETLE COMMUNITIES OF NORTHERN HEATH:

THEIR RESPONSE TO MANAGEMENT PRACTICES.

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1. INTRODUCTION

This introduction will explore the nature of the upland biota, its origins and conservation importance. Within this framework the ecology of the northern heath, and in particular the vegetation of the present study site, *Calluna-Vaccinium,* heath will be explored in terms of its geographical distribution, physiognomy, succession, zonation and management. The life cycle of the dominant plant of this vegetation community, *Calluna vulgaris*, together with the associated ecosystem dynamics will be addressed. The associated invertebrate fauna and its response to the ecosystem dynamics will then be explored. Subsequently the concept of the niche as it relates to community environment studies will be explored. Methods to elucidate these in a quantitative manner will be introduced and the suitability of carabid beetles as environmental indicators will be considered.

1.1. THE UPLANDS

The uplands, embracing the hills, moors and mountains above 123m, form the largest extent of undeveloped wildlife habitat remaining in Britain. They are typically above the limits of enclosed farmland and are composed predominantly of dwarf shrub heaths, grasslands and peat bogs. Their area, about 6.5 million ha, is almost 30 per cent of Britain.

Although relatively small in area and altitudinal range compared with the great alpine ranges of the world, the British uplands contain a great variety of landscapes and dependant biotic communities. These arise from marked differences in climate, geology, topography, soils and past land use, and complex interactions between these factors are such that no two upland districts are alike (Ratcliffe and Thompson, 1988).

1.1.1. THE CONSERVATION IMPORTANCE OF THE BRITISH UPLANDS.

Many facets of the uplands of Britain are of international importance. When compared to the great mountain systems of the world, the British uplands are insignificant in extent. However they are unique in nature due to the hyper-oceanic climate at the most insular, western Atlantic edge of Europe combined with widespread anthroprogenic perturbations which has produced a distinctive landscape and range of ecosystems.

Many of the soils of the uplands are believed to unique and support a wide range of plant communities that are of great importance. Foremost among these are the ombrotrophic bogs which are a localised global type, the largest extent of which occurs in the uplands Britain. The extensive development of acidophilous dwarf-shrub heaths and grasslands are diverse in nature. The communities dominated by

Ericaceae occur only in a fragmentary form in Europe and is regarded as an oceanic plant formation. *Calluna* heath is the best developed type which represents a unique ecosystem managed for red grouse. Two species of *Ulex, gallii* and *europaeus* contribute to a number of communities which form extensive stands which have a restricted world distribution. The sub-montane grassland communities reflect a greater degree of anthroprogenic influence than the ericoid heaths. *Juncus squarrosus* is widespread in the upland fringes of western Britain, yet elsewhere in the European mountains it is fairly localised. The upland grasslands are excellent examples of succession occurring under man-induced changes. Their species complement are widely distributed in continental Europe, but with different community relationships. The montane plant communities of the British uplands represent southern and oceanic outliers of Arctic-alpine fellfield and mountain tundra. Although they only cover a small area the British examples show considerable diversity and include several types which are either highly local or apparently absent elsewhere. The humid climate and varied topography of Britain are favourable for bryophytes and pteridiophytes. Britain has a richer Atlantic bryophyte flora than anywhere else in Europe. It is becoming increasingly apparent that most of Britain's upland plant communities are peculiar to this country in terms of species composition. For example, of the 82 British upland communities recognised in the National Vegetation Classification. The northern and montane vascular flora of Britain is drawn from at least seven phytogeogrephical elements and many species show such different ecological relationships, compared with continental Europe, that different ecotypes are evidently involved (Ratcliffe and Thompson, 1988).

There is probably a greater mixture of boreal, low-, mid- and high-artic, temperate and continental species of breeding birds in the British uplands than in any other comparably sized part of Europe. the species composition of at least two habitats is particularly distinctive. First the boreal-arctic peatland combination (with its often relatively large continental element) has no counterpart elsewhere. The second important element belongs to the montane plateaux and corries; it contains obvious outliers of Arctic Eurasia e.g. *Charadrius morinellus* and the circumpolar boreal to Arctic-alpine *Lagopus mutus*. On an international scale five species are significant in having main strongholds or very high population densities in Britain: *Falco peregrinus, Aquila chrysaetos, Lagopus mutus, Lagopus lagopus scoticus* and *Corvus corax.* Others, reaching almost greater numbers, at least locally, in upland Britain than elsewhere in Europe, include *Circus cyaneus, Falco columbarius, Tringa totanus, Vanellus vanellus, Calidris alpina, Numenius arquata* and *Pluvialis apricaria.* The British upland aviefauna is of considerable zoogeographical interest as their southern and/or western fringe populations may be important for the evolution of novel adaptations to changing environmental conditions (Ratcliffe and Thompson, 1988).

1.1.2. THE ORIGIN OF THE UPLAND BIOTA.

During the height of the last glaciation (50,000-15,000 BP) the uplands were glaciated and part of the continental ice sheet. Un glaciated south-east Britain held a transition from permanent ice through tundra and steppe to open scrub. Land bridges allowed subsequent migrations by plants and animals, but sea-level changes ended further immigrations thus causing a limitation in species diversity. Some native races of species began to diverge as a consequence, but isolation has been far too short for a significant degree of endemism to develop in the British biota.

An ameliorating climate since the last glaciation combined with widespread human influence has further impoverished or severely modified the upland flora and fauna. The climate became milder since deglaciation around 10000 BP. From around 4000 BP the climate became more oceanic. The influence of man on vegetation dates from at least 5000BP (Turner, 1965) and became significant from around 3900-3000 BP. Ensuing deforestation, burning and agricultural intensification in the uplands have produced mainly sheepwalk, deer forest and grouse moor with notable anthroprogenic vegetation. "Natural" vegetation is found only on the least productive ground in certain areas of the montane zone (the lower boundary corresponding with the climatic tree line), in the wettest bogs and inaccessible situations such as cliffs or lake islands. Many areas of the remaining uplands have "semi-natural" vegetation (*sensu,* Tansley 1939), and dominated by native plants which, although much changed in abundance, have been present since early Holocene times.

1.2. THE UPLAND FORMATIONS

The biotic communities of the uplands consists of two main types. At the highest levels and the more mountainous types of surface montane communities which are usually most prominent from altitudes of 611m and upwards; below this level there are various types of sub-montane communities, readily distinguished by the form and mode of life of the principal plants as well as by their relation to the main topographic features, and hence to the trends of the surface and soil. Thus on the steeper slopes and better drained areas there are grasslands and woodlands. Wherever the slopes are gentle the dwarf shrub communities occupy the leached and waterlogged surfaces (Pearsall, 1950).

Altitudinal deterioration in climate is matched by parallel changes in the vegetation and dependant animal communities, reflecting a fall in temperature and an increase in wind speed, rainfall and cloud cover. The resulting ecological zonation has been greatly modified in Britain by man. From the remaining fragments of natural vegetation it seems fair to compare this altitudinal zonation to that observable today in the mountains of extreme south-west Norway. It is noteworthy that such zonation is a small scale and local representation of the large-scale latitudinal zonation of vegetation formations which occur from northern Eurasia from the temperate zones to the polar regions .

In Britain, the lower mountain slopes were covered naturally by forest, except where the ground was too rocky or wet. In lower latitudes this was usually of *Quercus petraea* sometimes mixed with other broadleaves. Further north *Pinus sylvestris* with considerable amounts of *Betula pubescens* and *B. pendula* on more fertile soils. The difference corresponds to the transition from cool temperate broadleaf (nemoral) to boreal coniferous and *Betula* forest (taiga). With altitude there is a decline in stature of these species until they are reduced to tall shrubs and subsequently disappear. Above this there is naturally a zone of medium shrubs, mostly *Salix* spp., low *Juniperus communis* and taller forms of *Betula nana*. In Scandinavia this zone of natural birch woodlands and medium shrubs is distinguished as the sub-alpine zone, though little of this vegetation remains in Britain today. On top of this are successive zones of dwarf shrubs (low-alpine), high level grasslands, and moss and lichen heaths. This climatic sequence is complicated by topographical determined factors.

The sub-alpine zone of *Betula* woodland and medium shrubs has largely been eradicated in Britain. Patches of *Betula* and *Juniperus* scrub survive but are not generally of the climax type, and *Salix* scrub exists only on cliff ledges. This vegetation together with the woodland of the lower slopes has been subjected to anthroprogenic effects largely eradicating the original pattern of vegetation, replacing it with a complex pattern of dwarf-shrub communities (Ratcliffe and Thompson, 1988).

1.2.1. THE HEATHLAND FORMATION

There are several parts of the world where soils and climate are suitable for the development of dwarf shrub communities, but the type locality for heathland, as we know it, is north-west Europe - the are area where this vegetation formation was first described. The autecology of the dominant plant of the European heathlands, common heather (*Calluna vulgaris*), is an important component in our understanding of heathland communities.

Dwarf-shrub communities dominated by *Calluna* occur principally in the lands bordering the North Sea, the English Channel and the Atlantic coasts. This area extends from the north coast of Spain, northwards along the west coast of France, continuing into Belgium, through the Netherlands and across the north German plain. The heathland zone then extends into Jutland in Denmark and there were further areas of heathland in the southern provinces of Norway and Sweden. The whole of the British Isles falls within the zone suitable for heathland formation.

Within this area, the optimum conditions for *Calluna* are found in eastern England, the Netherlands, Northern Germany and Jutland.

Biejerinck (Webb, 1985) specified that *Calluna* required the following conditions:

1. Soils with small quantities of assimilable plant nutrients (oligotrophy)
2. Soil acidity in the range pH 3.5 to pH 6.7
3. Small seasonal fluctuations in the humidity of the soil and air
4. Protection from low temperatures by snow cover at high altitudes or on mountains
5. Adequate levels of light

These factors fall into two types: those dependant on soil conditions and those dependant on climate. However, open, dwarf-shrub communities only develop where there are factors which prevent the regeneration of woodland; thus Beijerinck added a further factor to include the activities of Man, grazing, or exposure.

1.2.2. HEATHLAND COMMUNITIES

Gimingham (1972) divides European heathlands into three main categories:

a. mountain heaths,
b. dry heaths and
c. humid and wet heaths.

All three categories occur in the uplands of Britain, though the first is confined to the montane zone. The latter two categories combine in the sub montane zone to form what is often termed "moorland". Within "moorland", there is a series of soil types and associated plant communities. On high rainfall areas blanket bog occurs, with peat up to 2 m deep. Such areas differ in many ways from the drier dwarf shrub communities, termed "northern heaths" by Gimingham (1972), which occur extensively at lower altitudes than blanket bog. The soils underlying the northern heaths are formed mainly over base-poor rock and there is often a high organic content in the top 50mm (Rodwell, 1991).

1.2.3. NORTHERN HEATH

Northern heath occurs around the upland fringes of northern and western Britain. However, at the more moderate altitudes where heaths continue to provide a biotically derived replacement for forest, the prevalence of heavy pasturing often severely restricts their contribution to the landscape or gives them a distinctly grassy aspect , particularly on somewhat better or marginally improved soils. Moreover, the continuing use of periodic burning to renew sub-shrub growth for either stock or grouse has favoured a widespread floristic impoverishment and convergence into a generalised *Calluna* dominated vegetation.

Nonetheless, it is still possible to detect some broad climate-related patterns among the communities. In the cool oceanic conditions of the upland margins of western and north-western Britain *Calluna-Erica* cinerea heath predominates, in the so called "Atlantic heather moor". Generally with the shift to a colder environment on somewhat higher ground through the hills of the north and west, and especially away from our more oceanic uplands (Figure 1.1.), this community is replaced by the *Calluna-Vaccinium myrtillus* heath. This is our most widespread and extensive Northern heath community, although its floristics and structure are often controlled not by climatic or soil variation across its range, but by response to burning, for it is a major component of sheep ranges and grouse moors, often occurring in patchworks of stands whose composition reflects particular combinations and timing of treatments. In broad terms, the *Calluna-Vaccinium* heath can be regarded as the British "Boreal heather moor". Two other less extensive communities of Northern heath occur. *Calluna-Vaccinium-Sphagnum* heath in situations of cool but equitable climate enhanced by shade and shelter of crags, and where there is relief from burning. *Calluna-Arctostaphylos uva-ursi* heath is centred on the east-central Highlands of Scotland, where the climate is much drier than to the north west and has greater extremes of temperature variation (Rodwell, 1991).

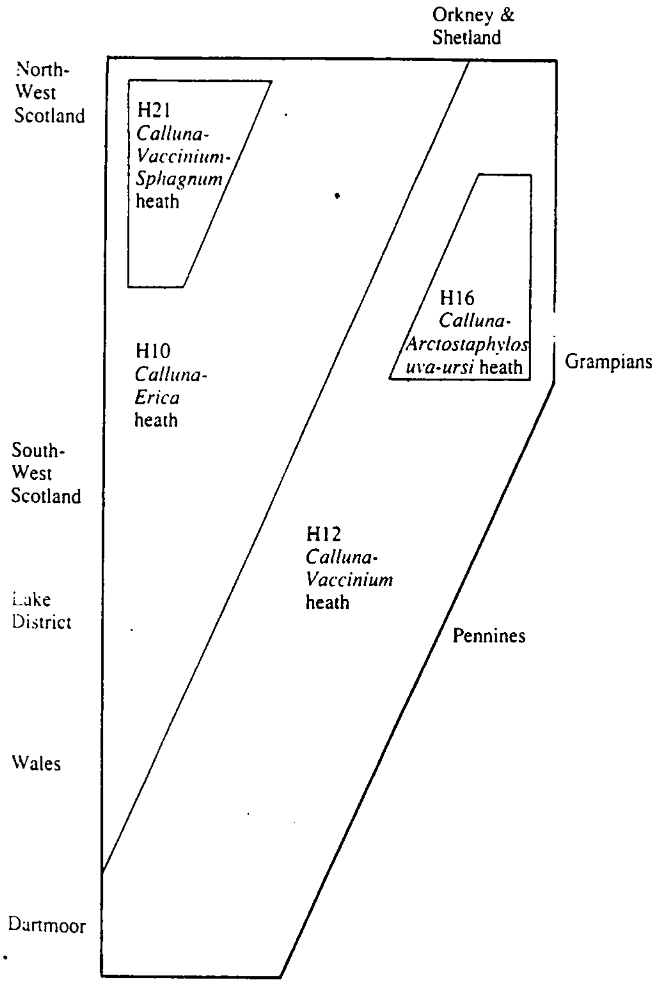


Figure 1.1. Atlantic and boreal trends in the heather moors of the northern and western uplands.

1.2.3.1. CALLUNA-VACCINIUM MYRTILLUS HEATH.

Physiognomy

The *Calluna-Vaccinium myrtillus* Heath is generally dominated by *Calluna vulgaris*, often overwhelming so: encompassing the majority of the *Calluna* dominated vegetation described from the less oceanic parts of the sub-montane zone. Throughout these areas the regular burning of grouse moor and hill grazings that encourages a predominance of species-poor building phase heather is commonly practised. However older stands, with a more open cover of degenerate *Calluna*, can often be found and there is structural variety also, in response to differences in grazing intensity and local climate, both of which can affect the height and extent of the sub-shrub canopy. More distinctly , when there is an opportunity for a contribution to the cover from other ericoids, capitalising upon the more open ground in the early or late stages of the *Calluna* growth cycle, or persisting among the developing *Calluna*, the potential diversity of this component of the vegetation is quite high (Rodwell, 1991).

Habitat

The *Calluna-Vaccinium myrtillus* Heath is the typical sub-shrub community of acidic to circumneutral, free-draining mineral soils throughout the cold and wet sub-montane zone. Climatic and edaphic variability across this range play some part in determining variation within the community but it is generally burning and grazing that exert the major influences on floristics and structure and, consequently, prevent succession to woodland.

The community can be found, predominantly between 200 and 600m, through-out the western and northern regions of the British Isles wherever the mean annual maximum temperature falls bellow 26°C. However, within this broadly-defined zone, the community is strongly concentrated in areas where the climate, and particularly the winter climate, is more severe, occurring most extensively in the central and north-east Highlands of Scotland, the central reaches of the Southern Uplands and the Northern Pennines, where, in the main, mean annual maxima rate less than 24°C, and in February the minima usually more than half a degree of so below freezing. Throughout these areas there are from 1000 to 1600mm of precipitation annually with usually 160-180 wet days yr^{-1}. In general the conditions are wet and cloudy and, in the harsh winters, there can be more than 40 days with snow lying (Rodwell, 1991).

Zonation and succession

The *Calluna-Vaccinium myrtillus* heath occurs in a wide variety of vegetation patterns with other dwarf shrub communities, mires and grasslands, where floristic differences are controlled primarily by variations in soils, climate and management treatments. Seral developments are usually held in check by burning and grazing and without these most stands would eventually progress to scrub and woodland, fragments of which can be found in association with the community at some sites.

The clearest soil dependant sequences occur where the free-draining soils which typically underlie *Calluna-Vaccinium* heath give way to soils with seasonally impeded drainage. In such situations the passage is typically marked by a transition to *Erica tetralix* wet heath and ultimately through to *Calluna-Eriphorum* mire where ombrogenous peats have formed. Where management treatments have been especially frequent or severe there is a progressive deterioration with a spread of *Juncus squarrosus* amongst a much reduced cover of dwarf shrubs. This is sometimes the prelude to the development of wet *Juncus-Festuca* grassland. In many sites, however, continuous heavy grazing has favoured a progressive loss of dwarf-shrub vegetation to grassland. The constant danger in such situations is the spread of *Pteridum aquilinum* particularly where the vigour of *Calluna* is reduced by burning and grazing. *Pteridum aquilinum* is likely to invade vigorously producing dense stands of the *Pteridium-Galium* community. Widespread interactions between these variables on less fertile peaty podzols involve transitions to *Nardus-Galium* grasslands, which are especially likely to develop were there has been grazing in the early stages of post-burn recovery.

Management.

As with all plagioclimax communities management is required to retard seral development. Two methods have been primarily used, often in combination, namely; burning and grazing. A third, mowing, has been employed in recent years where burning has been deemed unacceptable.

The need for a judicious programme of burning to maintain high and healthy grouse stocks was established early (Lovat, 1911) and has since been confirmed in the continuing work on the bird and its habitat The reasons for this response are well understood. The red grouse prefer to eat heather that is 2-3 years in age. Older or younger shoots are rejected. Thus red grouse are responding to nutritional factors in the heather that change due to burning or as a result of aging of the heather populations. Cover and nesting sites are provided by heather more than 10 years of age. In addition, opening or thinnings are necessary if grouse are to move freely through the heather. Thus, heather managed for grouse must contain a range of developmental phases (e.g. Miller *et al.*, 1970).

In Scotland, burning can legally take place between 1 October and 15 April (exceptionally to the end of April in a wet season or to 15 May beyond 457m) in England the legal period is reduced. Although research has shown that regeneration is better after autumn rather than spring burns March and Early April have been the traditionally favoured times. Usual practice is to burn with the wind, although slower fires can be maintained by back-burning and, of course, the moisture content of the vegetation and the soil can also affect the fire intensity. The size of the burn is also important since wider fires tend to have greater intensities. The crucial element is to aim for a ground temperature of less than 200°C if possible, though certainly below 400°C as even short exposures of temperatures above this level can be lethal to heather stem bases, while keeping the canopy temperature high enough to burn off the bulk of the above-ground material but not so high that the loss of inorganic nutrients in smoke is too high: 500°C seems to be an optimum temperature to satisfy these requirements (Rodwell, 1991).

When normal weather conditions prevail, it is the quantity and disposition of the fuel that is critical in the control of burn temperatures. Both the maxima and duration of high temperatures increase with the age of the vegetation. The biomass per unit area increases until at least 20 years since the last burn and the material becomes more woody with age. The vegetative regeneration post-burn is considerably impaired in plants which are more than 15 years old. Ideally, burning is timed to coincided with the end of the building phase, when the regrowth is between 12-15 years old. Longer rotations are employed in exposed situations and shorter ones in sheltered sites: an average canopy height of 30-38 cm appears to be a good upper limit. Many small burns are preferred, the optimum area being perhaps 0.5-1ha, with 2ha as an upper limit, and long thin strips c. 30m wide being preferred to rounded of squarish areas to maximise the interface of the burn with mature *Calluna* (Rodwell, 1991). Thus well managed grouse moors consist of a mosaic of different aged patches of more or less even aged *Calluna* produced by regular burning to maximise the extent of relatively nutritious pioneer and building regrowth. On many sites the structural and floristic differences can be related to this treatment.

Very frequency the post fire development are subject to the additional and immediate influence of grazing. Most burned stands are open to stock and wild herbivores and though moors are primarily managed either for grouse rearing or pasturing the two activities are frequently combined. Even where stock-rearing predominates, regular burning is often practised because although prudent moderate grazing alone ought to be sufficient to maintain a productive cover of *Calluna*, and thus of red grouse, this is hardly ever possible to achieve. It was perhaps possible before the clearances when small scale mixed farming predominated, with cattle being pastured instead of or along side sheep. But the shift towards heavy and more selective breeds of sheep the productivity declined and the occasional fires that had long been employed to retard tree invasion were replaced in many areas by more regular burning, often on a ten-year rotation.

Light grazing in the early stages of regeneration can facilitate early canopy closure, though with marked effects on the vegetation composition. Though *Calluna* is palatable, grazing often induces a plagiotrophic semi-prostrate habit which gives it an advantage over *Vaccinium myrtillus* or other less common species. In some situations preferential grazing of *Calluna* may callow the spread of the less palatable *Empetrum nigrum*. On less peaty soils grazing often favours the maintenance of grassy composition this kind of *Calluna-Vaccinuim* heath can also include mosaics of sub-shrubs and sward well on their way towards becoming *Nardus-Galium* grasslands in a grazing-mediated succession.

Where heavy follows burning on less fertile soils *Juncus squarrosus* tend to increase its cover.

