The biogeography of the magnesian limestone grassland flora of east Durham and Tyne & Wear

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THE BIOGEOGRAPHY OF THE MAGNESIAN LIMESTONE GRASSLAND FLORA OF EAST DURHAM AND TYNE & WEAR

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University of Durham

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ABSTRACT

1. The remaining fragments of Magnesian Limestone Grassland (MLG) in East Durham and Tyne & Wear were surveyed. Biogeographical theory and climate modelling techniques are applied in order to provide insights for conservation policy

2. Either Area or Perimeter is the most important variable in predicting species richness at all three scales. The Degree of isolation of a habitat isolate from other MLG habitat is also a significant predictor. Micro-habitat variation is of most importance at the smallest scale.

3. A Schematic model is presented which summarises the main processes determining MLG species richness at three interconnecting scales.

4. There is an exponential Species/Area relationship across the studied MLG fragments. It is very difficult to specify the exact mechanisms underlying this relationship however it appears that random and biological processes play a role.

5. Habitat sub-division appears not to depress species richness of MLG fragments. However this may be a result of smaller fragments supporting higher percentages of ecotonal species and also that these patches may be in historical disequilibrium.

6. There is a high degree of heterogeneity within the overall dataset. As different combinations of variables predict species richness within species' subsets representing different dispersal mechanisms.

7. There is a moderate nested structure across all studied MLG fragments

8. Few species occur in a high proportion of fragments and those that do tend to be non-characteristic MLG species. Conservation policy should focus on maximising the amount of habitat which is managed and protected, as opposed to saving specific species. Self-supporting metapopulations should be encouraged by viewing individual fragments as part of a wider network.

9. The distributional ranges of *Bromus erectus* and *Thesium humifusum* are highly correlated with three bioclimatic variables: MTCO, GDD5 and AET/PET. *Sesleria albicans'* distribution is also correlated with these bioclimatic variables but other non-climatic may also be important.

10. The distributional ranges of all three species change dramatically under the two future climate scenarios. There is a general pattern that the climate optimum for any species migrates in Northwards and Eastwards.

11. The present MLG community will disintegrate as species respond individualistically to climate change. It is likely that *Sesleria albicans* will no longer be the dominant grassland species

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LIST OF ABBREVIATIONS USED IN THE DISSERTATION

MLG	Magnesian Limestone Grassland
FSR	Fragment Species Richness
QSR	Quadrat Species Richness
SSR	Site Species Richness
RSR	Rare Species Richness (see * Table 2.2)
ADSR or ASR	Animal Dispersed Species Richness (see Appendix II)
WDSR or WSR	Wind Dispersed Species Richness (see Appendix II)
UDSR or USR	Unspecialised Species Richness (see Appendix II)

Perim	Perimeter
D58	Minimum Distance to a MLG fragment with a species richness of 58 or over
DN	Minimum Distance to the Nearest MLG fragment
N2.5 or No 2.5	The Number of MLG fragments within 2.5km
SR2.5	The Average Species Richness of those MLG fragments within 2.5km
N 5	The Number of MLG fragments within 5km
SRNN	The Species Richness of the Nearest fragment.
%BG	The Percentage of Bare Ground or Rock
% Prim	The Percentage of the MLG fragment's area consisting of Primary habitat
% Wide	The Percentage of a MLG fragment's flora which belongs to the Wide Element
No. Habit.	The Number of Adjacent Habitats
SA	Slope Angle
SD	Scrub Density

The above abbreviations may be preceeded by the following which describe the type of transformation applied:

Log	The Natural Log
Sqrt	Square Root
Asin	Arcsin

Also an (S) prefix clarifys that the variable was calculated for a site scale as opposed to a fragment scale.

SV	Saturation Value (Reed 1981)
MIPD	Mean Inter Population Distance (Quinn et al 1994)
CWS	County Wildlife Site

CSR	Climate Response Surface
MTCO	Mean Temperature of the Coldest month in °C
GDD5	The Annual Temperature Sum >5° in day degrees
AET/PET	The Ratio of Actual to Potential Evapotranspiration
AFE	*Atlas Flora Europaeae*

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CHAPTER ONE: INTRODUCTION

1.1 MAGNESIAN LIMESTONE GRASSLAND

Calcareous grassland supports one of the most diverse plant communities in the British Isles with over 330 characteristic species. However "huge losses among calcareous grasslands and their continuing vulnerability to either agricultural improvement or neglect have greatly enhanced the nature conservation interest of surviving stands." (Rodwell 1992). The Magnesian Limestone Grasslands (MLG) of North East England are no less vulnerable. Together with agricultural practice and myxomatosis, quarrying of the Magnesian Limestone has largely confined this vegetation community to a few intractable slopes and artificial habitats within a matrix of otherwise non-natural habitat. Dalby (1991) calculated that over 66% of the remaining MLG occurs within East Durham and Tyne&Wear. The core MLG community termed CG8 in the National Vegetation Classification occurs entirely within East Durham and Tyne & Wear with a total area of 67 hectares.