1.3. COMMUNITY DYNAMICS

1.3.1. THE HEATHER CYCLE

Heathland communities dominated by *Calluna Vulgaris* were among the examples Watt (1947) described in the first thorough treatment of cyclical processes in plant communities. He described a number of vegetational cycles in communities which were assumed to be "relatively stable over a reasonable period of time". Common to these examples was the development of gaps in the cover of a dominant species, which could be formed through the death of individuals or through some intrinsic feature of the plants' growth and morphology. Studies indicated that the dominant seldom recognised gaps immediately. Instead, a sequence of other species usually occupied the patch for a period before the dominant re-established. Where the population of the dominant was uneven-aged, gaps appeared irregularly in the canopy and the community structure took the form of a mosaic of patches of limited area, each at a different stage in the cycle. Thus, at a given time the patch composition reflects a series of phases which are "dynamically related to each other".

Watt (1955) developed his ideas of cyclic processes in heathland vegetation, distinguishing four phases in the morphological life-history of *Calluna* namely: pioneer, building, mature, and degenerate. Though not sharply differentiated these phases have been readily separated by subsequent workers (Gimingham, 1988) as follows:

1. *Pioneer.* Early stages in the establishment and growth. Regular branching from the axis of a single leading shoot, at first. Height up to *c. 6* cm, shape pyramidal, cover incomplete. Up to 6 years of age.

2. *Building.* Becoming bushy, branches radiating from the centre, productivity of peripheral shoots high and flowering vigorously. Height up to c. 0.5 m (or more), shape hemispherical, canopy dense, cover approaching 100%. Up to about 15 years of age (depending on habitat).

3. *Mature.* Extension growth declining, though green shoot production and flowering still high. Shape still hemispherical, but central branches inclined to spread sideways, initiating gap formation ; cover slightly reduced. Up to 20 years of age (or more).

4. *Degenerate.* Central branches dying, creating gap. Some other branches which have become partially buried in litter etc. may remain alive (because of adventitious rooting), sustaining a ring of foliage-bearing twigs. Cover much reduced. Eventually whole plant may die. Death at 30-40

years of age.

These phases are presented diagrammatically in figure 1.2.

The behaviour of individual *Calluna* plants results in canopy gap formation in the mature degenerate phases. Watt's studies in south east England indicated that the accumulated litter and mor humus beneath the gap was normally colonised by cryptograms, but that eventually the mor would decay or become dispersed, leaving a humus-stained mineral soil surface. In addition to cryptograms, a limited number of vascular plant species were noted as capable of occupying the gap. Watt noted "Seedling *Calluna* may become established on the mor but its chances of survival are greater on the mineral soil. Even then a number of years may elapse before an effective colonization initiates a new cycle. A new cycle may also be initiated by vegetative lateral spread from neighbouring bushes".

The cyclic nature of *Calluna* as originally proposed by Watt has been disputed by a number of researchers (Gimingham, 1988). However the observation that *Calluna* individuals pass through the sequence of phases as originally described is accepted, though it does not in itself constitute evidence of a cyclical process.

Records from permanent quadrats in the Netherlands suggested that mosaic patterns were caused not by cyclical processes, but by periodic catastrophic events such as severe drought or attacks of heather beetle, *Lochmaea suturalis* Thompson, leading to the death of individuals (Prentice *et al.* 1987). Other studies found that *Calluna*, instead of maintaining repeated cycles, has been replaced either by trees or by bracken (Marrs, 1986; Miles, 1981; Gong & Gimingham 1984). In cases like this, Watt's assumption of relative stability over a reasonable period of time does not apply, and the heath vegetation is evidently seral. Hence, the theory of cyclical process may only be invoked only when there is no potential for invasion by a more permanent and long-lived species. In addition to these changes pollution and management induced seral changes have occurred. Sufficiently grazed *Calluna* stands would thus be expected to exhibit cyclic processes if the cycle was not prematurely curtailed by burning or catastrophic events. Heather beetle is largely inhibited by the cold temperatures in the uplands of Britain in all but the warmest summers and snow cover provides insulation from damaging sharp frosts and rapid thaws.

The suggestion that *Calluna* was cyclic in nature provided a strong stimulus to the investigation of pattern in plant communities, by offering an explanation to be considered where habitat heterogeneity was insufficient to account for the mosaic. It provided a framework on which to base detailed research on the dynamics of even-aged stands of *Calluna* created by burning. In so far as it concerns the morphological life-history of *Calluna* it has been enormously valuable in interpretating the associated environmental changes and the varying responses of *Calluna* to environmental influences.

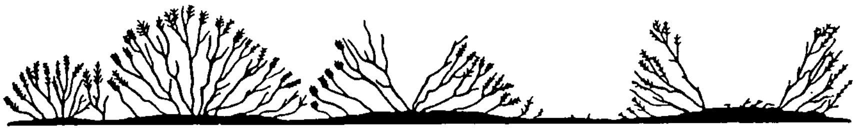
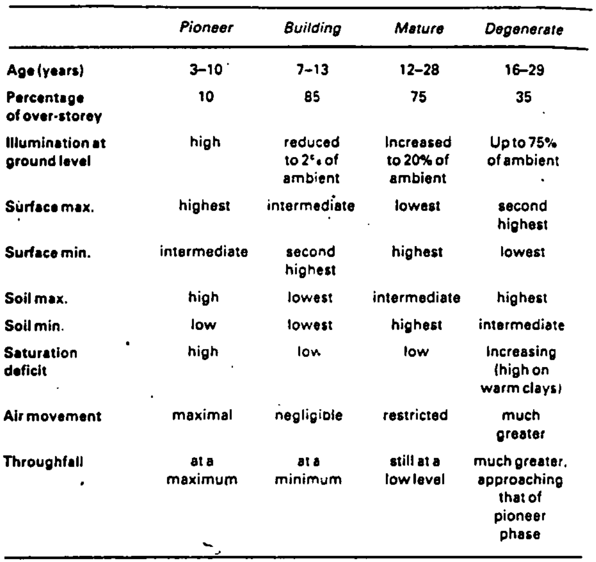


Figure 1.2. The heather cycle

1.3.2. THE ENVIRONMENTAL CHANGES

The structural changes which occur in heathland vegatation undergoing cyclical or successional change profoundly affect the climate near the ground. In turn, the occurrence and distribution of many species of animal may be affected, and so may the germination and establishment of seedlings beneath the canopy. Figure 1.3. summerises the characteristics of the micro climate beneth the vegetation in the different growth phases of a Calluna heath in Scotland (after: Barclay-Estrup,1971).



	Pioneer	*Building*	*Mature*	*Degenerate*
Age (years)	3–10	7–13	12–28	16–29
Percentage of over-storey	10	85	75	35
Illumination at ground level	high	reduced to 2% of ambient	Increased to 20% of ambient	Up to 75% of ambient
Surface max.	highest	intermediate	lowest	second highest
Surface min.	intermediate	second highest	highest	lowest
Soil max.	high	lowest	intermediate	highest
Soil min.	low	lowest	highest	intermediate
Saturation deficit	high	low	low	Increasing (high on warm clays)
Air movement	maximal	negligible	restricted	much greater
Throughfall	at a maximum	at a minimum	still at a low level	much greater, approaching that of pioneer phase

Figure 1.3. Characteristics of the micro climate beneth the vegetation in the different growth phases of a Calluna heath in Scotland (after: Barclay-Estrup,1971)

The rate at which the standing crop of Calluna increases declines with age until the standing crop reaches a maximum at about fifty years if age, see figure 1.4. Litter fall from young plants is negligible untill the third or fourth growing season, but then increses to rates of 200 to 250g m^{-1} at about 20 years of age. The composition of the litter also changes; at first, it is mostly short shoots, flowers and seed capsules, but during the building and degenerate phases, the woody component increases (Webb, 1986), see figure1.5.

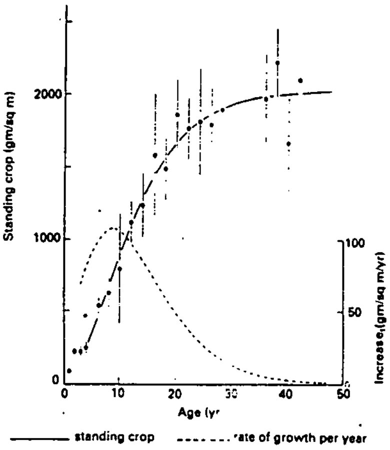


Figure 1.4. Heather growth following burning.

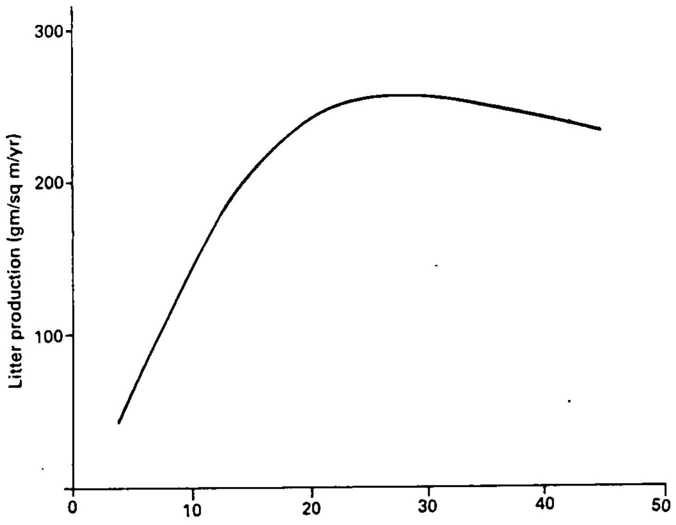
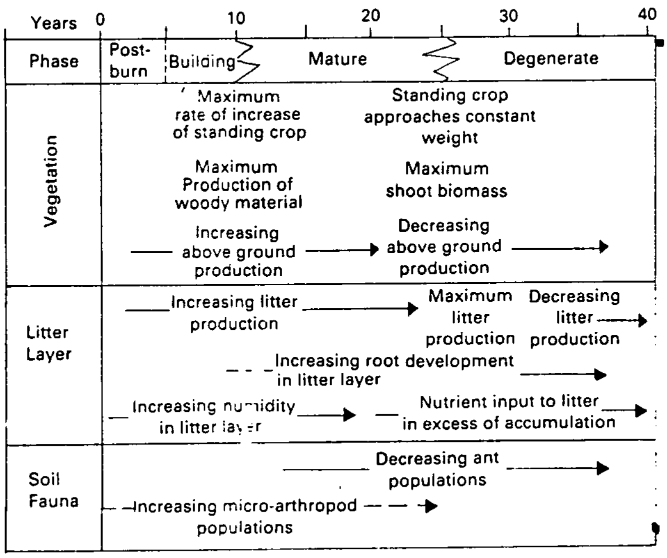


Figure 1.5. Rate of litter production over 50 years



Years	0 · 10 · 20 · 30 · 40
Phase	Post-burn · Building · Mature · Degenerate
Vegetation	Maximum rate of increase of standing crop Standing crop approaches constant weight Maximum Production of woody material Maximum shoot biomass Increasing above ground production → Decreasing above ground production →
Litter Layer	Increasing litter production → Maximum litter production Decreasing litter production → Increasing root development in litter layer → Increasing humidity in litter layer → Nutrient input to litter in excess of accumulation →
Soil Fauna	Decreasing ant populations → Increasing micro-arthropod populations →

Figure 1.6. Summary of changes within the heathland ecosystem in the years following a fire

1.4. THE FAUNA OF THE UPLANDS.

Coulson and Whittaker (1978), quoting Pearsall, write "one of the most noticeable features of upland life is the apparent smallness of the animal population". These authors suggest that this opinion is inaccurate as it is coloured by the general anthropocentric viewpoints of financial and aesthetic interest, They suggest that the invertebrates of are a highly important group in the uplands and that Pearsall writing in 1950 had neglected them because of the lack of work, at that time, on the phylum in the uplands as a result of their general inconspicuous nature and the difficulties of working with them, namely; quantification and taxonomy. Since 1950 much work has been undertaken on upland and, especially, moorland invertebrates making them probably the most studied community of invertebrates in Great Britain. A number of individual species have been studied in detail and consequently the upland invertebrates are the best studied group of invertebrates after those of agricultural / horticultural importance and single orders of high intrinsic / conservation importance such as Lepidoptera and Odonata.

Much of the earlier work (e.g. that summarised in Coulson and Whittaker (1978)) investigated the composition and distribution of species between habitats, their phenology and the structural, physiological and life-history adaptations to their environment.

Subsequently classifications of invertebrates from dwarf shrub communities and grasslands have been undertaken by Butterfield and Coulson (1983) and Coulson and Butterfield (1985, 1986) using similarity indices. The latter work was amplified upon by Coulson (1988) where the five communities, four from the uplands, identified were investigated in terms of invertebrate density, the number of species, their phenological distribution and the standing crop. These studies have established that northern heath has a characteristic invertebrate community.

More recently, techniques of classification based on the ordination of species by site matrices, have been used to characterise species communities associated with particular habitats in regional scale studies (Luff, Eyre and Rushton, 1989). This studied also identified northern heath as having a characteristic fauna. The dwarf shrub habitats of northern Europe have been examined by Eyre and Luff (1990) with regard to their carabid communities, northern heath exhibited a characteristic community.

1.4.1. THE FAUNA OF UPLAND DWARF-SHRUB HEATH.

The dominance of ericaceous dwarf shrubs is a key factor in shaping the faunal community. Watts *Calluna* growth phases provide a useful framework in which to examine the development of the heathland fauna. Changes in micro climate as the phases progress, for example, will be of direct relevance to the establishment of populations on the ground-dwelling, litter and soil animals, though this aspect has mostly been studied on lowland rather than upland heaths in Britain (Usher and Gardner, 1988).

As the *Calluna* life cycle proceeds, changes occur in the nutrient content of the foliage, which may in turn determine the pattern of utilisation by herbivores (Usher and Gardener, 1988). Similar changes occur in the production of litter; with the maximum occurring towards the end of the mature phase and the quality can influence the development of the soil and litter-dwelling fauna. There is little information on the development of other dwarf-shrub species, e.g. *Vaccinium myrtillus*. Similarly, the is little information on the associated influence on the faunal community, particularly during the pioneer and degenerate phases of the *Calluna* cycle when *Calluna* occupies less than 50 per cent ground cover (Usher and Gardner, 1988). The heathland fauna may have a profound effect on the vegetational development. This has been dramatically demonstrated where infestations of *Lochmaea suturalis* have severely restricted regeneration of *Calluna* in years when the temperature has be been sufficiently warm.

Usher and Gardner (1988) state that "the development of a soil fauna is primarily influenced by the growth phase of *Calluna*. During the pioneer phase the microclimate is harsh because much of the litter is blown away. As the canopy begins to close towards the end of the building phase, the microclimate beneath the plants stabilises and the developing litter layer retains more moisture. Under these conditions the soil and litter faunas develop rapidly. Litter production begins to decline as the plants reach the degenerate phase; the canopy opens out and the microclimate beneath the plants becomes less humid. Sufficient moisture is, however, retained by the existing litter and mosses to enable the soil fauna to retain its diversity".

Some of the soil fauna has been demonstrated to have seasonal migrations from the surface zone to deeper zones during the winter when the surface zone is subject to freezing (Usher and Gardner, 1988).

A feature of management is the successional patterns associated with the growth phases of *Calluna*. The ground-dwelling and ground-feeding taxa, such as Carabidae, Collembola and some Acarina and Araneae, were particularly abundant in upland pioneer stands, while the building and mature phases were dominated by shoot and sap feeders such as the Cercopidae, Psyllidae and Curculionidae (Gimingham, 1985).

Habitat heterogeneity is a key factor in governing diversity of the invertebrate fauna. Those phases with a more open canopy, i.e. pioneer and degenerate stands of *Calluna*, which exhibit greater floristic and microclimatic diversity when compared to building and mature phases, showed greater invertebrate diversity (Gimingham 1985). Further evidence was provided by the comparison of the invertebrate faunas of burnt and unburnt stands. Unmanaged stands including bushes of all ages unlike those that had been burnt and consequently many taxa were more numerous in unmanaged stands (Gimingham, 1985). In contrast to other habitats relatively little work has been undertaken on the quantitative response of invertebrates to the dynamic changes associated with management practices.

1.4.1. THE EFFECTS OF UPLAND LAND MANAGEMENT.

Northern Heath has been traditionally managed by burning and grazing and more recently by cutting and drainage. This section examines the impacts of such management upon the invertebrate fauna.

1.4.2.1. BURNING.

Regular burning on an approximately 15-year cycle reduces the diversity of the invertebrate fauna (Gimingham, 1985), but initially the soil fauna is not adversely affected as little heat penetrates the soil surface. The subsequent removal of litter by the wind has been demonstrated to cause a decrease in soil invertebrate populations (Chapman and Webb, 1978).

During the post-burn phase faunal diversity may be quite high as the developing stand of pioneer heather provides a wide variety of niches for ground- and plant-dwelling species. Little is known about the rate of recolonisation though Usher & Smart (1989) and Gardner and Usher (1989) suggest that recolonisation may be quite rapid. The effects of surrounding habitats is known but in lowland heathlands the proximity and diversity of surrounding habitats enhances diversity of the recolonising species (Webb, 1986). The interactions of the typical fauna and that from surrounding habitats is not known. Rotational burning of northern heath may well reduce the overall diversity because much of the area will be dominated by building and mature stands, which although supporting high populations of some herbivorous species, lack the diversity of the other phases and that of unburnt stands (Usher and Gardner, 1988).

Fishpool and Usher (1989) found differences in the carabid community between pioneer and later phase stands, the former being more diverse than the latter, consisting of species in addition to that found in the stands with a higher *Calluna* cover.

1.4.2.2. GRAZING BY DOMESTIC LIVESTOCK

The selectivity of grazing animals is likely to have a positive effect on invertebrates of unpalatable plants. Light grazing favours *Calluna* and prolongs the pioneer phase. This would have the positive effect on maintaining the associated invertebrate diversity. Heavy grazing stimulates graminoids and forbs (Welch 1984) and could thus stimulate the replacement of heathland species by those associated with grassland. The problem remains as to how to balance the requirements of domestic stock with the feeding and habitat preferences of the heathland fauna (Usher and Gardner, 1988). The grazing and burning interaction may be important since the congregation of grazing animals in recently brunt areas can significantly reduce *Calluna* regeneration and thus retard recolonisation of heathland species. Conversely the lengthening of the pioneer phase, once *Calluna* has re-established might have a positive effect on invertebrate diversity.

1.4.2.3. CUTTING

Heather cutting is used particularly where there are extensive stands of degenerate *Calluna* which can prove hazardous to burn due to the high fuel load, provided the terrain is not too steep or boggy. Preliminary work Gardner and Usher (1989) and Usher and Smart (1989) indicate that the invertebrate fauna may be impoverished compared to that of the pioneer phase subsequent to burning due to the retention of the litter layer in greater quantities.

1.4.2.4. DRAINING

Moor-draining or "gripping" has been employed on a number of soils. The immediate purpose is to increase the runoff and to lower the water-table to improve the vegetation and consequently livestock and game production (Usher and Gardner, 1988). The impacts of moor-draining on plant and animals appear to be very localised (Coulson, 1988). Coulson, Butterfield and Henderson (1990) found significant increases in a number of groups below the grip namely; Hemiptera, Diptera, Elateridae and Staphylinidae on an area adjacent to the present study site. They considered that the main effect was to drain pockets of deep wet peat and thus reduce the heterogeneity and consequently the diversity. In addition the loss of such areas restricts the spring emergence of invertebrates. These from a major contribution to food of young grouse (Butterfield and Coulson, 1975) and therefore drainage is unlikely to enhance grouse carrying capacity.

1.5. COMMUNITIES AND THE NICHE

A community is defined by (Krebs, 1985) as "any assemblage of populations of living organisms in a prescribed area or habitat ", and having "one or more of the following attributes: 1. co-occurrence of species, 2. recurrence of groups of the same species, and 3. homeostasis or self-regulation ".

The study of community ecology is pervaded by an important controversy over the nature of a community. Is the community an organised system of recurrent species or a haphazard collection of populations with minimal integration? Most of the argument about the nature of the community can be centred on two statements:

1. Associations are / are not discontinuous with one another.

2. Species are / are not organised into discrete groups corresponding to associations.

Two opposing schools have developed in ecology over the question of the nature of communities. The organismic school holds that communities are integrated units with discrete boundaries. The individualistic school holds that communities are not integrated units but collections of populations that require the same environmental conditions. The information available leans more towards the individualistic interpretation of the community. Communities are not descrite but grade continuously in space and time, and species groups are not consistent from place to place. However, in spite of this continuous variation, communities can be classified on the basis of the balance of probabilities with some species groups having a greater probability of occurring together than others. A community could therefore be viewed as a group of species which form a "node" of enhanced probability of co-occurrence upon a continuum.

Key to the concept of a community is the concept of the niche. An organism has a response, admittedly of varying magnitudes, to all environmental gradients related to its tolerance to that environmental variable. If we consider just two environmental gradients, such as temperature and humidity, and determine for each the range of values that allow the species to survive and multiply. This illustrated in figure 1.7.a. The area in which the species can survive contains its niche. If the concept of fitness, i.e. the degree of suitability (measured by a population parameter) is introduced an environmental gradient has a fitness distribution, a response curve, with an optimum. Most species have one optimum along the environmental gradient and decline to either side; most response curves are approximately bell shaped or Gaussian Figure 1.7.b.. Two curves combine to form a response surface, Figure 1.7.c. If another environmental gradient is introduced then the niche, as defined by the given variables, takes the form of a volume with the centre corresponding to the optimum, Figure 1.7.d. Now introduce other environmental gradients until all the ecological factors relevant to the species have been measured, ultimately we arrive at a n-dimensional hypervolume, which is termed the fundamental niche of the species. If two species have regions of co-occurrence in their hypervolumes of their fundamental niche then there is a competitive interaction resulting in the contraction of one or other or both niche volumes to form the realised niche. Other factors such as predator avoidance can also result in a contraction of the volume. It is the degree of niche overlap in a number of dimensions that determines the degree and probability of co-occurrences of a group of species. If the realised niche ranges / volumes and the optimum, in a limited number of important dimensions, of a species are determined it allows the investigation of a species response to an environmental gradient and its relationship to other species to be investigated. If these parameters of

compared it enables the investigation of the properties of the community in relation to the environment.

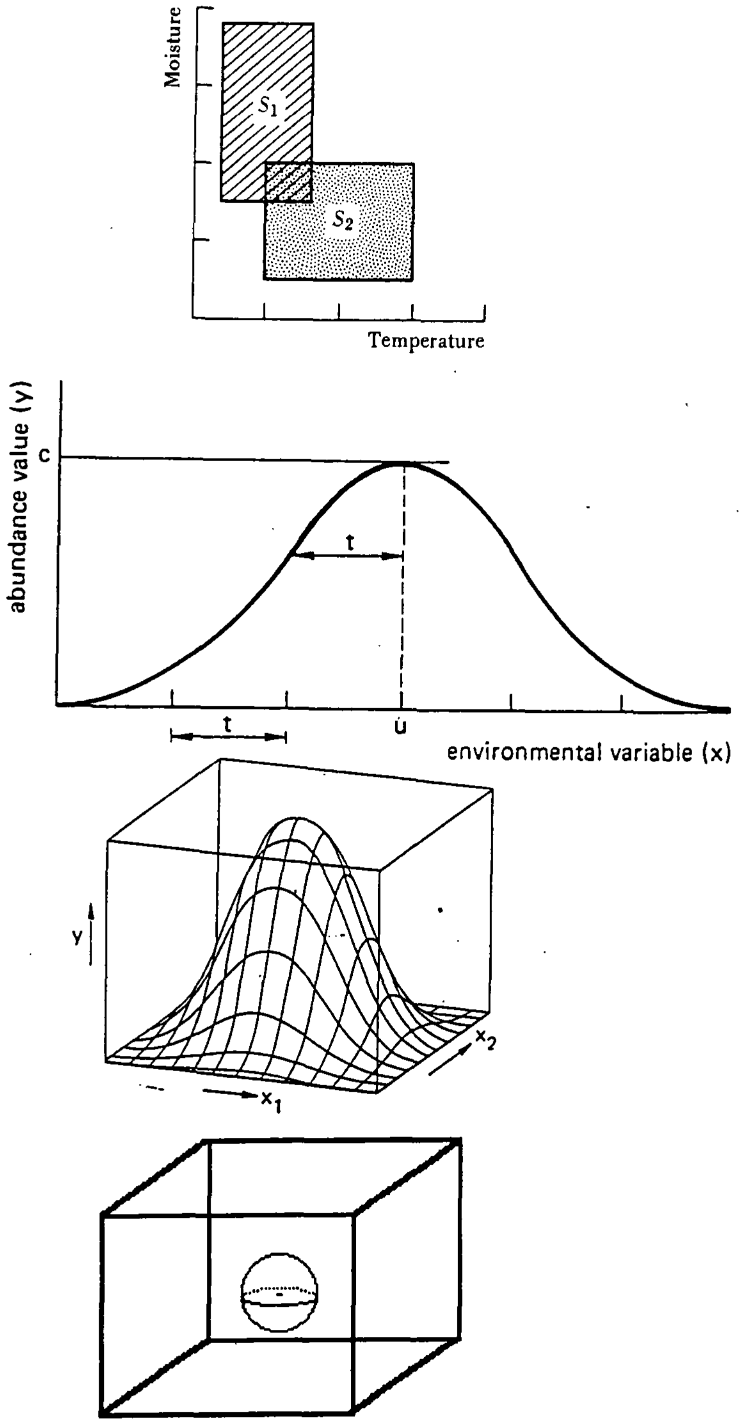


Figure 1.7 The Niche. a) The tolerances of two species with respect to moisture and temperature. b) The Gaussian unimodal response curve displaying the relationship between abundance value (y) of a species and an environmental variable (X). (U=optimum or mode; t= tolerance; c= maximum). C) a Gaussian response surface displays a unimodal relationship between the abundance value (Y) of a species and two environmental variables (x1 and x2). D) a 3 dimensional niche volume with the centre corresponding to the optima.

Tron?

Techniques based upon regression and ordination have been developed to allow the investigation of species and community relationships both in hypothetical geometric terms exploring the spatial relationship between sites and by direct means whereby environmental gradients are explored These are introduced in the following section and those employed in the present study are discussed in detail in the methods.

1.6. ANALYSIS OF COMMUNITY ENVIRONMENT RELATIONSHIP

Problems in community ecology often require the inference of species-environment relationships from community composition data and associated habitat measurements. Typical data consist of two sets: data on the occurrence or abundance of a number of species at a series of sites, and data on a number of environmental variables measured at the same sites. When the data are collected over a sufficient habitat range for species to show non-linear, non-monotonic relationships with environmental variables, it is inappropriate to summarise these relationships by techniques that are based on linear correlation coefficients, such as canonical correlation analysis. An alternative two-step approach has resulted, employing the following steps : (1) extract from the species data the dominant pattern of variation in the community composition by an ordination technique, and (2) attempt to relate this pattern (i.e., the first few ordination axes) to the environmental variables.

After having fitted a particular environmental variable to the species data by regression, we might ask if another environmental variable would provide a better fit. For certain species one variable may fit better, and for other species another variable. The question then arises: what is the best possible obtainable fit from the species data that is theoretically obtainable from the model of the equation.

This question defines an ordination problem, i.e. to construct the single "hypothetical environmental variable" that gives the best fit to the species data according to the model equation. This hypothetical environmental variable is termed the *latent variable*, or simply the (first) ordination axis. Subsequent axes can then be extracted from the residual variation (Ter Braak and Prentice, 1988).

The term "ordination" derives from early attempts to order a group of objects, for example in time or along an environmental gradient. Nowadays, the term is used more generally and refers to an "ordering" in any number of dimensions (preferably few) that approximates some pattern of the response of the set objects. The usual objective of ordination is to help generate hypotheses about the relationship between the species composition at a site and the underlying environmental factors. In indirect ordination methods organise the data solely on the pattern of object responses and use any additional information on environmental variables only at a later stage to aid interpretation. With direct methods of ordination the environmental factors of interest must be specified with an independent value at each site for each factor (for a species ordination) or the species responses to each factor (for a site ordination) thus direct ordination extracts axes based on known environmental variables rather than the latent variable.

Indirect gradient analysis has its drawbacks. If the measured environmental variables relate strongly to the first few ordination axes, "they can account for" (i.e., they are sufficient to predict) the majority of the variation in the species composition. If the environmental variables do not relate strongly to the first few axes, they cannot account for much of the variation, but they may still account for some of the remaining variation which may be substantial. These limitations can only be overcome by methods of direct gradient analysis (Digby and Kempton, 1987 and Ter Braak and Prentice, 1988).

1.7. CARABID BEETLES AS ENVIRONMENTAL INDICATORS AND THEIR APPLICABILITY TO THE STUDY OF NORTHERN HEATH.

"Ground beetles are a group of insects that serve as useful models to explore many facets of ecology... The British fauna is readily identifiable, and exhibits a range of feeding habits from specialist predators through generalist predator / scavengers to a few exclusive plant feeders (Rushton et al, 1991). They form a important proportion of the invertebrate communities of upland areas, in terms of species, numbers and standing crop (Coulson and Whittaker, 1978 and Coulson 1988).

Ground beetles have proved to be useful ecological indicators to habitats, both at the formation level (Luff et al, 1989) and Community level (Butterfield and Coulson, 1983). They also reflect the overall invertebrate communities in the uplands (Coulson and Butterfield, 1985). Numerous studies (E.g. many papers in Stork (1990), Rushton et al, 1990, Morris and Rispin, 1988 and Webb 1989) show that carabid beetle communities are particularly responsive to habitat manipulations.

Fishpool and Usher (1989) and Gardner and Usher (1989) have demonstrated differences between species composition of patches within managed upland heath. Gardener (1991) has shown differences between carabid communities between sites in relation to the flora and three other variables, though does not state them all or give any indication of their statistical significance.

However, ground beetles often reflect aspects of their habitats other than vegetation composition (Eyre and Rushton, 1989). These have yet to be studied except in the broadest sense with between site comparisons E.g. rainfall (Gardner, 1991).

Ground beetles exhibit relatively poor powers of dispersal as many, ca. 90% in moorlands (Bauer, 1989), are flightless. They thus exhibit basic compliance, at the community level, with island biogeography theory with respect to: island size (Bauer, 1989 and Webb, 1989); distance (Bauer, 1989), time (Terrell-

Nield, 1990); and habitat complexity / development (Gardner, 1991).

These attributes of carabid communities coupled with their usefulness in the quantification of conservation criteria (Eyre and Rushton, 1989) make ground beetles an ideal group in which to study the community response to moorland management.

1.8. AIMS

The aims of this investigation were to investigate the response of invertebrates of *Calluna-Vaccinium* heath, using the carabid beetles as indicators, to the effects of burning and grazing in concert using floristic attributes of the vegetation, structural measures and microclimatic as a framework to quantify the habitat response to the interaction of management practices.

2. METHODS.

2.1. STUDY AREA AND SAMPLE SITES.

The study was carried out on Waskerly Moor in Weardale, County Durham, England (National Grid Reference NZ 04). Fourteen sample sites were used distributed within NZ 0044, NZ 0045, NZ 0145 and NZ 0245, see figure 2.1. for the approximate locations of each sample site. The study areas vegetation was comprised of Calluna vulgaris-Vaccinium myrtillus heath, Calluna vulgaris sub community (National Vegetation Classification community H12a). The study area is managed for both grouse and sheep and is thus managed by burning. The vegetation is therefore comprised of a patchwork of variously aged stands of Calluna. The majority of the patches were comprised of mature to degenerate phase *Calluna*, the remaining were predominantly post-burn or pioneer phase *Calluna*. This pattern appears to reflect a management history where burning was reintroduced after a period of cessation of this practice for a period.

The stocking rate of sheep was relatively high and on the lower areas of the moor, though not in the vicinity of the sample sites, this is reflected in the vegetation in the form of invasion by Pteridium aquilinum.

Sample sites A, C, D, J and N. where pioneer phase sites, L, E and H where post-burn sites, M, F, G, K and B where mature to mature / degenerate phase sites and I was a building phase site. Appendix 1 gives details of the vegetation cover and structure.

2.2. PITFALL TRAPPING

Ten pitfall traps were set at each sampling site, in a row with 3m intervals between them. They consisted of 200ml polystyrene cups with a neck diameter of 6 cm containing 2% formalin with a small quantity of detergent added to lower the surface tension and thus act as a wetting agent. Catches were collected at 2-3 weekly intervals between 9th of April and 12th July. The carabid beetles were identified using Lindroth (1974) and nomenclature follows this author.

2.3. ENVIRONMENT SAMPLING

2.3.1. VEGETATION SAMPLING.

The percentage cover of each vascular plant species was assessed using a point quadrat to sample 100 points from within a $1m^2$ horizontal quadrat. This was repeated ten times per sample site. The vegetation height was Measured using a drop disk of 100g and 20cm diameter. The height was measured in 25 locations within each of the 14 sampling sites.

2.3.2. SOIL SAMPLING

Five 5cm diameter soil cores were taken from each site. The percentage water content of the soil was determined by drying the cores at 50°C to constant weight and calculating the water loss and subsequently the percentage. The organic matter content was determined by ashing the soil in a muffle furnace at 450°C and calculating the loss due to combustion.

2.3.3. MICRO-TOPOGRAPHY

The micro topograohy was determined by measuring the variation in the soil surface in relation to a horizontal plane, determined by a spirit level.

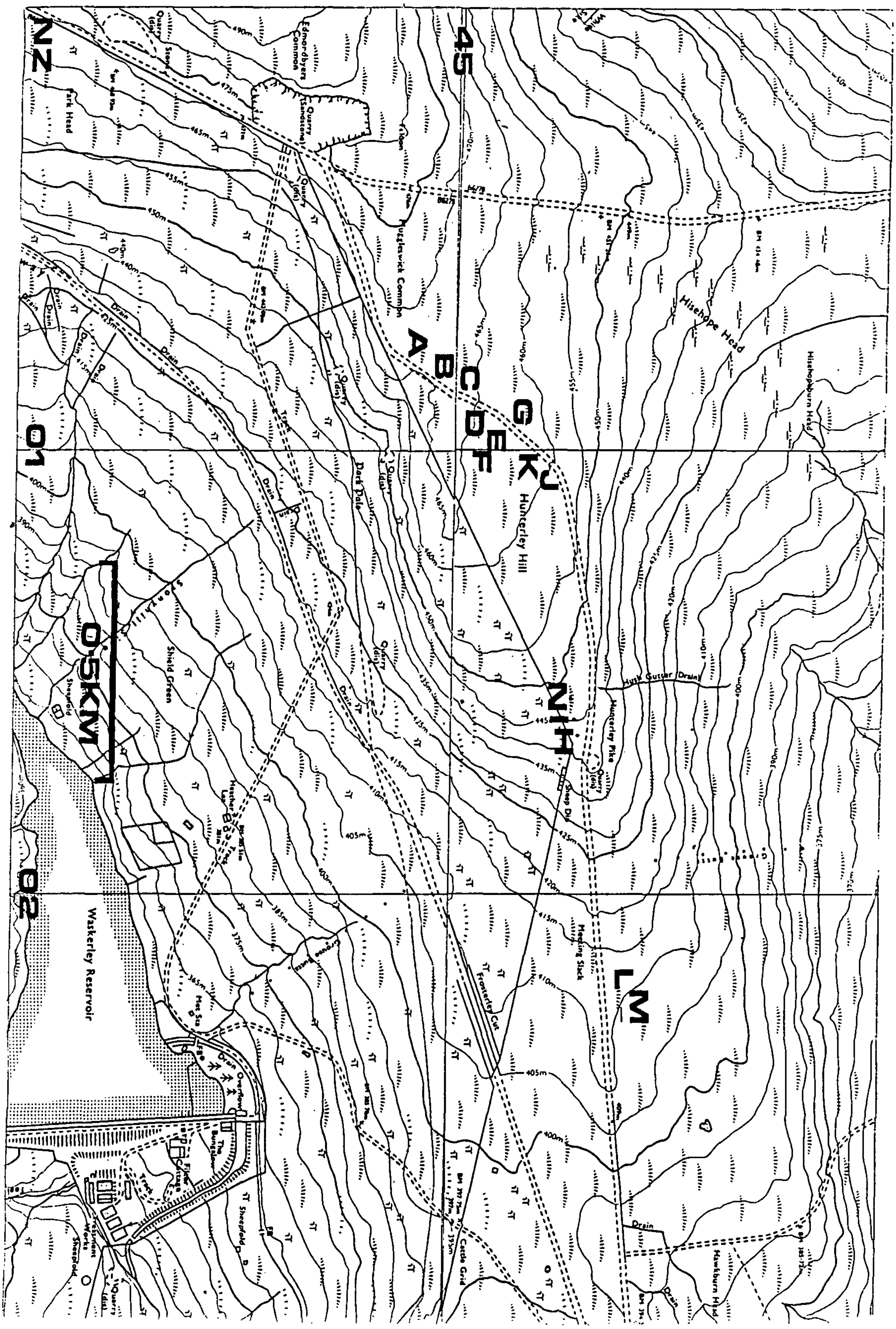


Figure 2.1. The approximate location of the 14 sample sites.

Wrong way round

2.4. DATA ANALYSIS

2.4.1. SPECIES DISTRIBUTION.

Visual inspection of species abundance plots suggested that the data fitted Fisher *et al.* (1943) log series model. The log series model was fitted to the species data as per (Magurran, 1988). The observed species abundance's were put into abundance classes in $\log^2$. 0.5 was added to the upper boundary of each class so that it would be unambiguous to assign the observed species abundance's to each class.

The log series takes the form:

$$\alpha x,\ \frac{\alpha x^2}{2},\ \frac{\alpha x^3}{3} \ldots \frac{\alpha x^n}{n}$$

where αx is the number of species with one individual, $\alpha x^2/2$ the number of species with two individuals, etc.

To fit the series it was necessary to calculate the number of species that were expected to have one individual, two individuals and so on. These expected abundance's were then put into the same abundance classes used for the observed distributions and a χ^2 test is applied to statistically compare the two distributions.

The two parameters needed to fit the series are x and α. x is estimated by iterating the following term

$$S/N = [(1-x)/x][-\ln(1-x)]$$

Where S = total number of species and N = total number of individuals.

When α and x had been obtained the number of species expected to have 1, 2, 3,...n individuals were calculated. These values were summed for the appropriate abundance classes and used as the observed values.

2.4.2. ANALYSIS OF COMMUNITY ENVIRONMENT RELATIONSHIPS

2.4.2.1. REGRESSION ANALYSIS

Linear, least squares, regression analysis was performed on the whole data set to investigate the species environment relationship and the relationship between environmental variables using SPSS-PC.

Weighted average regression using CANOCO (Ter Braak, 1987) was used to investigate the relationships between environmental variables.

2.4.2.2. CLUSTER ANALYSIS

TWINSPAN is a polythetic divisive method of classification and thus has considerable benefits over agglomerative methods based upon similarity measures as the outcomes of the higher levels of the hierarchy are not strongly dependant on the way in which the samples are clustered at the lower levels but instead base their classification upon the overall structure of the data at the outset. Thus the higher levels of the hierarchy are relatively insensitive to the details of the clustering at the lower (Digby and Kempton, 1987).

The stages of a TWINSPAN analysis are as follows (Hill, 1979):

1. Identification of a direction of variation in the sample data by ordinating the samples in a primary ordination using the method of correspondence analysis (Hill, 1973).

2. Division of the ordination through its middle to obtain a crude dichotomy of the samples.

3. Identification of differential species that are preferential to one or the other side of the crude dichotomy.

4. Construction of a refined ordination, using the differential species as a basis.

5. Division of the refined ordination at an appropriate point to derive the desired dichotomy.

6. Construction of a simplified ordination, the "indicator" ordination, based on a few of the most highly preferential species. This ordination is then evaluated to see whether the dichotomy suggested by the refined ordination can be reproduced by a division of the indicator ordination.

With the exception of borderline cases, the refined ordination is used to determine the dichotomy. The indicator ordination is essentially an appendage, in order to provide a succinct characterisation of the dichotomy.

The idea of differential species is essentially qualitative, and to be effective with quantitative data must be replaced by a quantitative equivalent. This equivalent is the "pseudo species" (Hill, 1979). The essential idea is that much of the quantitative information can be retained by expressing it on a relatively crude scale. The levels of abundance that are used to define the crude scale are termed "pseudo species cut levels. The method of pseudo species allows quantitative values to be used as differential species and as indicators, thus samples with many of species A can be separated from samples with only a few individuals of species A by defining the sample with many individuals as having two or more pseudo species (Hill, 1979).

2.4.3.3. ORDINATION

Transformation of data.

Transformation of species abundance's are necessary for a number reasons:
At one extreme, abundance values may have an enormous range, over orders of magnitude. General experience suggests a preference for abundance values with an intermediate range of approximately 0 - 10 (Gauch, 1982 and Digby and Kempton, 1987).This range allows both quantitative and qualitative information to be expressed without either dominating the other. A number of reasons bear upon the recommendation to use an intermediate range.

1. Biological processes responsible for the abundance's are of an exponential nature leading to an enormous range of abundance's. Consequently, only the few dominant species rather than the entire species composition, control the results of many analysis's unless a transformation is applied to put the species on a more equitable footing.

2. Sampling limitations and spatial and temporal fluctuations in species populations imply that for most community data the reliable information can be carried by one digit.

3. The results of multivariate analysis are affected little by finer differences in the input data.

4. Minimise of scale dependence.

The logarithmic transformation , ln(Y+c), has a predominant place in quantitative ecology: it has the effect of compressing large values relative to small values in the data matrix (Digby and Kempton, 1987). The constant c is usually chosen to take a small positive value so as to reduce differences between small data values and particularly , to cope with zero values. This form of transformation is particularly relevant, as in this study, where the data conforms to the underling log series diversity model. The value of c used was 1.

Indirect ordination

The method of ordination varies with the underlying regression model. The latent variable can be obtained by an alternating sequence of regressions and calibrations, the methods used depending upon the model selected:

1. Start with some (arbitrary) initial site scores $\{x_i\}$ with zero mean.
2. Calculate new species scores $\{b_k\}$ by the regression model chosen.
3. Calculate new site scores $\{x_i\}$ by the corresponding calibration method.
4. Remove the arbitrariness in scale by standardising the site scores using the method appropriate to the regression model.
5. Stop on convergence, i.e. when the newly obtained site scores are close to the site scores of the previous cycle of iteration, else repeat from step 2.

The final scores do not depend on the initial scores (Ter Braak and Prentice, 1988).

Ordination can provide latent variables in any number of dimensions; one latent variable is derived first, and the second latent variable can be obtained by applying the same process again but with one extra step - after step 3 the trial scores are made uncorrelated with the first latent variable by orthogonalization.

The resultant axes can be thought of as hypothetical environmental gradients, which are subsequently interpreted in terms of measured environmental variables in the second step of the analysis by regressing the site scores for a given axes against the environmental variable for that site.

The method of ordination used was detrended corespondance analysis (DCA). DCA is a derivitive of Corespondence Analysis (CA) (Hill 1973) an ordination method which employs weighted averages as a heuristic alternative to Gaussian -type models. Ter Braak and Looman (1986) showed by simulation of presence-absence data that weighted average estimation estimates the optimum of a Gaussian logit curve as effciently as the maximum likelihood technique of Gaussian logit regression given certain conditions. However there is a problem with second and higher axes in CA. The problem is the well known but not well-understood "arch effect". If the species data come from an underling one-dimentional Gaussian model the scores of the second ordination axis show a parabolic ("arch") relationship with those of the first axis; if the species data come from a two-dimentional Gaussian model in which the true site and species scores are located homogeneously in a rectangular region in two-dimentional space, the scores of the secondordination axis lie not in a rectangle but in an arched band (Hill and Gauch, 1980). The arch effect arises because the axes are extracted sequentially in order of decresing "varience". (Ter Braak and Prentice, 1988). As a result of the arch effect, the two-dimentional CA solution is gererally not a good approximation to the two-dimentional Gaussian ordination. Hill and Gauch (1980) developed DCA as a heuristic modsification of CA designed to remove both the edge effect and the arch effect. The method emploed in this study was detrending by polynomials as implemented by CANOCO (Ter Braak, 1987), as less "zealous" method of detrending than originally employed by Hill and Gauch (1980) (Ter Braak and Prentice, 1988). It has been shown that DCA often works remarkably well in practice and gives a good approximation to Maximum likelihood Gauissian ordination in simulated data sets were the species have identically shaped Gaussian surfaces (Ter Braak and Prentice, 1988).