The coincidence of Durham and Tyne & Wear's northern geographical position (55°N), climate regime (700-750 mm precipitation per annum and 3.75 average hours of bright sunshine per day) and geology facilitates the presence of a unique calcareous grassland community. The associated flora contains a mixture of species with varied overall geographical distributions within the UK and Europe. The flora demonstrates affinities to both the Arctic-Alpine grasslands (Association: Elyno-Sesleriatea) and the lowland thermophilous calcareous grasslands (Association: Festuco-Brometea) (Shimwell 1968). Therefore many of the more restricted species in the Durham MLG flora are close to either their northern or southern range limits within the British Isles.

It is not therefore surprising that the MLG of North East England has been the focus of much scientific attention. There have been a series of reviews, starting with the that of Heslop-Harrison & Richardson (1953) and concluding with the latest Dalby (1991). These reviews stress the importance of conserving this resource. In addition various ecological studies have taken subsections of the total habitat and explored the internal dynamics of this community, eg. the colonisation of secondary sites and the effect of successional scrub encroachment. Studying the effects of different management regimes however has proved to be more difficult given the short time scale of many studies. Management of these plagioclimatic grasslands is believed to be extremely important for their survival as natural succession promotes woodland. Though in some areas on the Durham escarpment the interplay of lithology and hydrology is thought to have prevented woodland from ever becoming established (Bartley, Chambers & Hart-Jones 1976).

However few studies have attempted to relate modern ecological theory to the remaining scattered MLG habitat fragments. This study attempts to apply such theories not as an esoteric exercise but in order to gain new insights for conservation policy. Furthermore in order to produce balanced and comprehensive conclusions the sample population included all known MLG habitat in East Durham and Tyne & Wear with two exceptions (See Section 2.1).

Growing concern regarding the potential impacts of global climate change upon species and ecosystems has fuelled research into response prediction. The varied biogeographical affinities of Magnesian Limestone Grassland species together with habitat fragmentation renders this particular community very sensitive to environmental change. Therefore this study uses modelling techniques to predict the magnitude and direction of change for a few key species. Thereafter implications for long term conservation management are discussed.

1.2 THE FACTORS PREDICTING SPECIES RICHNESS AT THREE SCALES

The study of species richness is highly scale dependent (Magurran 1988). Therefore this study attempts to identify how species richness at differing scales is related. Additionally factors influencing species richness may well operate on different scales. This study also evaluates the role of a number of environmental variables in predicting species richness at three selected scales. Stepwise Multiple Linear Regression is used in conjunction with Simple Regression analysis to determine those variables most important in explaining variation in species richness. This technique has been applied in many similar studies such as Reed (1981) and Johnson & Simberloff (1974). However the use of this technique in ecological studies is heavily criticised by James & McCulloch (1990). In this study therefore great care is taken in checking that no assumptions are violated especially regarding: the effect of co-linearity between predictor variables; the existence of any data that disproportionally influences the regression line and finally, the stepwise selection procedure itself is compared with alternatives.

1.3 THE SPECIES/AREA RELATIONSHIP

A strong relationship between species richness and area is an attribute common to many datasets, though it is most commonly studied in relation to isolated "islands". However both the nature and the underlying mechanisms of the relationship are highly disputed. There are three central hypotheses that predict both its form and its causes. The null hypothesis is termed the Random Placement Hypothesis (Arrhenius 1921). This states that a Species/Area relationship is produced merely as a result of random placement of species through space. Therefore the relationship has no biological significance and is purely a sampling phenomenon.