Direct ordination.

Canonical correspondence analysis (CCA) is a constraint ordination technique, the results of which are based on species presence or abundance and values of environmental variables simultaneously. CCA differs from CA in that the ordination axes are constrained to optimise their relationship with a set of environmental variables, the direction in which they operate can be indicated in the ordination diagram by arrows, i.e. a biplot. Before calculation of the biplot co-ordinates the environmental variables are standardised to zero mean and unit variance. This is necessary when using environmental data which are on different, and often arbitrary, scales of measurement. The co-ordinate of the head of the arrow on axis s must be $[\lambda s\ (1 - \lambda s]^{1/2}$ times the intraset correlation of the environmental variable with axis s, where λs is the eigenvalue of axis s and it is assumed that the species scores are standardised. By connecting the origin of the plot (the centroid of the site points) with each of the arrowheads, we obtain the arrows representing the variables, with their lengths proportional to their rate of change in the weighted average as inferred from the biplot. Their length is therefore a measure of how much the species distributions differ along that environmental variable. Important environmental variables therefore tend to be represented by longer arrows than less important ones, Only the direction and relative lengths convey information. By inspection of the angles between arrows, one may visualise the association (correlation) between species presence or abundance and increasing values of the environmental variables. Species are represented by points in the ordination diagram. These points represent approximate values of the weighted averages of the species with respect to environmental variables. The word "approximate" means that the ordination diagram does not explain the exact values and, therefore, does not "explain" the total variance in all these weighted averages, but a fraction $(\lambda_1 + \lambda_2)$/(sum of all canonical eigenvalues), whereλ_1 and λ_2 are the first and second canonical eigenvalues. Statistical validity of the resulting environmental axes can be evaluated by an unrestricted Monte Carlo permutation test (Ter Braak, 1986 and 1987). The test is carried out by randomly permuting the sample numbers in the environmental data. For each random data set generated in this way, the first eigenvalue and the sum of all eigenvalues (trace) are calculated. If the species occurrences or abundance's are significantly related to the examined environmental variables, then these values calculated from the original data are among the 5% highest values calculated from at least 100 random data sets. The first eigenvalue is used for testing the importance of the first ordination axis. The trace is used as an overall test of the effect of the environmental variables on the species.

3. RESULTS

A total of 32 species of carabid beetles, representing 16 genera, were identified from the 14 sample sites. Some 4433 individuals were collected with the vast majority belonging to just 3 genera, namely *Carabus, Pterostichus* and *Trechus*, with 11.5% , 36.5% and 23% of the catch respectively totalling over 70% of the catch. Six other genera each contributed over 1% of the catch namely *Notiophilus, Nebria, Calathus, Trichocellus, Bradycellus* and *Bembidion* with 2.39%, 6.72%, 7.56%, 4.22%,1.62% and 6.29% respectively. The seven remaining genera being represented by a few individuals only. Table 3.1 shows the number of each species caught at Waskerly. Appendix 2 shows the species numbers for each of the sampling sites.

TABLE 3.1. Numbers of carabids captured in pitfalls at 14 sites on Waskerly Moor and the number of site occurrences.

Species number	Species name	Number of Sites	Number of individuals
1	*Carabus arvensis*	2	2
2	*Carabus nemoralis*	12	74
3	*Carabus nitens*	6	18
4	*Carabus problematicus*	14	355
5	*Carabus violaceus*	12	53
6	*Pterostichus strenuus*	14	133
7	*Pterostichus adstrictus*	11	1320
8	*Pterostichus diligens*	12	93
9	*Pterostichus niger*	6	17
10	*Pterostichus nigrita*	2	2
11	*Pterostichus madidus*	7	42
12	*Notiophilus biguttatus*	7	43
13	*Notiophilus germinyi*	11	63
14	*Miscodera arctica*	4	15
15	*Nebria salina*	10	293
16	*Nebria brevicollis*	2	5
17	*Calathus micropterus*	14	250
18	*Calathus melanocephalus*	12	85
19	*Patrobus septentrionis*	1	1
20	*Loricera pilicornis*	3	5
21	*Amara lunicollis*	6	7
22	*Leistus rufescens*	3	9
23	*Harpalus aeneus*	1	1
24	*Trechus obtusus*	14	1004
25	*Trechus quadristriatus*	2	3
26	*Trichocellus cognatus*	14	187
27	*Bradycellus harpalinus*	5	6
28	*Bradycellus ruficollis*	10	58
29	*Bradycellus collaris*	6	8
30	*Amaria familiaris*	1	1
31	*Bembidion unicolor*	14	278
32	*Bembidion sp*	1	1

3.1. SPECIES ABUNDANCE

Visual examination of Figure. 3.1., rank of species (ascending order) against abundance suggested that the Carabidae of the Study site fitted Fisher's logarithmic series model of species diversity (Fisher *et al*, 1943). Figure. 3.2 shows the same data but with a logarithmic plot of abundance. This shows an approximately linear relationship after plotting ón a logarithmic scale.

Regression and correlation of this the data, using log transformed abundance data, is displayed in Figure 3.3. This shows a highly significant correlation (r =0.9933; p <0.001; df = 31).

The observed species distribution, expected distribution according to Fisher's model and χ^2 for the 11 abundance classes necessary to fit the model to the data are given in Table 3.2. No statistical difference was detected between observed species distribution and the expected distribution of the log series model ($\Sigma\chi^2 = 6.32$; $P > 0.70$; df = 10).

TABLE 3.2. The observed species distribution, expected distribution according to Fisher's model and χ^2 for 11 abundance classes

Class	*Upper boundary*	*Observed*	*Expected*	χ^2
1	2.5	7	6.6	0.02
2	4.5	2	2.6	0.14
3	8.5	4	2.8	0.51
4	16.5	2	2.9	0.28
5	32.5	2	2.9	0.28
6	64.5	5	2.9	1.52
7	128.5	3	2.9	0.00
8	256.5	5	2.7	1.52
9	512.5	1	2.5	0.90
10	1024.5	1	2.2	0.65
11	∞	1	2.0	0.50
Number of species		33	33	$\Sigma\chi^2 = 6.32$

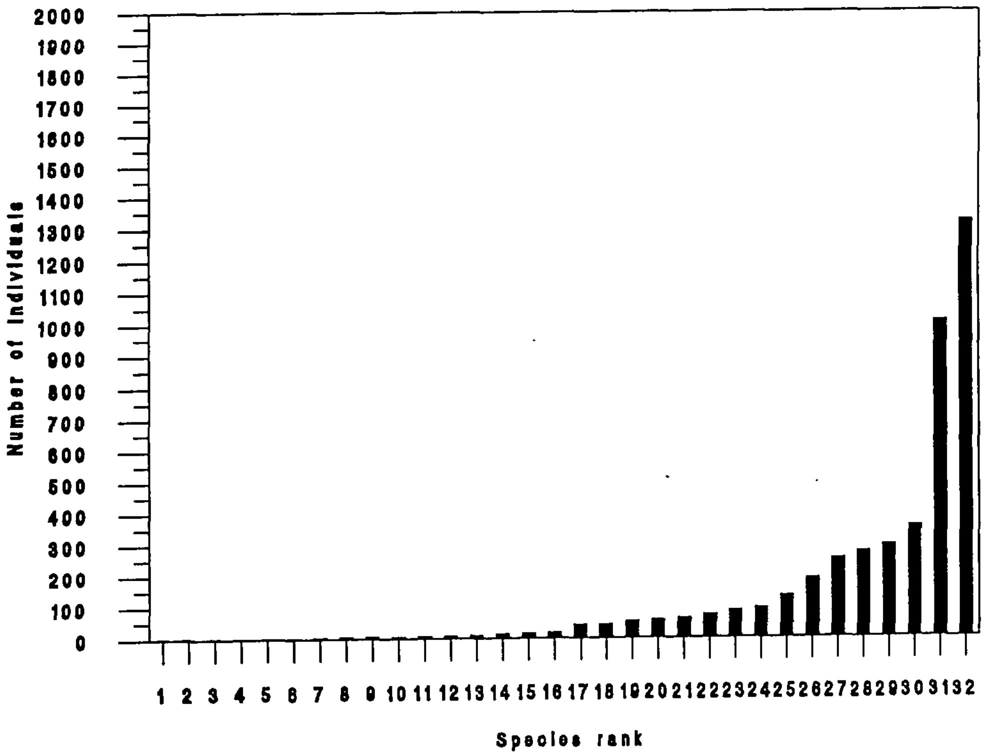


Figure 3.1. Species abundance distribution

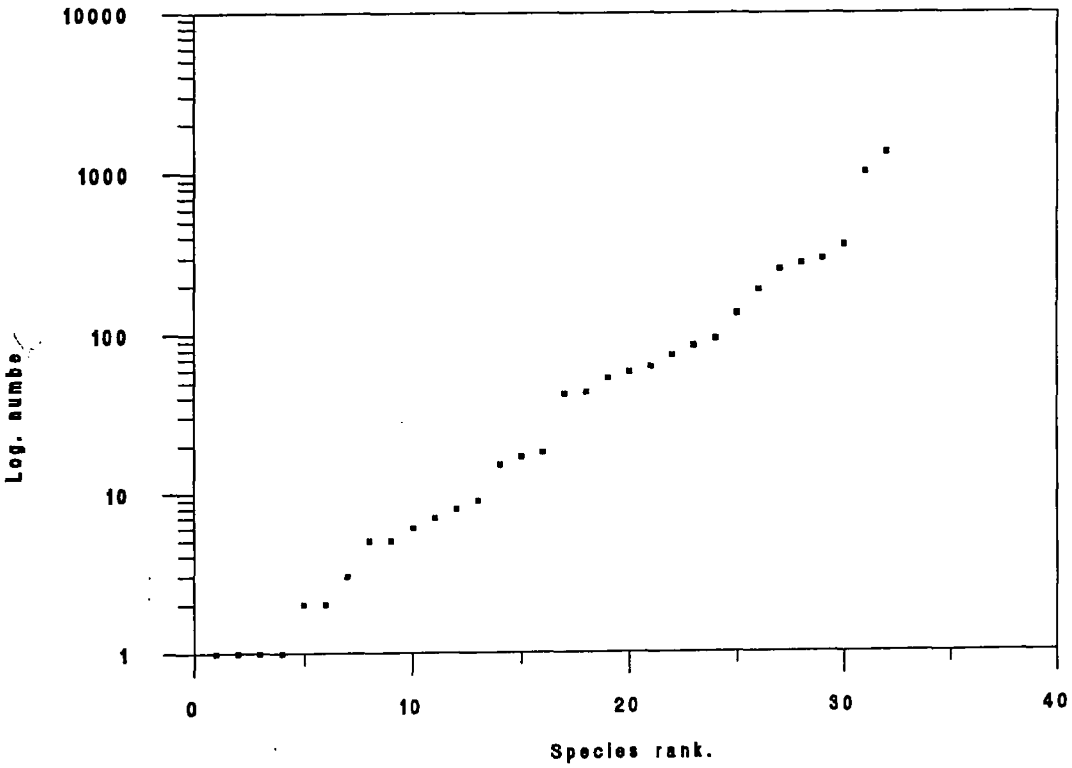


Figure 3.2. Species abundance distribution, logarithmic scale.

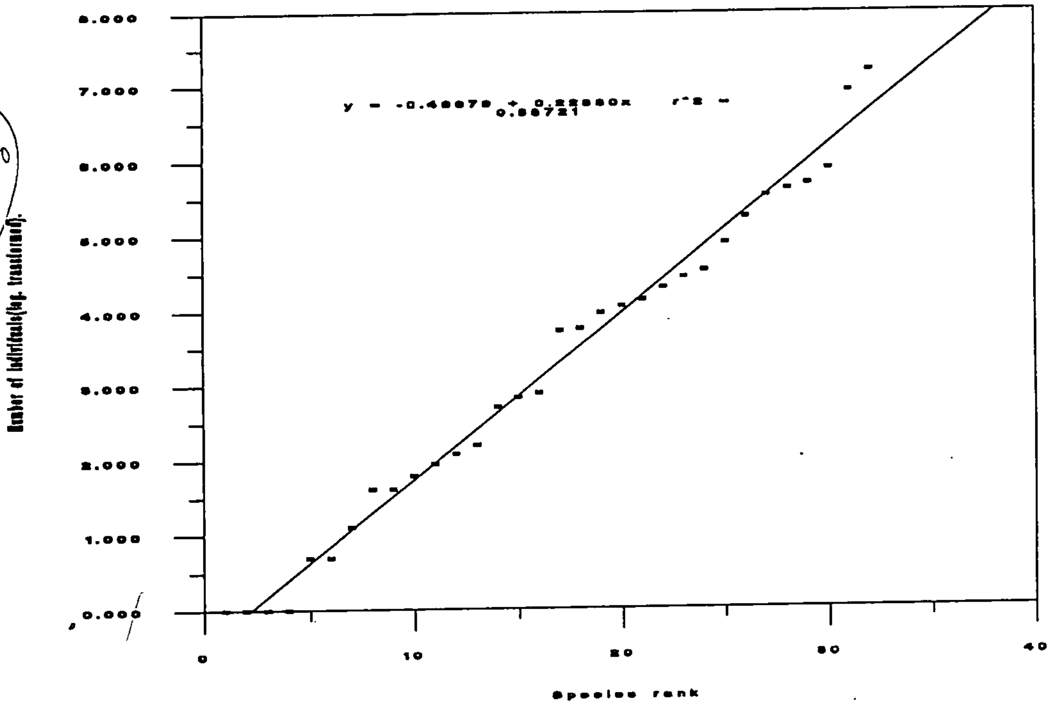


Figure 3.3. Regression of logarithmic species abundance distribution.

3.2. SPECIES RICHNESS AND DIVERSITY INDICES

Table 3.3. shows the number of species, the number of individuals trapped and diversity indices for the catches from the 14 individual sampling sites.

The recent post burn sites, E, H & L, had the highest number of species with over 20 species each. The late pioneer sites, A, C, D, J & N, have 17 to 22 species and the building to degenerate phase sites, B, F, G, I, K & M, have the lowest number of species with 13 to 15 species.

The same pattern is reflected in the number of individuals caught at each sites. Sites E, H, & L trapped on average 466 individuals, 31% of the total. Sites A, C, D, J & N trapped on average 326 individuals, 37% of the total and sites B, F, G, I, K & M trapped on average 233 individuals, 32% of the total. Figure 3.4. illustrates the relationship between the number of individuals trapped and the number of species trapped, it shows a highly significant relationship ($r = 0.7290$; $p < 0.01$; $df = 12$).

The diversity indices are somewhat inconsistent in their ranking of the sites, table 3.4. Though the results of Spearman's rank correlations which are presented in table 3.5. show that the ranks of all the indicies, bar the Margalef, are significantly correlated with each other ($p<0.01$; df 12) Therefore the results of these indicies are comparable and need not be considered individually. Some of the difference in the Margalef index can be attributed to its different sensitivity to sample size. However the general pattern suggests that the sites in the late pioneer phase, C, D, J & N, have the highest diversities. The post-burn sites, E, H &L, have intermediate diversities and the post pioneer sites, B, F, G, K & M, have lower diversities. Two sites, A & I (pioneer and building phase respectively), do not fit this trend.. Site A has low scores for most of the indices, a reflection of the relatively high species richness (Margalef = 3.070) with an uneven (J evenness = 0.536; Var. H' = 0.007) species structure. Site I has a consistently high diversity score, a reflection of its intermediate species richness (Margalef = 2.219) and even community structure (J evenness = 0.780; Var. H' = 0.003).Some of the variation in the diversity idices could therefore be related to the relationship between the number of individuals caught and the number of species caught.[39]

TABLE 3.4. Comparison of diversity measures

D	*Y*	D_{mg}	*HB*	*J*	*H'*	
1***	1***	0.17	0.98***	0.94***	0.98***	*D*
	1***	0.15	0.96***	0.96***	0.97***	*Y*
		1***	0.25	-0.04***	0.29	D_{mg}
			1***	0.89***	0.99***	*HB*
				1***	0.89***	*J*
					1***	*H'*

*** $p < 0.001$

D = Simpson index, Y = Yule index, D_{mg} = Margalef index, HB = Brillioun index,
J = Lloyd and Ghelardi's index and H' = Shannon index.

TABLE 3.3. Species richness, the number of individuals trapped and diversity indices for the 14 sampling sites.

Index	A	B	C	D	E	F	G	H	I	J	K	L	M	N
No. of sp.	18	15	22	17	21	15	13	22	14	18	13	20	15	17
N	254	277	434	287	558	220	203	512	351	384	230	328	120	271
Simpson	1.052	1.080	1.188	2.013	1.441	0.830	1.141	1.421	1.758	1.293	0.877	1.111	1.175	1.658
Yule	1.063	1.091	1.196	2.039	1.449	0.841	1.156	1.427	1.775	1.303	0.887	1.120	1.202	1.678
Margalef	3.070	2.489	3.458	2.825	3.162	2.596	2.259	3.365	2.219	2.858	2.208	3.282	2.924	2.858
Brillouin	1.449	1.460	1.736	2.173	1.883	1.319	1.498	1.904	1.982	1.650	1.363	1.565	1.528	1.966
J eveness	0.536	0.569	0.588	0.803	0.641	0.523	0.614	0.639	0.780	0.598	0.566	0.553	0.625	0.731
Shannon	1.548	1.541	1.817	2.275	1.951	1.417	1.594	1.976	2.059	1.727	1.453	1.656	1.692	2.071
Var. H'	0.007	0.006	0.005	0.003	0.003	0.009	0.007	0.003	0.003	0.004	0.008	0.006	0.015	0.004

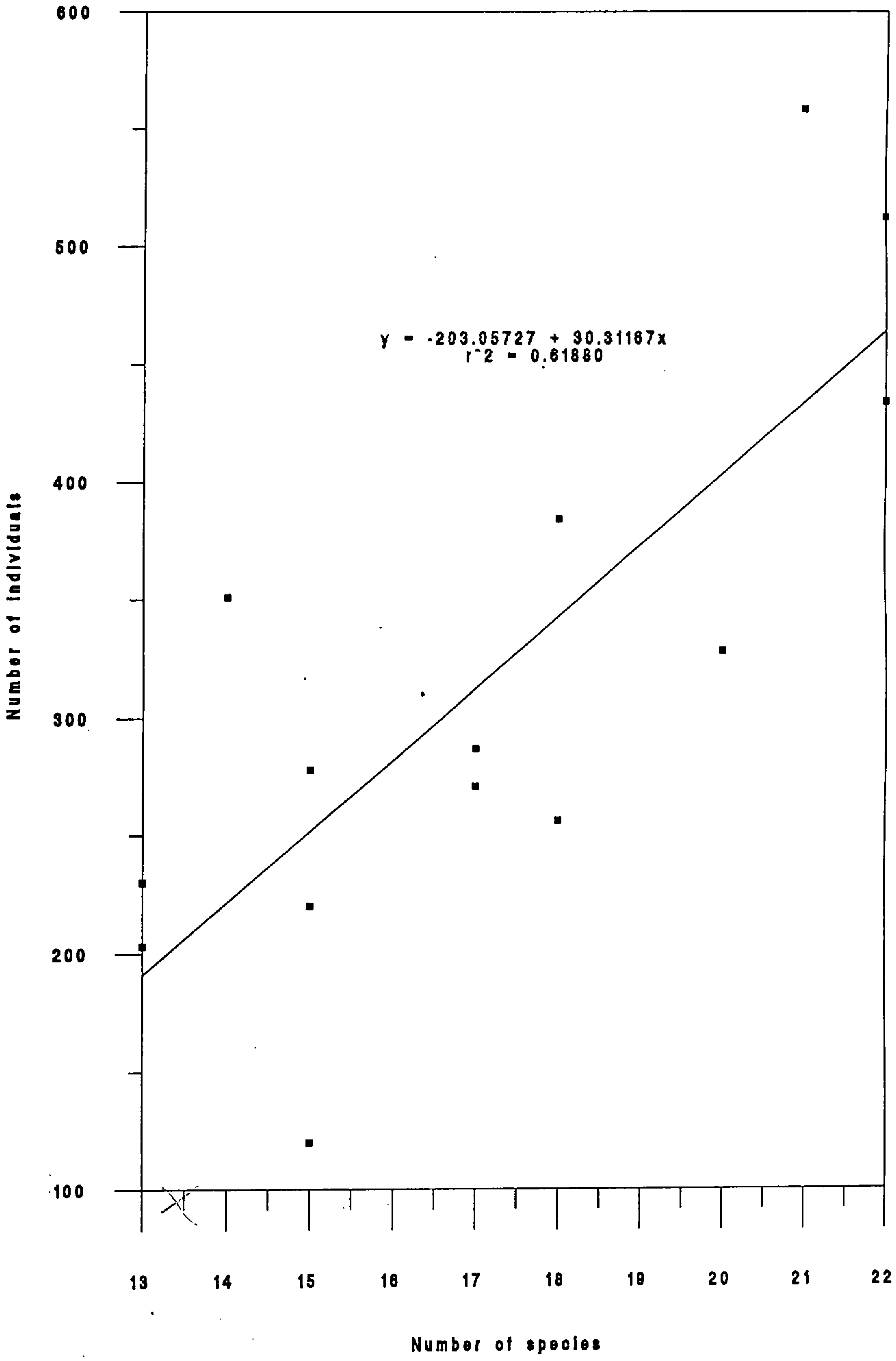


Figure 3.4. The relationship between the number of species and individuals trapped per sample site.

3.3. ENVIRONMENTAL VARIATION

Average (weighted) values of the environmental variables for the 14 sample sites (Table 3.5.). The high standard error on some of the environmental variables indicate that there was considerable variation between sampling sites reflecting the considerable between sample site heterogeneity of the study site. Indicate that the main differences between the sites concern the degree of *Calluna* cover and vegetation height and to a lesser extent the organic content of the soil, though the variance measures are difficult to interpret.

Inter-correlations of the environmental variables are explored in tables 3.6. & 3.7., Pearson product-moment correlations and weighted correlations respectively. The significance of these correlation's are also given in tables 3.6 and 3.7 respectively. A strong set of significant inter-correlations exists between the various environmental variables, particularly between the percentage cover of *Calluna* with the other environmental variables indicating that the percentage cover of *Calluna* is the dominant and governing factor for the variation between sampling sites.

Table 3.5. Average (Weighted) values of the environmental variables from the 14 sample sites.

NO.	ENVIRONMENTAL VARIABLE	WEIGHTED MEAN	STANDARD DEVIATION
1	Micro-topography	10.11	9.43
2	Micro-topography variance	654.07	422.92
3	Bare Ground	47.78	35.37
4	Bare ground variance	306.06	410.56
5	*Calluna* cover	39.37	38.64
6	*Calluna* cover variance	126.93	169.82
7	Moss cover	*	*
8	Moss cover variance	126.93	168.85
9	Sorrel cover	1.13	2.39
10	Sorrel cover variance	15.55	33.63
11	*E. tetralix* cover	1.18	3.15
12	*E. tetralix* cover variance	21.57	56.82
13	Woody debris	35.40	32.80
14	Woody debris variance	1.87	1.86
15	% water content of soil	29.90	9.52
16	Vegetation height	13.08	13.44
17	Vegetation height variance	32.42	64.68
18	% Organic content of soil	86.42	10.62

* high co-variability with another variable therefore not calculated.

Table 3.6. Inter-set correlation (Pearson's) of environmental variables.

Environmental variable	1	2	3	4	5	6	8	9	10	11	12	13	14	15	16	17
1. Micro-topography	1															
2. Micro-topography variance	0.84***	1														
3. Bare Ground	-0.10	-0.05	1													
4. Bare ground variance	0.08	0.37	0.34	1												
5. *Calluna* cover	0.05	-0.10	-0.96***	-0.55*	1											
6. *Calluna* cover variance	0.08	0.44	0.06	0.77**	-0.28	1										
8. Moss cover variance	0.08	0.42	0.11	0.71**	-0.38	0.66**	1									
9. Sorrel cover	0.18	0.19	0.45	0.29	-0.46	-0.06	0.06	1								
10. Sorrel cover variance	0.07	0.08	0.45	0.26	-0.45	-0.07	0.05	0.99***	1							
11. *E. tetralix* cover	-0.27	-0.07	0.16	0.07	-0.22	0.09	0.02	-0.16	-0.16	1						
12. *E. tetralix* cover variance	-0.26	-0.60*	0.15	0.07	-0.22	0.10	0.04	-0.17	-0.17	0.99***	1					
13. Woody debris	-0.24	-0.21	0.97***	0.20	-0.89***	-0.60	0.05	0.34	0.36	0.09	0.08	1				
14. Woody debris variance	-0.27	-0.09	0.67**	0.33	-0.73**	0.19	0.25	0.18	0.21	0.71**	0.70**	0.61*	1			
15. % water content of soil	0.18	-0.09	-0.53*	-0.40	0.60*	-0.31	-0.52	-0.27	-0.29	0.15	0.14	-0.56*	-0.38	1		
16. Vegetation height	0.09	-0.07	-0.93***	-0.58*	0.97***	-0.29	-0.38	-0.44	-0.44	-0.18	-0.18	-0.87***	-0.69**	0.52	1	
17. Vegetation height variance	0.17	-0.10	-0.51	-0.33	0.54*	-0.11	-0.25	-0.25	-0.25	-0.13	-0.13	-0.49	-0.42	0.60*	0.53	1
18. % Organic content of soil	0.09	0.26	0.00	0.23	-0.90***	0.22	0.41	0.08	0.05	-0.34	-0.33	0.03	-0.17	-0.72**	0.01	-0.34

Variable 7 exhibited high co-variability with another variable therefore not calculated by CANOCO.
* P<.0.05; **P< 0.01; *** P<0.001

Table 3.7. Inter-set correlation (weighted)of environmental variables.

Environmental variable	1	2	3	4	5	6	8	9	10	11	12	13	14	15	16	17
1. Micro-topography	1															
2. Micro-topography variance	0.84 ***	1														
3. Bare Ground	-0.09	-0.11	1													
4. Bare ground variance	0.06	0.37	0.22	1												
5. *Calluna* cover	0.04	-0.08	-0.95***	-0.46	1											
6. *Calluna* cover variance	0.06	0.44	-0.01	0.81	-0.25	1										
8. Moss cover variance	0.10	0.46	-0.01	0.70	-0.30	0.71**	1									
9. Sorrel cover	0.18	0.17	0.37	0.24	-0.38	-0.07	0.02	1								
10. Sorrel cover variance	0.07	0.06	0.37	0.21	-0.38	-0.09	0.00	0.99 ***	1							
11. *E. tetralix* cover	-0.27	-0.08	0.11	0.06	-0.19	0.07	0.02	-0.17	-0.17	1						
12. *E. tetralix* cover variance	-0.26	-0.06	0.10	0.06	-0.19	0.08	0.04	-0.18	-0.18	0.99***	1					
13. Woody debris	-0.21	-0.26	0.97***	0.08	-0.88***	-0.12	-0.08	0.25	0.27	0.03	0.03	1				
14. Woody debris variance	-0.23	-0.08	0.62*	0.23	-0.69**	0.16	0.18	0.12	0.14	0.70**	0.70**	0.55*	1			
15. % water content of soil	0.14	-0.10	-0.52	-0.37	0.61*	-0.32	-0.48	-0.22	-0.24	0.20	0.19	-0.55*	-0.35	1		
16. Vegetation height	0.08	-0.04	-0.92***	-0.51	0.97***	-0.29	-0.31	-0.37	-0.37	-0.14	-0.14	-0.84***	-0.65*	0.54*	1	
17. Vegetation height variance	0.15	-0.09	-0.52	-0.30	0.56*	-0.13	-0.22	-0.23	-0.22	-0.12	-0.12	-0.49	-0.41	0.62*	0.54*	1
18. % Organic content of soil	0.12	0.29	0.01	0.26	-0.11	0.26	0.44	0.07	0.05	-0.37	-0.37	0.04	-0.20	-0.71**	-0.02	-0.36

Variable 7 exhibited high co-variability with an other variable therefore not calculated by CANOCO.
* P<.0.05; **P< 0.01; *** P<0.001

3.4. COMMUNITY ENVIRONMENT RELATIONSHIP ANALYSIS

3.4.1. REGRESSION ANALYSIS

Few of the linear (least squares) correlation coefficients of individual species against the environmental variables where significant therefore the method was inappropriate and the results are not presented.

3.4.2. CLUSTER ANALYSIS

The results of the TWINSPAN analysis are presented in Fig 3.5. and 3.6. The classification of the sites is slightly unstable depending upon the psuo speices cut levels used and upon the cut level of omission of rare species used. However in the majority of the analysis's the samples were separated into two main classes at the first division, one, site group 1, with mature or virtually no *Calluna* the other, site group 2, with Pioneer *Calluna*. All analysis's suggest three main ecologically meaningful groupings at the second division with Carabidae assemblages corresponding to three stages of heather development, namely: post-burn / early pioneer, late pioneer and building to degenerate. At subsequent divisions the groupings can be interpreted in relation to the developmental phases of *Calluna* though whether this is justifiable, given the size of the end groupings.

In general the TWINSPAN analysis was characterised by five species groupings, see figure3.6., they were as follows:

Species group A is comprised of: *Pterostichus madidus, Carabus arvensis, Harpalus aeneus, Amara familiaris, Pterostichus niger, Leistus rufecens, Bradycellus collaris, Carabus violaceus, Bradycellus harpalinus* and *Bradycellus ruficollis.*

Species group B. is comprised of: *Trechus obtusus, Calathus micropterus, Pterostichus strenuus, Calathus melanocephalus, Trichocellus cognatus, Carabus nemoralis* and *Carabus problematicus*

Species group C. is comprised of :*Notiophilus germinyi, Pterostichus adstrictus, Pterostichus diligens* and *Bembidion unicolor.*

Species group D. is comprised of: *Notiophilus biguttatus, Amara lunicollis, Loricera pilicornis, Miscodera arctica* and *Nebria salina.*

Species group E. is comprised of: *Carabus nitens, Pterostichus nigrita, Nebria brevicollis, Patrobus septentrionis, Trechus quadristriatus* and *Bembidion sp.*.

Species group A characterises the sample sites with higher *Calluna* cover, site group 1a. The species of which group A is comprised also occur in more open sites but at lower frequencies or are less constant in site group 2. Characteristic species are *Carabus violaceus, Pterostichus niger, P. madidus* and *Bradycellus ruficollis.*

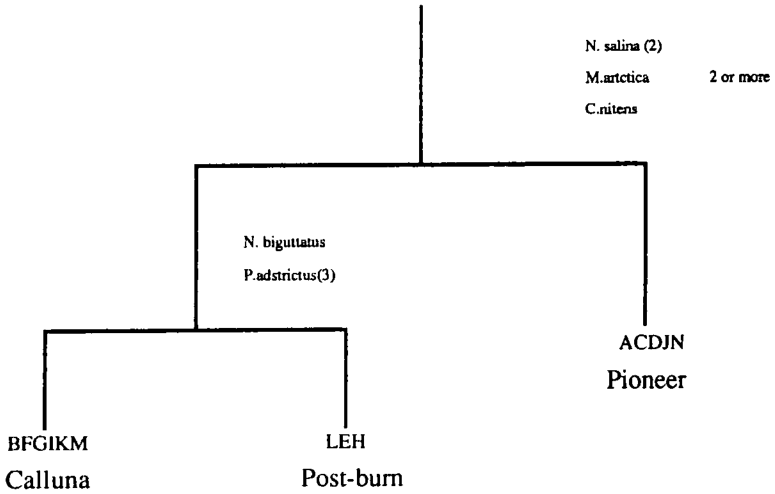
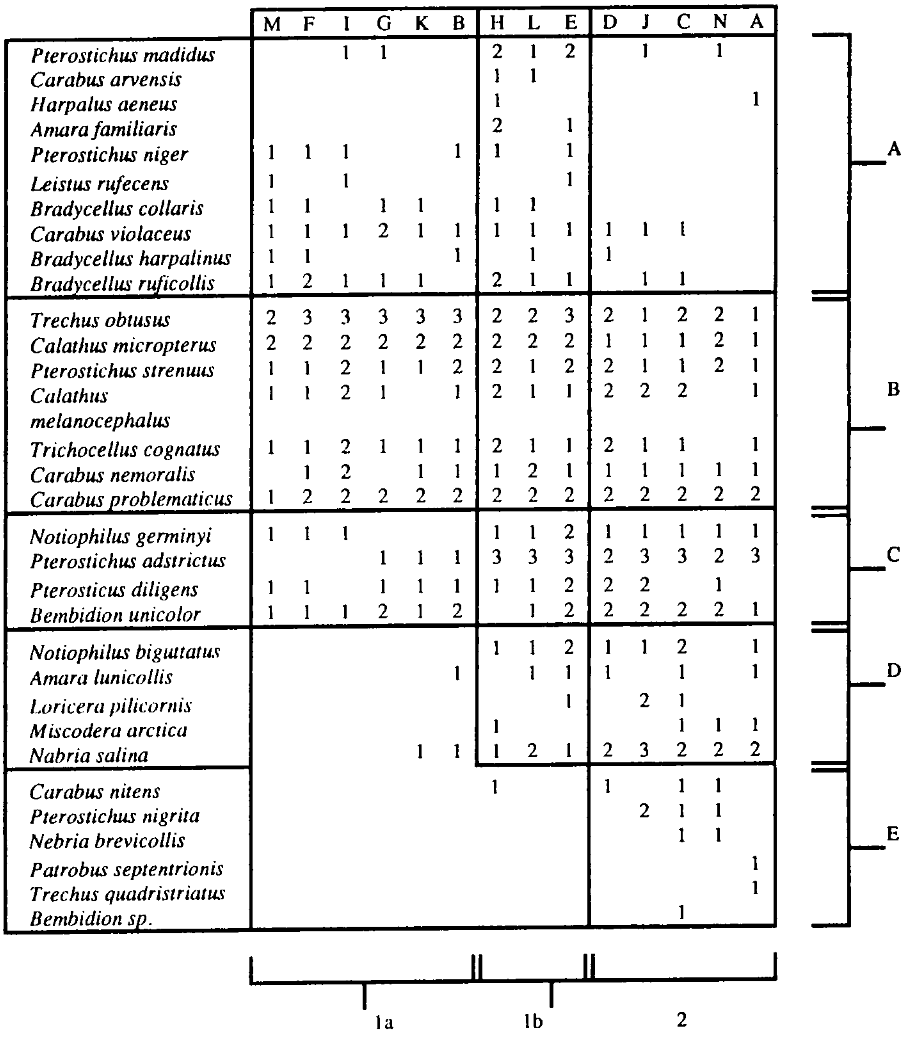


Figure 3. 5. TWINSPAN analysis of 14 carabid sample sites on Waskerly Moor; the indicator species at each division are given Psudospecies level in brackets. Sites are coded A-N. Details of the endgroups are given in figure 3.6. and in the text.



	M	F	I	G	K	B	H	L	E	D	J	C	N	A
Pterostichus madidus			1	1			2	1	2		1		1	
Carabus arvensis							1	1						
Harpalus aeneus							1							1
Amara familiaris							2		1					
Pterostichus niger	1	1	1			1	1		1					
Leistus rufecens	1		1						1					
Bradycellus collaris	1	1		1	1		1	1						
Carabus violaceus	1	1	1	2	1	1	1	1	1	1	1	1		
Bradycellus harpalinus	1	1				1		1		1				
Bradycellus ruficollis	1	2	1	1	1		2	1	1		1	1		
Trechus obtusus	2	3	3	3	3	3	2	2	3	2	1	2	2	1
Calathus micropterus	2	2	2	2	2	2	2	2	2	1	1	1	2	1
Pterostichus strenuus	1	1	2	1	1	2	2	1	2	2	1	1	2	1
Calathus melanocephalus	1	1	2	1		1	2	1	1	2	2	2		1
Trichocellus cognatus	1	1	2	1	1	1	2	1	1	2	1	1		1
Carabus nemoralis		1	2		1	1	1	2	1	1	1	1	1	1
Carabus problematicus	1	2	2	2	2	2	2	2	2	2	2	2	2	2
Notiophilus germinyi	1	1	1				1	1	2	1	1	1	1	1
Pterostichus adstrictus				1	1	1	3	3	3	2	3	3	2	3
Pterosticus diligens	1	1		1	1	1	1	1	2	2	2		1	
Bembidion unicolor	1	1	1	2	1	2		1	2	2	2	2	2	1
Notiophilus biguttatus							1	1	2	1	1	2		1
Amara lunicollis						1		1	1	1		1		1
Loricera pilicornis									1		2	1		
Miscodera arctica							1					1	1	1
Nabria salina					1	1	1	2	1	2	3	2	2	2
Carabus nitens							1			1		1	1	
Pterostichus nigrita											2	1	1	
Nebria brevicollis												1	1	
Patrobus septentrionis														1
Trechus quadristriatus														1
Bembidion sp.												1		

Figure 3.6. TWINSPAN output for the 14 carabid catches together with the psudospecies level. The species groups are coded A-E and site groups 1, 1a and 2. The individual sample sites are coded A-N.

Species group B. is comprised of ubiquitous species with a similar numerical distribution, within the confines imposed by the use of pseudo species, between the two site groups. *Carabus problematicus* is particularly characteristic. Other preferential include *C. nemoralis,* and *Trichocellus cognatus.*

Species group C. is comprised of species which although ubiquitous show a stronger preference for post burn and pioneer phase sites, characteristic species include: *N. germinyi P. adstrictus, P. diligens.*

Species group D. strongly characterises the post-burn and pioneer phase sites, site groups 1b and 2. The group is comprised of species with a higher pseudo species level. Characteristic species include *N. salina* and *N. biguttatus.*

Species group E. also characterises site group 2. It is comprised of the less common species, namely e.g. *C. nitens*

Three site groups are recognised by the analysis: 1a characterised by species group A, B and C and comprised of sites M, F, I, G, K and B and building the degenerate phase *Calluna* sites. Site group 1b is characterised by species groups A, B, C, and D and is comprised of the three post burn sites, H, L and E. Site group 2 is characterised by species groups B, C, D and E. It is comprised of the pioneer phase sites D, J, C, N, and A.

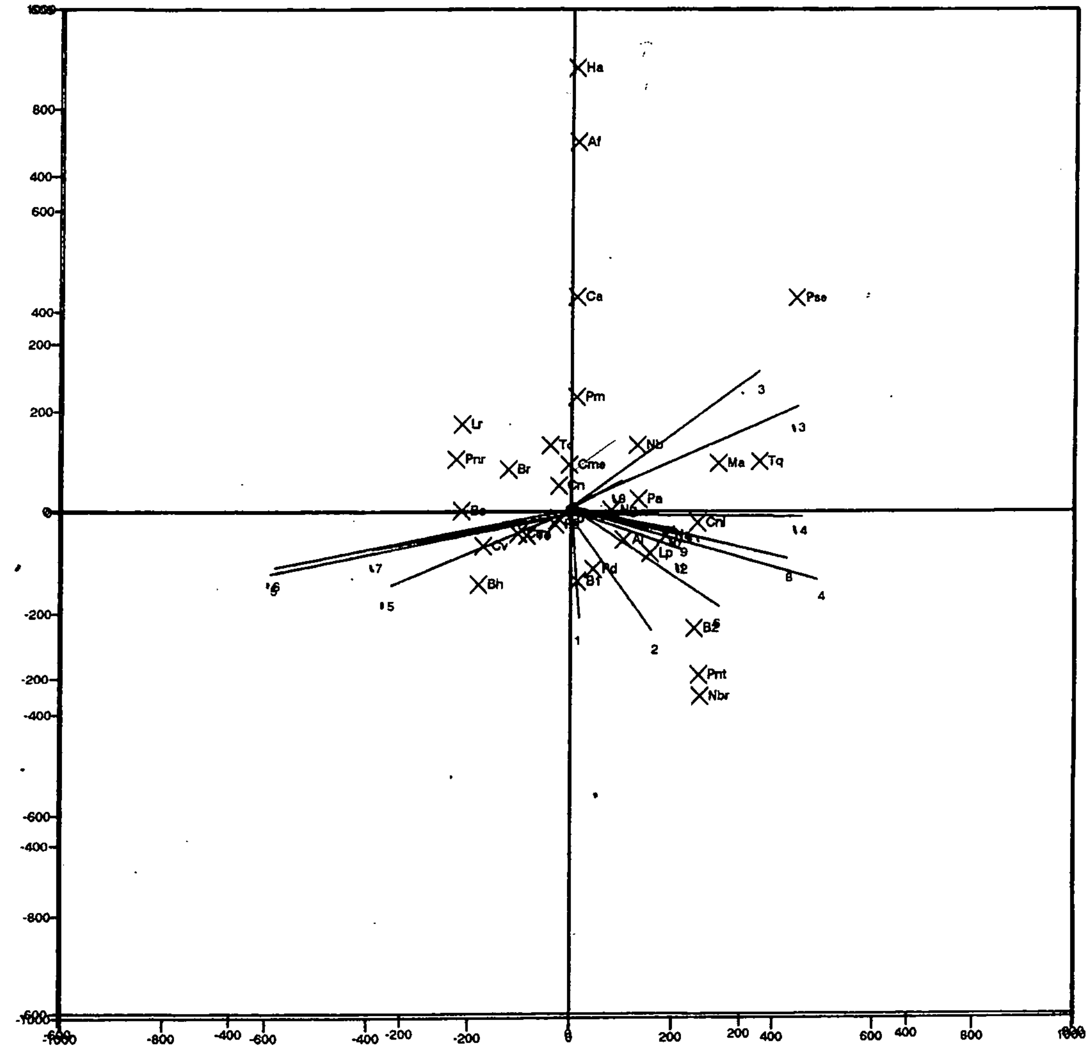
3.4.3. ORDINATION.

3.4.3.1. INDIRECT ORDINATION

Ordination diagrams of the results of a Detrended Correspondence Analysis (DCA), using log (ln(Y+1)) transformed species abundance values, are presented in Figures 3.7. 3.8. and 3.9.for species, sites and environmental variables respectively.

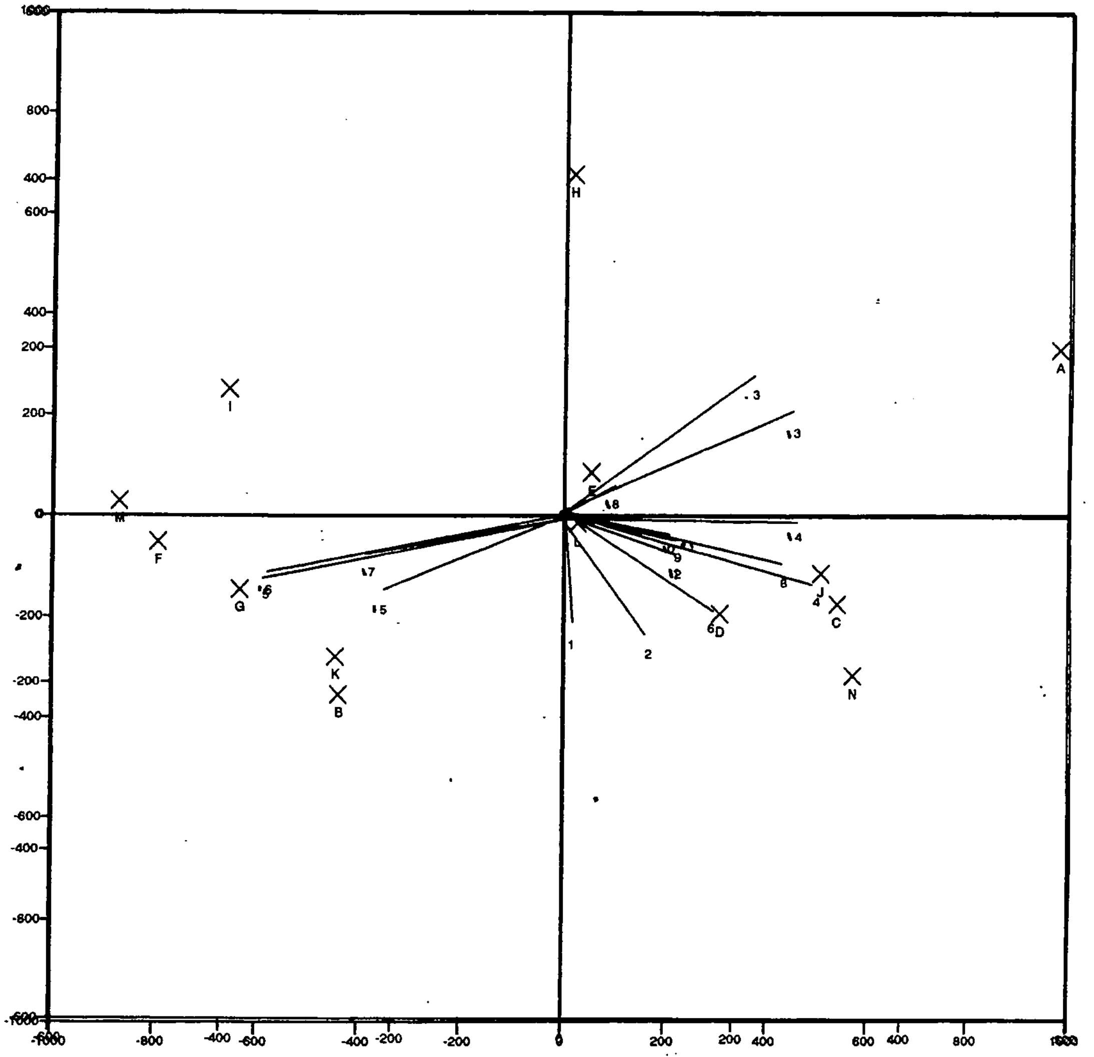
DCA explores the maximum amount of variation in the species data. The axes can be interpreted as hypothetical environmental variables with the maximum discriminate ability. There is relatively little variation in the species data reflected in the low eigenvalues, 0.215, 0.064, 0.045 and 0.026 for axes 1-4 respectively. The majority of the community variation is displayed in axis 1, eigenvalue = 0.215, which has a considerable higher value than all the remaining axes , eigenvalues < 0.077. This suggests that one variable, or a set of co-variables, dominates the variation displayed by the species data.

The plot of the first two axes of the DCA data for each of the sites is shown in figure 3.8. Lines join the positions of the sites in each TWINSPAN cluster on the plot. The most obvious feature is the arrangement of the sites in each group along the first axis; the mature *Calluna* sites having much lower axis one scores than the pioneer sites and the post-burn sites with scores midway between the two. The closest sites to the origin (the point of average community composition) on axis one are sites H, E, & L,



DCA Environment biplot
See Fig. 3.9 for key

Figure 3.7. Detrended correspondence analysis species diagram. X: Cn = *Carabus nemoralis;* Cni = *Carabus nitens;* Cp = *Carabus problematicus;* Cv = *Carabus violaceus;* Ps = *Pterostichus strenuus;* Pa = *Pterostichus adstrictuus;* Pd = *Pterostichus diligens;* Pn = *Pterostichus niger;* Pm = *Pterostichus madidus;* Nb = *Notiophilus biguttatus;* Ng = *Notiophilus germinyi;* Mi = *Miscodera arctica;* Ns = *Nebria salina;* Cm = *Calathus micropterus;* Cme = *Calathus melanocephalus;* Lp = *Loricera pilicornis;* Al = *Amara lunicollis;* Lr = *Leistus rufescens;* To = *Trechus obtusus;* Tc = *Trichocellus cognatus;* Bh = *Bradycellus harpalinus;* Br = *Bradycellus ruficollis;* Bc = *Bradycellus collaris and* Bu = *Bembidion unicolor.*



DCA Environment biplot
See Fig. 3.9 for key

Figure 3.8. Detrended correspondence analysis diagram of the sample sites .

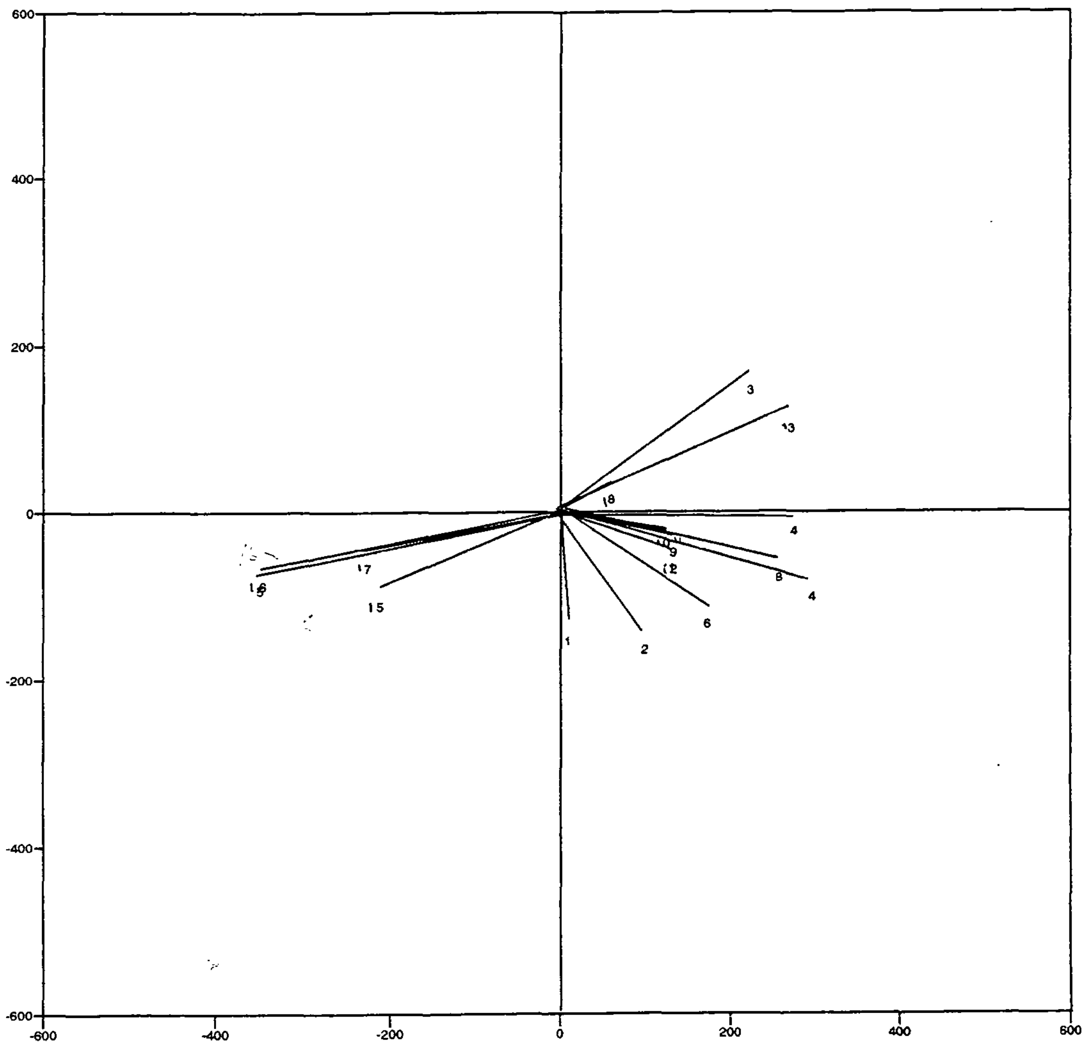


Figure 3.9. Detrended correspondence analysis diagram of the environment variable biplots

1	Micro-topography
2	Micro-topography variance
3	Bare Ground
4	Bare ground variance
5	*Calluna* cover
6	*Calluna* cover variance
7	Moss cover
8	Moss cover variance
9	Sorrel cover
10	Sorrel cover variance
11	*E. tetralix* cover
12	*E. tetralix* cover variance
13	Woody debris
14	Woody debris variance
15	% water content of soil
16	Vegetation height
17	Vegetation height variance
18	% Organic content of soil

the three youngest sites, illustrating the preponderance of the more ubiquitous species , i.e. those near the origin on the species plot figure 3.7. The first axis appears to be directly related to the successional status of the vegetation to some degree, though in a complex manner.

The ordination which is related to that used in the TWINSPAN analysis shows that in fact the dichotomy produced by TWINSPAN is in fact comprised of three clusters with the central one spanning the origin and not an artificial division imposed upon the data. The sites were therefore split into two at the first division of TWINSPAN, however the ordination suggests that splitting into three would be more appropriate.

The ordination displays no direct evidence for a cyclic change in the carabid community paralleling that in the plant community. However the polarisation of the axis with the post-burn sites in the centre necessitates a reversal of the direction of community change at some point. However this need not be a steady transition from one state to another but may occur as a jump. The second axis shows no clear discrimination between sites.

The ordination of species shows a number of outlying species, all of which are rare, namely; *Harpalus aeneus, Amara familiaris, Patrobus septentrionis, Carabus arvensis, Pterostichus nigrita* and *Nebria brevicollis*. These are all outliers on the second axis and their status as outliers can be attributed to their rarity. Therefore axis 2 has less real variation than that displayed in the ordination diagram. The species ordination diagram shows a gradual gradation along both axes, outliers excepted, indicating that there is no major separation of the species into separate groupings. However the groupings imposed by TWINSPAN can be discerned, though there is considerable overlap.

Figure 3.9. is a DCA biplot diagram of the environmental variables. The length of the arrows relative to each other is indicative of the amount of variation in the species and thus site data explained by the variable in question. It shows that the environmental variables can be divided into three types. the first group, that displayed in the lower right hand quadrant of figure 3.9., is indicative of environmental heterogeneity and is comprised of either those environmental variables that measure this directly i.e. the variance measures, namely: variance of bare-ground, variance of woody debris, variance in *Calluna* cover, variance in *Rumex* cover, variance in *E. tetralix* cover and micro-topographic variation, or they are variables which show very considerable between site variation namely *Rumex*, moss and *E. tetralix* cover.

The second group, that displayed in the upper right hand quadrant is that indicative of the openness of the sample site. This group is comprised of three variables namely: bare ground cover, woody debris cover and moss cover variance.

The third group, in the lower left quadrant is that associated with *Calluna* development. The group comprises of four variables namely: *Calluna* cover, *Calluna* height, *Calluna* height variance and water content of the soil.

The lengths of the biplot arrows are indicative of the corresponding environmental variables relative importance in explaining the variation displayed by the species data.

Results of weighted correlation's coefficients of site axis values correlated against the respective site environmental values, without and with the deletion of outling species are presented in Table 3.8 and 3.9. respectively, together with their significance. These tables show that of the eighteen environmental variables only eight could be significantly correlated to the community at each site, namely: bare ground, bare ground variance, *Calluna* cover, moss cover variance, woody debris, woody debris variance, % water content of soil, vegetation height and vegetation height variance.

Table 3.8. Inter set correlations of environmental variables with axes (r x 1000).

NO.	ENVIRONMENTAL VARIABLE	Axis 1		Axis 2	
1	Micro-topography	22		-499	
2	Micro-topography variance	242		-544	
3	Bare Ground	658	*	453	
4	Bare ground variance	714	**	-304	
5	*Calluna* cover	-841	***	-279	
6	*Calluna* cover variance	417		-425	
7	Moss cover	~		~	
8	Moss cover variance	624	*	-220	
9	Sorrel cover	324		-107	
10	Sorrel cover variance	303		-67	
11	*E. tetralix* cover	320		-174	
12	*E. tetralix* cover variance	323		-179	
13	Woody debris	540	*	622	*
14	Woody debris variance	665	**	-7	
15	% water content of soil	-509		-342	
16	Vegetation height	-833	***	-258	
17	Vegetation height variance	-545	*	-171	
18	% Organic content of soil	143		132	

~ high co-variability with another variable therefore not calculated by CANOCO.
* P<.0.05; **P< 0.01; *** P<0.001

Table 3.9. Inter set correlations of environmental variables with axes after deletion of outling species (r x 1000).

NO.	ENVIRONMENTAL VARIABLE	Axis 1		Axis 2
1	Micro-topography	-11		-12
2	Micro-topography variance	212		-86
3	Bare Ground	673	**	250
4	Bare ground variance	691	**	-170
5	*Calluna* cover	-851	***	-137
6	*Calluna* cover variance	402		-246
7	Moss cover	~		~
8	Moss cover variance	615	*	-123
9	Sorrel cover	312		-153
10	Sorrel cover variance	296		-155
11	*E. tetralix* cover	345		-143
12	*E. tetralix* cover variance	349		-145
13	Woody debris	562	*	330
14	Woody debris variance	695	**	83
15	% water content of soil	-514	*	-121
16	Vegetation height	-842	***	-117
17	Vegetation height variance	-550	*	100
18	% Organic content of soil	125		-225

~ high co-variability with another variable therefore not calculated by CANOCO.

* P<.0.05; **P< 0.01; *** P<0.001

3.4.3.2. DIRECT ORDINATION

Only those environmental variables found to be significantly related to their respective site scores were used in direct gradient analysis as the number of environmental variables exceeded the number of sampling sites, the variables used were: bare Ground, bare ground variance, *Calluna* cover, moss cover, moss cover variance, woody debris, woody debris variance, vegetation height and vegetation height variance. After the first analysis some of these were omitted due to their high co-variability with others as indicated by their variable inflation factor (Ter Braak, 1987) these were moss cover, moss cover variance and woody debris.

Ordination diagrams of the results of a canonical correspondence analysis, using log (ln(Y+1)) transformed species abundance values, are presented in Figures 3.10., 3.11. & 3.12. for species, sites and environmental variables respectively. Figure 3.13. shows the cumulative percentage of the variance displayed by the data which is explained by the selected environmental variables.

The first thing to note about the CCA ordinations are their remarkable similarity with those produced by DCA. However they are "mirror" images due to a reflection about the origin on the first axis since the sign of a gradient produced by an ordination is arbitrary (Digby and Kempton, 1987). A Spearman's rank correlation of the site scores of axis 1, i.e. that axis displaying most of the variation in both ordinations, shows a highly significant relationship. This suggests that the environmental variables used in the CCA ordination are approximate to the hypothetical latent variable displayed by the species data.

Figure 3.13. shows the cumulative percentage of the variance explained by successive axes of the CCA ordination. It shows that a high percentage, 92.4%, of the variation displayed in the species data are accounted for by the first four axes of the ordination. The majority, 62.2% is displayed by the first axis with relatively little being displayed by axes 3&4 , just 15% in total. In interpreting percentages of variance accounted for, it must be kept in mind that the goal is not 100%, because part of the total variance is due to noise in the data.

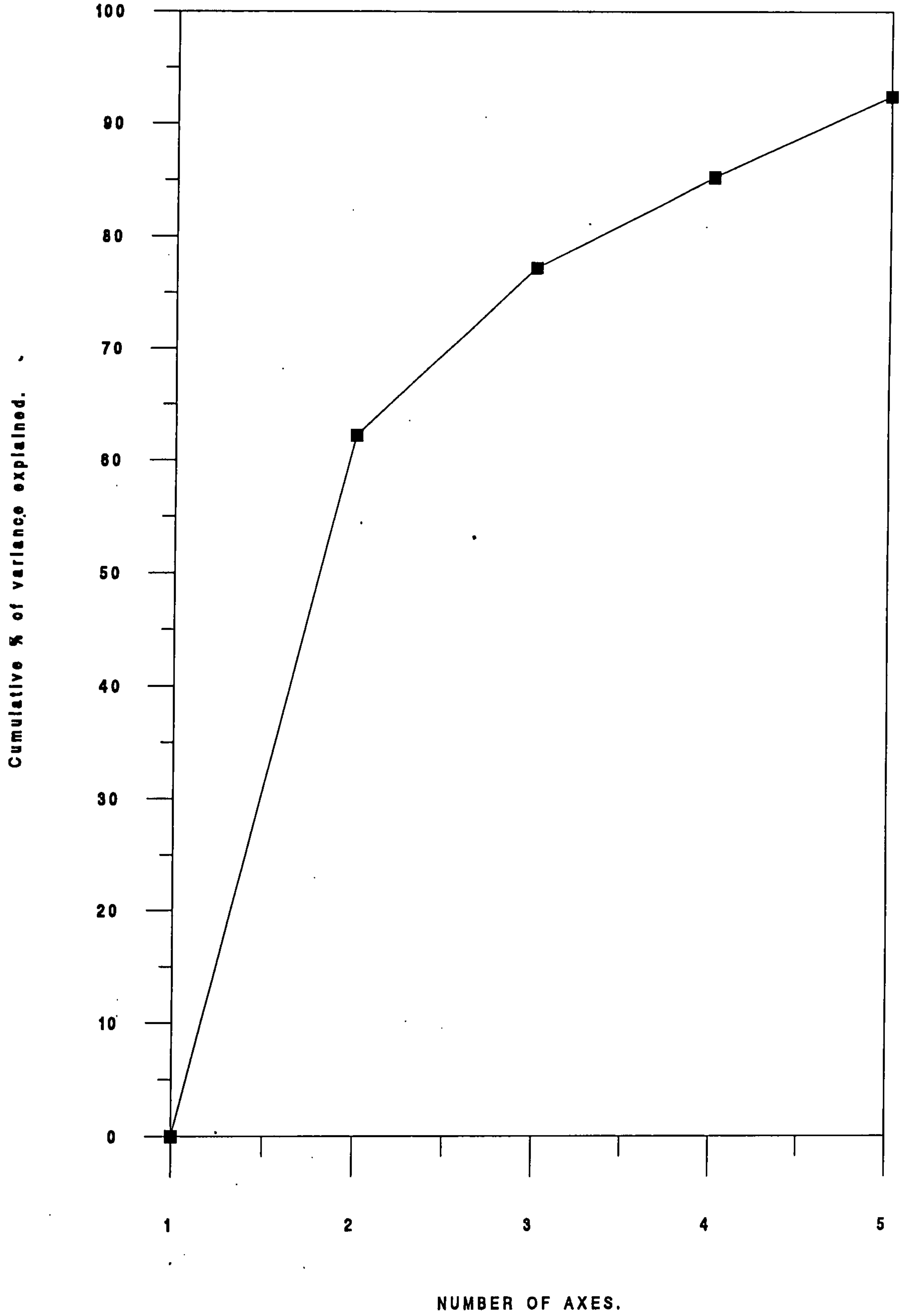


Figure 3.13. Percentage of variance explained by the first four axes.

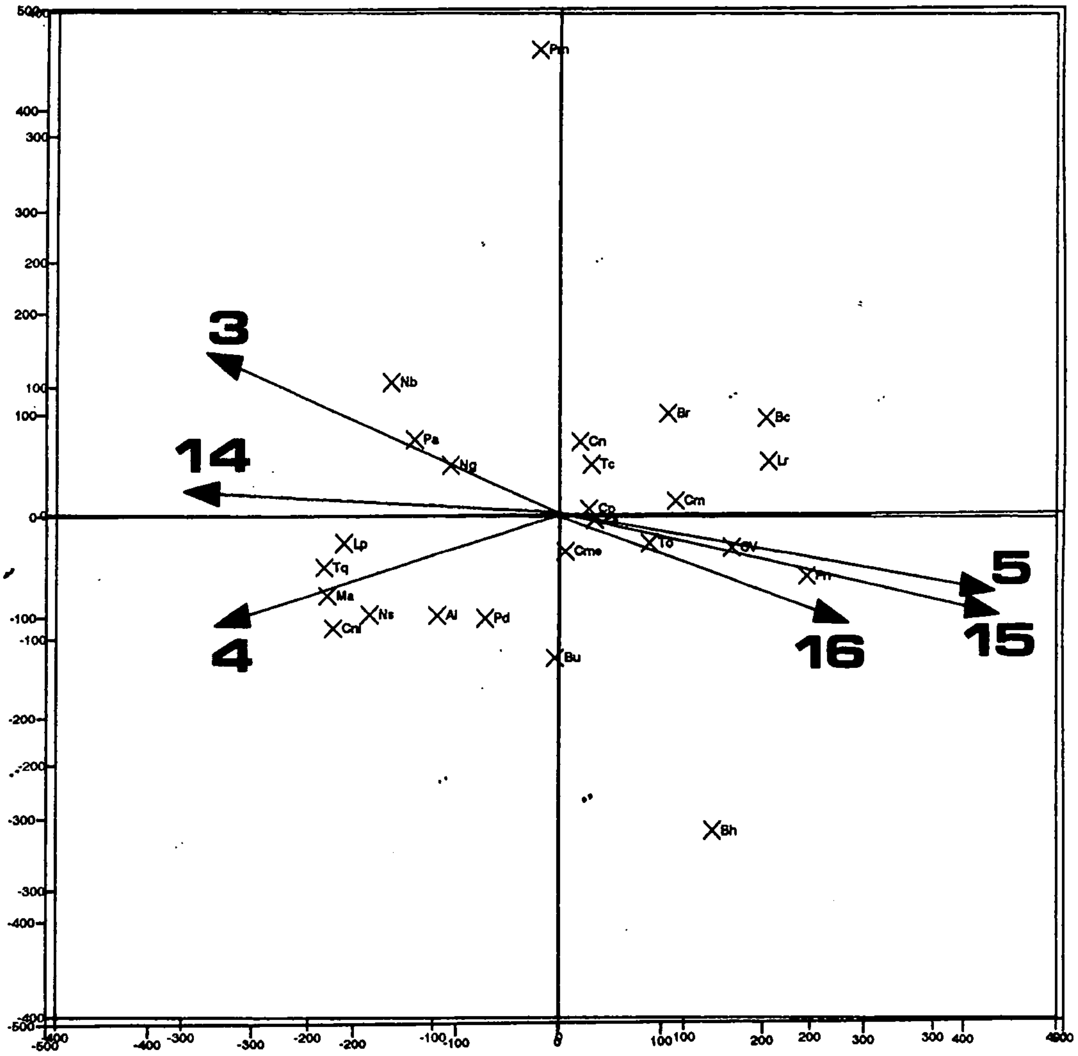
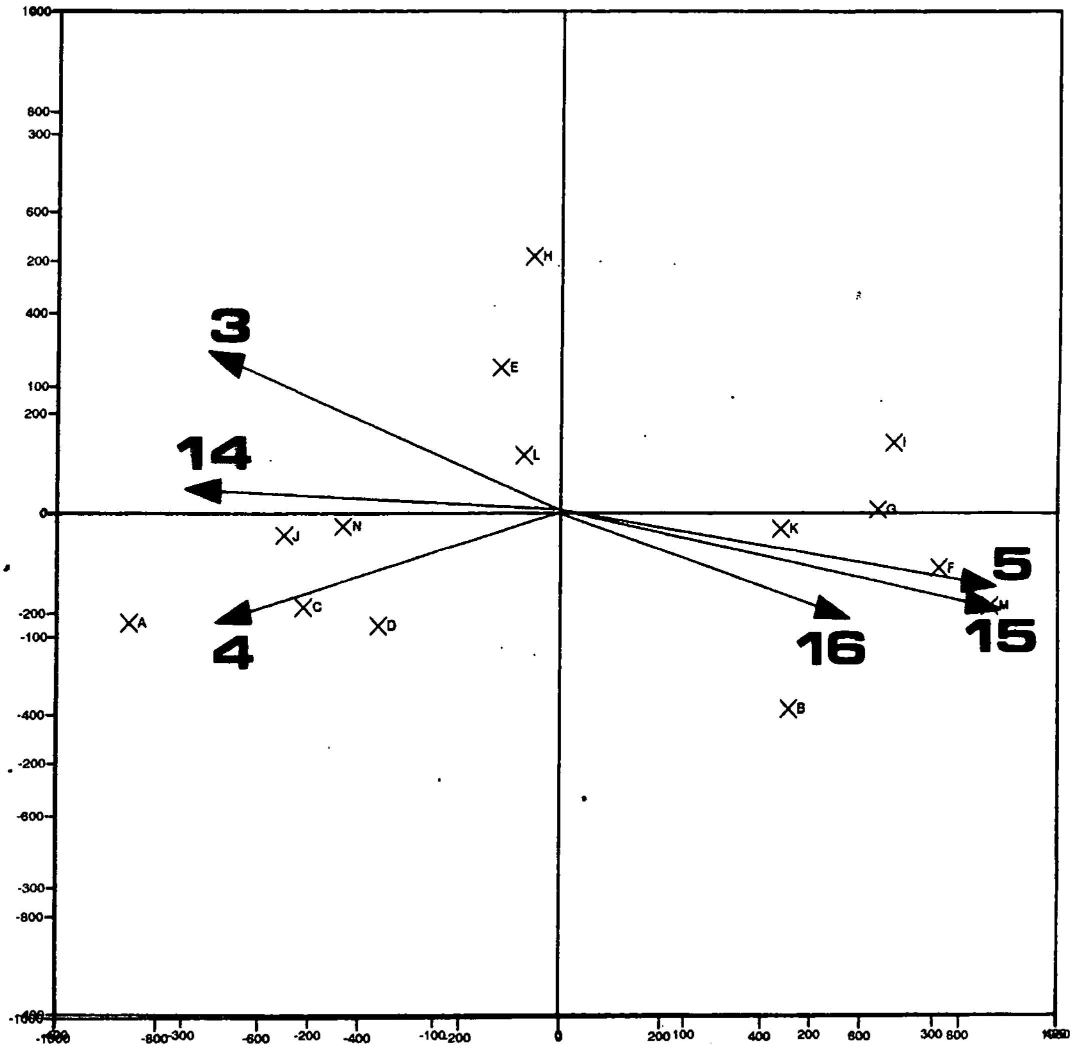


Figure 3.10. Canonical correspondence analysis diagram for caribidae. X: Cn = *Carabus nemoralis;* Cni = *Carabus nitens;* Cp = *Carabus problematicus;* Cv = *Carabus violaceus;* Ps = *Pterostichus strenuus;* Pa = *Pterostichus adstrictuus;* Pd = *Pterostichus diligens;* Pn = *Pterostichus niger;* Pm = *Pterostichus madidus;* Nb = *Notiophilus biguttatus;* Ng = *Notiophilus germinyi;* Mi = *Miscodera arctica;* Ns = *Nebria salina;* Cm = *Calathus micropterus;* Cme = *Calathus melanocephalus;* Lp = *Loricera pilicornis;* Al = *Amara lunicollis;* Lr = *Leistus rufescens;* To = *Trechus obtusus;* Tc = *Trichocellus cognatus;* Bh = *Bradycellus harpalinus;* Br = *Bradycellus ruficollis;* Bc = *Bradycellus collaris and* Bu = *Bembidion unicolor.*

CCA Environment biplot
See Fig 3.12 for key



CCA Environment biplot
See Fig 3.12 for key

Figure 3.11. Cononical correspondence anaysis diagram of the sample sites .

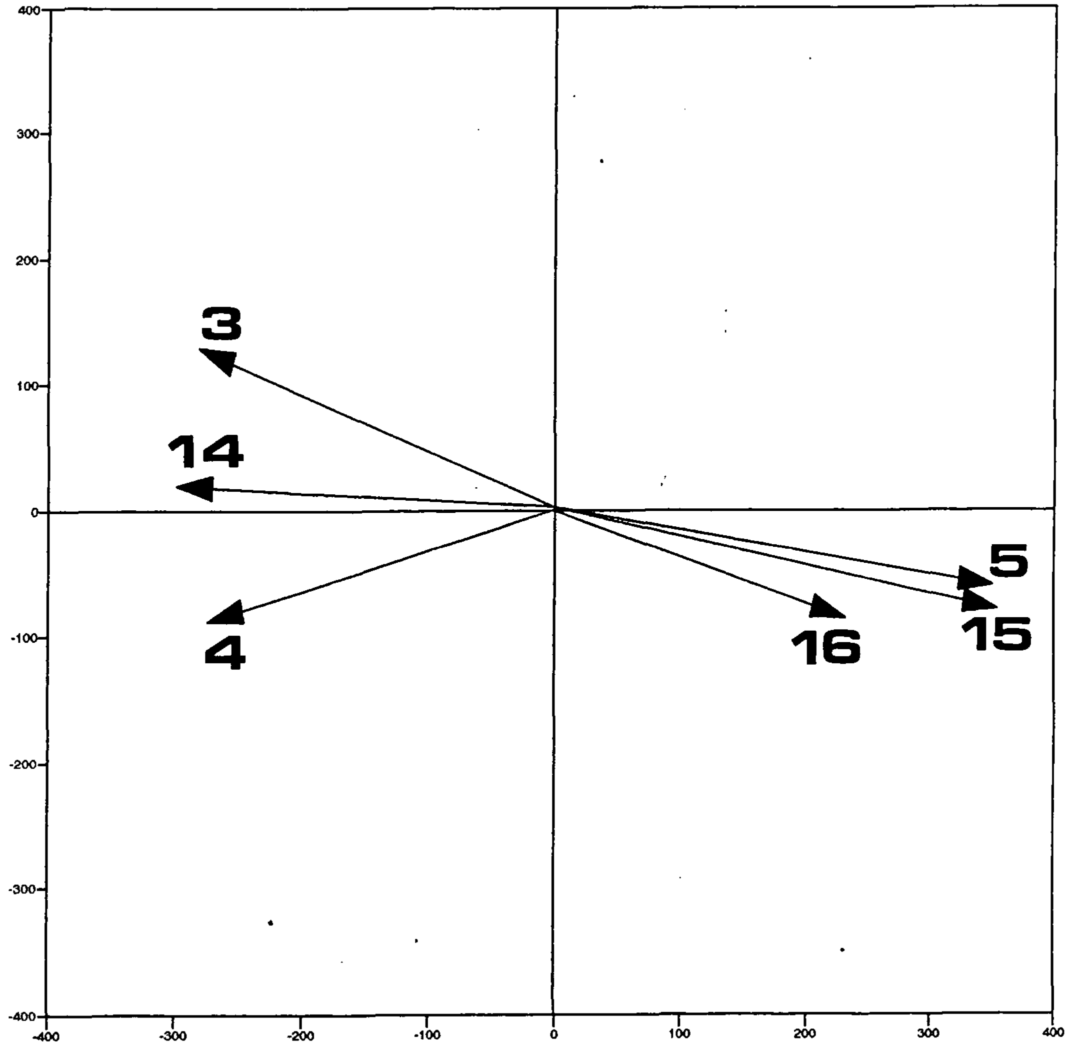


Figure 3.12. Canonical correspondence analysis digram of the environmental variable bi-plots.

3	Bare Ground	14	Woody debris variance
4	Bare ground variance	15	% water content of soil
5	*Calluna* cover	16	Vegetation height

The Monte Carlo permutation test showed that Axis 1 showed a distribution that was highly different from a random distribution at $P < 0.001$ significance level. However the trace test on all axes was not significant, this may be a reflection of the low variance in the axes 3 & 4 (eigenvalues 0.027 & 0.021 respectively) which suggests that these axes may be attributable to random noise in the data set. If indeed this is the case then one would expect the overall test not to be significant. It was not possible to test this as CANOCO only allows for an independent test on the first axis. The fact that the first axis accounted for 62.2% of the variation in a low variation data set (Axis 1 eigenvalue 0.199) suggests that the data set is overwhelmingly dominated by one environmental gradient.

The site ordination diagram indicates three main groupings: A, C, J, D & N., K, G, I, F, B &M. and one of E, L & H. The environment biplot indicates three main groups of environmental variables governing the ordination of both sites and species, in the lower left-hand quadrant are factors indicating the within site heterogeneity. In the Upper left-hand quadrant are variables that indicate the openness of the site and in the lower right-hand quadrant are factors that indicate the structural complexity degree of *Calluna* cover.

The biplot diagram indicates that the environmental variables measured are operating approximately equally on both axis I & II, thus suggesting that the variables measured are not those that are governing community organisation. However it would appear that the variables measured are a convenient "descriptor" of a product variable of the two axes. The Inter set correlations of environmental variables used in the CCA with site axes after deletion of outling species are given in table 3.10. togeather with their significance. They show that all six environmental variables used were significantly correlated with the first axis but only one, the percentage of bare ground was significantly correlated with axis 2, again illustrating that there is only one major axis ovf variation in the data.

Table 3.10. Inter set correlations of environmental variables used in the CCA with axes after deletion of outling species (r x 1000).

NO.	ENVIRONMENTAL VARIABLE	Axis 1		Axis 2	
3	Bare Ground	-698	**	580	*
4	Bare ground variance	-679	**	-392	ns
5	*Calluna* cover	872	***	-354	ns
14	Woody debris variance	-729	**	83	ns
16	Vegetation height	862	***	-265	ns
17	Vegetation height variance	568	*	-388	ns

* P<.0.05; **P< 0.01; *** P<0.001

Table 3.11. shows t-values of the regression coefficients. Only one value exceeded the critical value of a

students t-distribution. However the students t-test is not appropriate for tests of significance of canonical coefficients, because they have a larger variance. But the t-values have an exploratory use. In particular when the t-value of a variable is less than 2.1 in absolute value, then the variable does not contribute much to the fit of the species data in addition to the contributions of the other variables in the analysis. The variable then does not have an effect that is uniquely attributable to that particular variable. Bare ground variance, woody debris variance and to a lesser extent vegetation height variance therefore do not contribute much independently to the fit of the species data in addition to that contributed by the other variables .

Table 3.11. T-values of regression coefficients (x 100)

NO.	ENVIRONMENTAL VARIABLE	Axis 1		Axis 2	
3	Bare Ground	194	ns	310	*
4	Bare ground variance	-57	ns	-31	ns
5	*Calluna* cover	222	ns	40	ns
14	Woody debris variance	-145	ns	-124	ns
16	Vegetation height	36	ns	212	ns
17	Vegetation height variance	75	ns	-205	ns

* P<.0.05; ns= not significant.

4. DISCUSSION

4.1. PITFALL CATCHES AND THEIR RELEVANCE TO COMMUNITY STUDIES

According to Greenslade (1964) pitfall traps are quite suitable for studies of reproduction and the activity patterns of carabids, while there are several objections attached to the method when quantitative interpretation of the data are made. The size of the catch may be influenced by the trap itself and the biology of the species in question. However for the purposes of community studies a measure of absolute abundance is not necessary since broad abundance classes convey sufficient information. The following sections address the factors which govern whether this degree of accuracy can be achieved.

4.1.1. TRAP ATTRIBUTES.

Luff (1975) compared the trapping efficiently of traps of different size. He concluded that 6-10 cms was a suitable diameter to use. Traps of different sizes catch species at different efficiencies, efficiency is defined as the ratio of capture of individuals to the number of encounters. In this study traps of 6cm diameter were used. This trap size in Luffs study caught species at an efficiency of between 71 and 89%, with a mean of 72.8 %.

The most commonly used preservatives are formaldehyde and ethylene glycol. The former, and that used in this study, has the advantage of being both cheaper and better suited both for killing and preserving. Formaldehyde may exert some attractive effect on carabid beetles although there seems to be little or no difference in the reactions of the different species (Luff, 1968).

Luff (1975) suggested that a trap position in relation to that of other traps would result in the catch per trap being reduced when traps are placed close together in a grid. This effect was minimised by having traps in one row with a large spacing, 3m, between.

The material out of which the trap is constructed can effect the retention rate. Luff (1975) measured escape rates of 4% per day from dry plastic traps. It can be assumed that the escape rate was negligible with the use of a preservative and wetting agent. This also had the additional advantage of reducing predation within the trap.

4.1.2. BIOLOGICAL ASPECTS OF PIT FALL TRAPPING.

Pitfall trapping is a relative method of estimating the composition of a community. Southwood (1978) suggests that "The biological interpretation of relative population estimates is extremely difficult. Their size is influenced by the majority or all of the following factors:

1. Changes in actual numbers - population changes.
2. Changes in the number of animals in a particular "phase".
3. Changes in activity following some change in the environment.
4. The responsiveness of that particular sex and species to the trap stimulus
5. Changes in efficiency of the traps."

Factor 2 is not of relevance to this study as only adults were to be considered.

Factor 1 could be of significance if different species populations changed relative to each other at different times of the year and if a study only sampled part of the year. This was in fact the case as only three months were sampled. The sampling programme thus biased the sample towards species such as *C. nemoralis* and *C. problematicus* which are prominent in the spring and away from species such as *C. arvensis* which are prominent latter on in the year. Seasonal differences were also noted within species, early in the sampling programme *C. problematicus* was trapped predominantly in the post burn / pioneer sampling sites, latter becoming more ubiquitous.

Hance (1990) detected considerable differences in phenology between species, therefore this may be of significance to the results as a complete phenological cycle was not sampled, the length required for this is not certain as some species in the uplands e.g. *Carabus problematicus* remain as adults for over two years (Butterfield, 1986). A year of trapping would be the minimum trapping period required to take into account seasonal phenological patterns but this would necessitate all years exhibiting similar patterns this evidently is not the case many invertebrates exhibit loose cyclic patterns over a number of years attributable to parasites, long life cycles with a synchronous emergence of adults only in certain years and climatic effects which occur only in some years e.g. the heather beetle.

These factors are only significant in community studies if the sample bias due to phenology occurs differently between sampling sites at different times of the year. This aspect has been investigated in carabid beetles by Maelfait and Desender (1990). Although their results are to some extent mixed they conclude that ".... it is possible to use short sampling periods to distinguish the carabid communities of comparable habitats. When these short periods are used, observed differences should be interpreted with care. As we have shown, differences in capture yields may not simply reflect habitat preference. Phenology patterns, phenological shifts and seasonal migration from one habitat to another have to be taken into account. This implies that site assessment studies using carabid beetles requires considerable expertise".

Any community study based on a short period of sampling therefore has to assume that these community fluxes "average" out between sampling sites due to the different between site effects of the differential species change. In fact niche theory would suggest that this is the case as otherwise vacant niches would occur, however this may of course not be filled by a species of the same family. Implicit in this is that the community is ordered through competition. Factors other than competition may be affecting the community such that competition has little or no affect. Where populations are bellow carrying capacity any observed differences in the community are purely the result of niche differentiations.

Changes in the environment could affect the trap yields differently but this an effect of between sample site differences and functioning. Thus in short term studies where there has been no significant seral development such that there is no convergence of habitat type and thus community towards a "seral average" over time then these differences in environment are a function of community differentiation and need not be considered.

Factor 4, The responsiveness of that particular sex and species to the traps. This factor operates differently between sites and within sites. Obviously the more mobile a species or sex is the more likely a species is to come into contact with a trap and thus be trapped, assuming no differentiation between species in any other respect. It has been demonstrated that considerable differences occur between species within the same habitat. Barriers and obstructions alter the probability of a species coming into contact with a trap if these are different between sites then there is a difference in probability in capture between them.

The effects of the vegetation cover on the behaviour of each species have been considered by some authors, but are difficult to quantify. Greenslade (1964) found that habitats with an open field layer allow greater speed of movement, resulting in higher catches than those obtained in habitats with a dense vegetation cover. This applies in particularly to the larger species, which move faster than the smaller ones, are more easily trapped, and hence may be over represented in the samples. Conversely, Luff (1975) found the small species were in fact more easily trapped than the larger ones. However, most habitats contain some vegetation, and because this obstructs the movement of the larger species more than that of the smaller species, the effect of the greater mobility of larger species should thereby be reduced.

Desender & Maelfait (1986) showed that the catches of pitfall traps and an absolute estimate (soil cores) were not significantly correlated and that the ratio of the two methods varied between species. They suggest that the catches of different carabid species in ..."traps will hardly be related to the real relative abundances of the species, because of differences in biology between the species concerned". Some overestimated species are highly mobile animals actively hunting during the daytime. The underestimated species are those with a pronounced preference for night activity; their feeding strategy probably brings about a reduced ground surface activity.

It has generally been accepted that larger carabid beetles can be expected to cover greater distances than smaller ones. However, Desender and Maelfait suggest that it is "mainly the diurnal activity cycle and feeding ecology of a species which are the influencing factors" in its representation in a pitfall catch.

Halsall and Wratten (1988) with a time lapse video study found significant differences between capture rates for different species. These differences were unrelated to size, speed of movement and diurnal behaviour. They also found that there where few differences in capture rates when the type of substrate, trap type and season were changed.

Baars (1979) also working in *Calluna* dominated vegetation found that carabid beetles showed a satisfactorily linear relationship between pitfall catches and the mean density as determined by an absolute measure in different structural types of vegetation if trapped over a complete phenological cycle.

Since the numbers of beetles caught in pitfall traps depends on both the abundances and the activity of each species, the trapping results are commonly expressed by the "activity density" (Refseth, 1980). This is thought to yield a good estimate of the role of a species in an ecosystem, and data obtained from pitfall traps ought therefore to yield valuable information about the numerical and ecological status of each carabid species.

However, in zoo-sociological studies of the present type, in which the results from several sample sites are to be compared, it is actually not necessary to have exact estimates of population densities. Refseth (1980) stated that when the sizes and numbers of traps and the duration of the sampling periods are all approximately equivalent, the catches made will be an expression of the relative abundances of the different species and hence yield comparable data. It therefore seems very important to ensure that standard sampling techniques are used in making systematic studies of carabid communities.

Luff (1990) suggested that "the use of carabid communities as indicators of environmental quality and change depends on their being a sensitive and consistent reflection of their environment..." the " species caught is relatively independent of local small scale habitat variations. The use of incidence (i.e., presence / absence) data is therefore acceptable for gross habitat classification". He also suggests that "quantitative carabid data, incorporating some measure of relative abundance of each species in the catch at each site may be very sensitive to local variations in habitat type... . Classifications of carabid habitats based on such data... must therefore either rely on samples taken from spatially uniform habitats, or be based on enough sub-samples (e.g. individually sited pitfall traps) so as to average out local habitat variations". this is supported by the work of Nemilea *et al.* (1992).

Reasons for the differences in communities trapped in each habitat could be either differing activity of each species, or changes in their trapability. Clearly there was less overall carabid activity in the *Calluna* sample sites compared to the post burn ones. This may be the result from greater difficulty of movement in the vegetation (Greenslade, 1964) or because the *Calluna* sample sites provided more food and shelter, so that searching activity was reduced. There was no evident relationship between species body size and their habitat preference. It seems likely therefore that, at least in part, the differences in the communities caught in each habitat reflect true differences in the effective abundance of the various species present. Whether these in turn relate to actual population density is immaterial; the community caught in the pitfall traps is still a sensitive indicator of habitat type.

4.2. Analysis of species habitat relationships

4.2.1. MULTIVARIATE ANALYSIS

CANOCO and TWINSPAN both use weighted averaging to estimate the optimum of the species. This method is an estimate of Gaussian regression. Ter Braak and Looman (1986) and Ter Braak (1986) have shown that the method as employed in correspondence analysis approximates the maximum likelihood solution of Gaussian ordination, if the sampling distribution of the species abundances is Poisson, and if:

a. ~~1.~~the species' tolerances are equal,
b. the species' maxima are equal,
c. the species' optimum are homogeneously distributed over an interval *A* that is large compared to the tolerance, and,
d. the site scores are homogeneously distributed over a large interval *B* that is contained in *A*.

The wording "homogeneously distributed" is used to cover either of two cases, namely 1. that the scores are equispaced, with spacing small compared to the tolerance, or 2. that the scores are drawn randomly from a uniform distribution. Conditions 1 to 3 imply a species packing model with respect to the ordination space. The species scores resulting estimate the optimum of the species in this model.

Conditions 1 and 2 are unlikely to hold for most natural communities but the usefulness of the methods relies on their robustness against violations of these conditions (Hill and Gauch, 1980).

Dargie (1986) demonstrated that gradients in beta diversity and species richness cause different forms of distortion in correspondence analysis ordinations. However, detrending largely removes the beta diversity effect and reduces, but does not eliminate the influence of species richness. Beta diversity is defined as the degree of change in species diversity along an environmental gradient (Magurran, 1988).

Van Groenewoud (1992) tested CA and DCA using simulated community data of known structure and varying complexity. He showed that where the community response was unequal with respect to the first and subsequent environmental gradient the resulting ordination did not recover the community well. The analysis showed that the first community gradient will be recovered in an acceptable manner only if the variation in the community due to the second or higher order gradients are small. This was in fact the case in the present study, axis 1 eigenvalue = 0.199 subsequent axes < 0.077.

CCA however uses the site values of the environmental gradients to compute the species optimum and therefore should recover the data with a greater degree of acceptability than those methods recovering a latent variable. This suggestion has yet to be tested.

CANOCO can only ordinate sites accurately in environmental space where the community at that site is comprised of species which respond to the environmental gradients supplied. Species which are ubiquitous or those which show an average response to an environmental variable will be placed at the origin, the average point in ordination space, of the ordination diagram. Thus if a sites community is comprised entirely or almost so of ubiquitous species then it will be placed at the centre of the ordination space when the environmental characteristics of the site would place it else where.

This would appear to have happened with sites e, h and l (all post burn sites), which are placed at the origin even though their environment is at one corner of the ordination space. The community at these sites was largely comprised of generalist species a reflection of the highly perturbed nature of the sites.

If a species is highly narrow (selective) in its habitat use, but the mean of its environment space is the same as that of the average habitat, the species would be judged to be unselective by the model, a problem when the results are to be used in modelling habitat requirements.

These properties of the multivariate methods employed thus have to be considered when interpreting ordination diagrams.

4.3. THE COMMUNITIES OF CARABID BEETLES IN NORTHERN HEATH

4.3.1. COMMUNITY STRUCTURE

The classification produced in this study can be compared with a number of other studies, they are summarised in table 4.1. which examines the occurrence of species that were trapped in this study in the other classifications.

In the course of this investigation three assemblages / communities of carabid beetles have been recognised; one from post burn sites, one from pioneer phase *Calluna* sites and one from building to degenerate phase *Calluna* sites. The pioneer phase sites can be considered to be species enriched versions of the building to degenerate phase *Calluna* sites as the pioneer phase sites contain most of those species found in this group. It should be noted that the community from post-burn sites is distinguished from the pioneer phase grouping only by the lack of high numbers of preferential species, it can therefore be viewed as an early stage in this communities development from the common core community. This is not immediately apparent from the TWINSPAN dendrogram which only displays the mathematical relationship, not the ecological relationship between the sites.

4.3.2. COMMUNITY AFFINITY

The two communities remaining, i.e. when that associated with the post-burn is considered to be an almost total sub-set of the pioneer phase grouping, are comparable to communities 2 and 3 in Luff *et al.* (1989) classification of the Carabidae communities of north-east England. Luff *et al* describe their communities thus: "Habitat group 2: well drained upland localities... including heather moor, probably on shallow mineral soils". These authors cite typical species as including *N. germinyi, T. cognatus* and *C. melanocephalus.* " Habitat group 3: wetter upland... localities, often with a peat substrate". These sites had similar upland species as those found in habitat group 2 but also contained species preferring damp conditions such as *P. diligens.*

Whilst the species groupings are broadly comparable, the habitat differs in morphology, though not in micro-climate. Site group 1a of this study is broadly comparable, in species composition, to that of habitat group 3 of Luff *et al.* Site group 2b of this study is comparable to site group 2 of Luff *et al.* However both groups of this study were derived from *Calluna - Vaccinium myrtillus* vegetation on a shallow peat substrate forming a typical example of dry northern-heath vegetation. Consequently the two classifications are not comparable in habitat types. It is likely that the micro-climate of site group 1a is damper than that of site group 2b therefore the site types derived from this study correspond to that of Luff *et al.* in this regard.

Eyre and Luff (1990) have constructed a preliminary classification of European grassland habitats using carabid beetles. Their classification title is somewhat of a misnomer as they define grassland as non woodland sites, it therefore contains dwarf-shrub habitats. The study groupings 1a and 2b(1b & 2b) were comparable to habitat C and Habitat B. of this classification respectively. Habitat B is described as well-drained, upland heaths in the United Kingdom with a high incidence of *N. salina, C. melanocephalus, P. madidus* and *T. obtusus*. Habitat c. is described as UK and Norwegian damp, upland heaths with *P. diligens, P. nigrita, Agonum fuliginosum* and *Patrobus assimilis*. These habitat groups are comparable to groups 2 & 3 of Luff *et al.*

The pioneer phase sites of this study also show a slight degree of association with habitat A and habitat F of Eyre and Luff, described as Norwegian upland sites and Netherlands, West German and Polish lowland dry heaths lowland heath sites in that pioneer phase sites share species with these habitat groupings that were not recorded from habitats B and C of Eyre and Luff. *M. arctica* was in common with the Norwegian upland sites and *C. nitens* and *Harpalus aeneus* were in common with the continental lowland heath sites. However many of the characteristic species of these groupings were not present on the study site of this investigation. These findings suggest that Eyre and Luff's classification does need refining, as indeed they suggest by their title.

The communities of this study can also be compared with those derived from classifications that examined upland sites in grater detail. These studies can be grouped into three groups, that examining the invertebrate communities of the uplands in general (Coulson and Butterfield, 1985), that examining the carabid communities of the uplands in general (Butterfield and Coulson, 1983) and those examining the carabid communities of upland heath in particular (Gardner, 1991 and Fishpool and Usher 1989).

The post-burn and pioneer phase sites were most closely attributable to peat community I of Butterfield and Coulson (1983) which occurred on dry heath and included two sites near the current study site. It is characterised by Calluna associated species such as *T. cognatus* and *B. ruficollis* together with widespread open habitat species such as *P. madidus, C. melanocephalus* and *N. salina*. However this study found that *M. arctica, C. nitens* and *P. adstrictus* where more characteristic, reflecting the greater areas of bare ground on these sample sites.

The building to degenerate phase sample sites of this investigation closely resemble peat community II of Butterfield and Coulson (1983) which was comprised of sites on areas where dry heath and deep wet are adjacent. Characteristic species include those of peat community I together with typical wet habitat species such as *P. diligens*. This study found that P. strenuus another species typical of wet habitats was also indicative of this type of habitat. The habitat description of Butterfield and Coulson does not fit these sample sites exactly since they were comprised of what would be considered dry heath botanically, however these sites were predominantly building to mature phase sites which in the study of Barclay-Estrup (1971) had the most humid micro-climate and could therefore be considered roughly comparable to the description of Butterfield and Coulson.

The studies of Gardener (1991) and Fishpool and Usher (1989) relate more directly with this investigation than those already discussed as the predominantly investigate northern heath and use TWINSPAN in their clustering. Their TWINSPAN analysis relate closely to that of the present study. Gardeners' group B and Fishpool and Usher's group III relate closely to site group 1a of this study, all three grouping share similar vegetation, i.e. that with a closed *Calluna* canopy, and characteristic species namely *B. ruficollis*, *T. obtusus*, *C. melanocephalus*, *C. violaceus* and *C. problematicus*. Their site group C and II relate closely to site groups 1b, 2a and 2b of this study all are comprised of dry *Calluna* heath with an open canopy or sites which have been recently burnt. They share characteristic species which include: *P. adstrictus*, *N. salina* and *M. arctica*.

Although few carabid species are restricted to high altitude there are a number of species which are more frequently encountered in upland areas. Goodier (1968) lists eight species which were found above 609m in the mountains of Wales but rarely found at lower altitudes. Two of these, *Miscodera arctica* and *Pterostichus adstrictus* were found during the present study. Of the 12 species that are found in the British Isles out of the 17 species found at altitudes above 900m in southern Norway (Refseth, 1980) 5 were also found during this investigation. These species were: *Carabus violaceus*, *Miscodera arctica*, *Calathus melanocephalus*, *C. micropterus* and *Notiophilus germinyi*. However the habitats were not comparable.

Table 4.1. Comparison of carabid community classifications.

	Fishpool and Usher (1989)		Luff et al. (1991)		Butterfield & Coulson (1983)		Eyre and Luff (1990)		Gardner (1991)		This study		
	III	II	2	3	I	II	B	C	B	C	1a	1b	2
Carabus arvensis							*	*	*	*		*	
Carabus nemoralis		*								*	*	*	*
Carabus nitens	*	*										*	*
Carabus problematicus	*	*	*	*	*	*	*	*	*	*	*	*	*
Carabus violaceus	*	*	*	*	*	*	*	*	*	*	*	*	*
Pterostichus strenuus				*			*	*			*	*	*
Pterostichus adstrictus	*	*	*	*	*	*	*	*	*	*	*	*	*
Pterostichus diligens		*	*	*	*	*	*	*	*	*	*	*	*
Pterostichus niger			*	*	*	*	*	*	*	*	*	*	
Pterostichus nigrita		*	*	*	*	*	*	*	*	*			*
Pterostichus madidus	*	*	*	*	*	*	*	*	*	*	*	*	*
Notiophilus biguttatus	*	*	*	*			*	*	*	*		*	*
Notiophilus germinyi	*	*	*	*			*	*	*	*	*	*	*
Miscodera arctica		*							*	*		*	*
Nebria salina	*	*	*	*	*	*	*	*	*	*	*	*	*
Nebria brevicollis		*	*	*			*	*	*	*			*
Calathus micropterus			*	*	*	*	*	*	*		*	*	*
Calathus melanocephalus	*	*	*	*	*	*	*	*	*	*	*	*	*
Patrobus septentrionis													*
Loricera pilicornis		*	*	*	*	*	*	*	*	*		*	*
Amara lunicollis							*	*			*	*	*
Leistus rufescens	*		*	*			*	*	*	*	*	*	
Harpalus aeneus												*	*
Trechus obtusus	*	*	*	*	*	*	*	*	*	*	*	*	*
Trechus quadristriatus	*	*							*	*			*
Trichocellus cognatus	*	*	*	*	*	*	*	*	*	*	*	*	*
Bradycellus harpalinus		*	*	*			*	*			*	*	*
Bradycellus ruficollis	*	*	*	*	*	*	*	*	*	*	*	*	*
Bradycellus collaris											*	*	
Amaria familiaris			*	*								*	
Bembidion unicolor					*	*	*	*	*	*			

4.3.3. COMMUNITY ENVIRONMENT RELATIONSHIPS

It is clear that the carabid communities on managed *Calluna-Vaccinium* heath are strongly related to the degree of vegetation development. The comparison of DCA and CCA site scores, which showed no significant differences between the ranks of sites on axis 1, clearly showed that the major part of the variation in the community (Axis 1 explained 62 per cent of the community variation after deletion of outlying species) can be predicted / accounted for by the structural characteristics of the vegetation. This is shown by the CCA ordinations similarity to the DCA ordination which only explores variation within the species matrix in terms of a latent variable which has the maximum explanatory effect. Therefore the combination of environmental variables used in the final analysis can be seen as accurately describing the latent variable. Experimentation would be required to determine whether it is actually the environmental variables used or the associated variables they reflect, namely, microclimatic differences such as humidity, insolation, maximum and minimum temperature. These factors can be related directly to vegetation development and several carabid species have been shown to exhibit distinct preferences in respect to temperature, moisture and light Gardner (1991). It is therefore not surprising that the species composition should be influenced by these variables.

As 92 per cent, though part of this figure may be due to noise, of the variation in the species data was explained by the six environmental variables supplied in the final analysis, after the deletion of outliers (to reduce noise), it would suggest that the environment is simple and community space is largely limited to four dimensions.

Species particularly characteristic of pioneer areas were *Pterostichus adstrictus*, *Miscodera arctica* and *Carabus nitens*. All three have been associated with dry open ground with sparse vegetation in the uplands by Lindroth (1974). Holliday (1984) and Richardson and Holliday (1982) found *P. adstrictus* more abundant in burned spruce forest than undamaged woodland and attributed this to the abundance of rotting logs for breeding in the former. *P. adstrictus* is a highly mobile species which flies into open sites (J.E.L. Butterfield personal communication). Thus the species may have been attracted to the charred remains of the *Calluna* or alternatively some other feature that is associated with post-burn and pioneer phase patches, the association with burnt sites is clear as both Fishpool and Usher(1989) and Gardner and Usher (1989) concur. Lindroth (1974) described both *Miscodera arctica* and *Carabus nitens* as being associated with moss in addition to those factors already mentioned therefore it is not surprising that these species were associated with the pioneer phase sites as moss was most abundant on sample sites of this phase.

Species associated with the later stages of heather development included *Pterostichus nigra, P. strenuus* and *P. dilgens* all of which have been associated with wet areas by Lindroth (1974) therefore is not too surprising to find them to be associated with a high canopy cover which has been demonstrated by Barclay-Estrup (1971) to have a low saturation deficit and consequently a relatively high humidity.

Some species e.g. *C. problematicus* where considered by Lindroth (1974) to be widespread heathland species and, namely; others *Bradycellus ruficollis* and *Trichocellus cognatus* to be specifically associated with *Calluna.*

The remaining species tend to be either species that were considered to be widespread heathland species or associated with open country by Lindroth (1974).

Burnt northern heath and pioneer Calluna represent in hospitable habitat for carabids since burnt stands have both higher summer temperatures than *Calluna* clad heath, which may favour some species, and lower winter minimum temperatures. Such stands are also more susceptible to freezing (Fullen, 1986). *Calluna* reduces wind speed and the lack of this protection combined with high insolation and high temperatures could result in increased desiccating in burnt and pioneer *Calluna* stands. Despite these effects in both habitats they contain a higher number of species than the stands with a high *Calluna* cover, probably as a reflection of the greater habitat heterogeneity.

4.3.4. SIGNIFICANCE FOR CONSERVATION MANAGEMENT.

It is clear that there are at least three communities of carabid beetles to be found in the *Calluna-Vaccinium* community of northern heath. That associated with pioneer phase *Calluna* being the most distinctive in that it had species clearly associated with it unlike the other phases. Consequently management is required to maintain this habitat. Indeed the management practised on the study site might be ideal, though perhaps requiring a reduction in stocking level, as the grazing subsequent to burning retards the development from pioneer phase thus prolonging a stands suitability for this community. However the deflections of the vegetation community associated with this form of management if prolonged would prove to be deleterious in the long term.

Like Gardner (1991) also studying in northern heath and Refseth (1980) studying in low-alpine heath and sub-alpine forest this investigation has demonstrated that the carabid fauna were well correlated with the structural complexity. However unlike Refseth it is suggested that a separate classification for carabid communities would considerably increase upon the level of information obtained by plant and bird species. Indeed this study concurs with the suggestion of Eyre *et al.* (1986) that invertebrate community data may be more useful for assessing the impacts of environmental change than either plant or bird data, since invertebrate adapt to changes of smaller magnitude and more rapidly additionally the abundance of individuals and species is generally larger therefore any change can be determined at a finer resolution. Since the carabid community, and presumably the invertebrate community as a whole, can not be predicted from vegetation type alone it is important that with respect to conservation evaluation that factors other than vegetation type are considered, the results together with those of Fishpool and Usher (1989) and Gardner (1991) suggest that structural characteristics of the vegetation at the very least should be considered when evaluating northern heath.

APPENDIX 1

var	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
site																		
1	2.10	236.91	69.00	676.67	6.10	8.77	20.00	405.56	3.00	45.56	0.00	0.00	60.50	380.28	17.74	0.50	1.10	96.44
2	15.67	467.23	11.89	44.61	85.00	27.78	1.70	5.57	0.00	0.00	0.00	0.00	0.00	0.00	58.04	21.80	149.50	55.98
3	5.36	811.06	52.90	1378.77	14.00	590.44	21.00	380.22	0.00	0.00	0.00	0.00	34.10	272.54	21.70	1.00	1.20	92.84
4	14.24	1241.88	34.10	331.66	29.20	341.96	31.50	472.50	0.00	0.00	3.20	63.51	20.00	344.44	22.55	10.30	12.30	92.91
5	17.02	672.21	89.50	44.28	7.10	39.43	3.50	8.50	0.00	0.00	0.00	0.00	78.00	412.22	21.85	2.95	1.70	84.12
6	6.88	536.78	1.00	2.67	98.40	6.27	0.20	0.40	0.00	0.00	0.00	0.00	0.00	0.00	35.18	26.80	14.10	94.77
7	10.85	446.74	9.40	31.82	88.10	58.77	2.60	17.60	0.00	0.00	0.00	0.00	0.00	0.00	33.42	34.00	30.70	96.50
8	1.81	230.52	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	95.00	111.11	26.38	0.00	0.00	89.07
9	5.65	615.71	1.80	3.51	97.00	10.67	5.00	53.78	0.00	0.00	0.00	0.00	0.00	0.00	34.00	33.60	41.90	80.40
10	0.20	374.20	64.70	377.57	17.60	104.71	6.00	37.56	0.00	0.00	11.50	205.83	43.50	644.72	38.52	7.36	12.80	71.18
11	11.82	688.19	4.80	31.51	84.00	79.78	9.20	78.62	0.00	0.00	0.00	0.00	0.00	0.00	28.86	33.60	29.30	96.79
12	1.53	290.51	83.90	289.43	6.60	91.16	0.70	1.12	7.70	115.12	0.10	0.10	63.50	344.72	24.06	1.50	1.80	81.59
13	14.25	587.21	5.30	28.68	89.00	121.11	5.70	52.68	0.00	0.00	0.00	0.00	0.00	0.00	38.05	33.10	272.50	87.75
14	37.69	1858.80	66.10	765.88	10.80	157.07	15.10	198.77	5.50	62.28	0.00	0.00	33.00	123.33	31.38	5.10	4.10	93.63

1, Micro-topography, 2, Micro-topography variance , 3, Bare Ground, 4, Bare ground variance, 5, *Calluna* cover, 6, *Calluna* cover variance, 7, Moss cover, 8, Moss cover variance, 9, Sorrel cover, 10, Sorrel cover variance, 11, *E. tetralix* cover , 12, *E. tetralix* cover variance, 13, Woody debris, 14, Woody debris variance, 15, % water content of soil, 16, Vegetation height, 17, Vegetation height variance, 18, % Organic content of soil

APPENDIX 2

	A	B	C	D	E	F	G	H	I	J	K	L	M	N		TOTAL
Carabus arvensis	0	0	0	0	0	0	0	1	0	0	0	1	0	0		2
Carabus nemoralis	1	4	5	1	5	1	0	8	27	3	4	13	0	1		74
Carabus nitens	3	0	3	1	0	0	0	1	0	6	0	0	0	3		18
Carabus problematicus	10	16	20	11	47	16	13	26	85	23	14	23	7	45		355
Carabus violaceus	0	2	1	1	3	7	11	1	13	1	7	1	4	0		53
Pterostichus strenuus	1	10	5	22	12	5	4	20	20	6	8	2	2	16		133
Pterostichus adstrictus	135	1	228	75	229	0	1	225	0	147	9	173	0	98		1320
Pterostichus diligens	0	3	29	24	12	2	1	3	0	10	2	2	1	3		93
Pterostichus niger	0	3	0	0	2	1	0	1	7	0	0	0	3	0		17
Pterostichus nigrita	0	0	1	0	0	0	0	0	0	0	0	0	0	1		2
Pterostichus madidus	0	0	0	0	17	0	1	17	2	1	0	1	0	3		42
Notiophilus biguttatus	2	0	3	7	15	0	0	9	0	5	0	2	0	0		43
Notiophilus germinyi	1	0	3	9	27	1	0	3	1	7	0	3	1	6		63
Miscodera arctica	7	0	4	0	0	0	0	1	0	0	0	0	0	3		15
Nebria salina	63	1	29	39	5	0	0	2	0	131	1	11	0	10		293
Nebria brevicollis	0	0	1	0	0	0	0	0	0	0	0	0	0	4		5
Calathus micropterus	1	37	1	3	19	10	40	13	38	6	24	12	27	18		250
Calathus melanocephalus	7	5	11	12	2	1	5	22	12	2	0	3	2	0		85
Patrobus septentrionis	1	0	0	0	0	0	0	0	0	0	0	0	0	0		1
Loricera pilicornis	0	0	2	0	2	0	0	0	0	1	0	0	0	0		5
Amara lunicollis	1	1	1	1	2	0	0	0	0	0	0	1	0	0		7
Leistus rufescens	0	0	0	0	3	0	0	0	4	0	0	0	2	0		9
Harpalus aeneus	1	0	0	0	0	0	0	1	0	0	0	0	0	0		1
Trechus obtusus	6	150	27	24	129	142	105	28	100	4	144	65	60	21		1004
Trechus quadristriatus	2	0	0	0	0	0	0	0	0	0	0	0	0	1		3
Trichocellus cognatus	3	1	8	17	6	6	2	97	29	2	3	4	3	5		187
Bradycellus harpalinus	0	1	0	1	0	2	0	0	0	0	0	1	1	0		6
Bradycellus ruficollis	0	0	3	0	1	21	6	13	3	3	2	4	2	0		58
Bradycellus collaris	0	0	0	0	0	2	1	1	0	0	2	1	1	0		8
Amaria familiaris	0	0	0	0	1	0	0	0	0	0	0	0	0	0		1
Bembidion unicolour	9	42	48	40	19	3	13	20	9	25	9	4	4	32		278
Bembidion Sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0		1
Total	256	278	434	287	558	220	203	512	351	384	230	328	120	271		4433

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