Secondly, the Equilibrium Theory of Island Biogeography is possibly one of the longest lived yet most controversial theories in ecology. The hypothesis states that the number of species on an "island" is the result of a dynamic equilibrium between the immigration and extinction of species. It is argued that the number of species at equilibrium on a small island would be lower than that on a large island because population levels are depressed and extinctions more likely. In addition islands a long way from the source of immigrants are predicted to have fewer species than those closer. Though the theory states that species richness is correlated with the degree of isolation and area, it is the latter that has attracted most attention. The Species/Area relationship in this case is determined by the Power Function ($S = CA^z$, where C equals the intercept and Z the slope). The slope of the Species/Area relationship is interpretable as an index of isolation with values between 0.20 and 0.35 if the dataset is in accordance with the hypothesis, ie immigration and extinction are in equilibria.

However as McGuiness (1984) discusses testing the Equilibrium hypothesis via the nature of the species-area relationship is notoriously difficult as there is no clear null hypothesis. Therefore the fitting of the power function model is arbitrary. The theory was constructed from data collected from oceanic islands and has in the past been applied to continental habitat "islands". However the applicability of the theory to continental habitat isolates is questioned in this study. It is shown that the presence of transients in continental samples reduces the number of new species encountered with increasing area, reducing the slope of the Species/Area relationship.

Finally the Habitat Diversity Hypothesis (Williams 1943) pinpoints a very different mechanism causing the Species/Area relationship. The theory states that within a range of areas from $10cm^2$ to 1 hectare (this encompasses the majority of the studied MLG fragments) the Species/Area relationship best fits the Exponential model as a result of the random placement of a species. However for "islands" ranging from 1 hectare to 10^7km^2, area is presumed to act via the addition of new ecological conditions resulting in a Power Function relationship.

In this particular study as the "island" sizes are relatively small and the habitat relatively constant (due to the strict physio-chemical requirements of the species associated with calcareous grasslands) there is no strong habitat gradient between sites. However species richness at a quadrat scale (0.25m^2) is significantly related to a number of habitat variables, eg. the height of the vegetation or the amount of bare ground. Furthermore it is certain that not all micro-habitat variation that influences species richness significantly is captured within the measured variables. In addition at a larger scale, habitats adjacent to the MLG fragments may influence species richness as non-characteristic species invade from the edges.

Several additional analyses proved helpful in identifying the mechanisms underlying the Species/Area relationship. Quinn & Harrison (1988) have devised a technique that allows the effect of habitat subdivision on species richness to be further examined. Reed (1981) used a Saturation Value calculated for each "island" in order to pinpoint individuals not conforming to the predicted overall relationship represented by the regression line.

1.4 THE FACTORS PREDICTING THE NUMBER OF SPECIES (i) WITH A PARTICULAR DISPERSAL MECHANISM AND (ii) A LOW REGIONAL FREQUENCY, IN AN INDIVIDUAL FRAGMENT

Species richness within subsets of species can be predicted using different combinations of variables than those used to predict overall richness. In this study Animal-dispersed species, Wind-dispersed species, species with an Unspecialised dispersal mechanism and Rare species are analysed separately for relationships with the predictor variables. Not only does this help to pinpoint particular processes contributing to the overall pattern but assesses heterogeneity within the community as a result of species-specific characteristics.

1.5 THE DISTRIBUTION OF SPECIES ACROSS THE TOTAL HABITAT

Wright & Reeves (1992) developed a statistical analysis to test the degree to which biotas with lower numbers tend to be subsets of the biotas of richer sites, ie. do the rarest species only occur in the fragments which are most species rich? They conclude that a nested pattern among a set of habitat patches implies a regional structure which is maintained dynamically by biological processes. Whilst the Nestedness statistic does not take direct account of the area of each fragment, a significant nested structure implies that species are not randomly distributed through space as proposed by the Random Placement hypothesis. Moreover Wright & Reeves concluded that nestedness is best correlated with the degree to which the system is dominated by Immigration or Extinction. However in this study as the dataset only shows a moderate nested structure it is difficult to identify the precise causal mechanisms. It is possible though to determine the degree to which different species and habitat subsets contribute to the overall structure. Kadmon (1995) found that there was a strong differential in the contribution made by different species subsets representing different dispersal mechanisms.

1.6 CONSERVATION IMPLICATIONS

The SLOSS (Single Large Or Several Small) debate has been at the forefront of conservation theory since it was first formalised by Simberloff & Abele (1982). It recognises that there is only a limited area of habitat that can be protected given pressure on land use and few resources. The nature of the Species/Area relationship and also the effect of subdivision on species numbers indicates which combination of reserves would maximise species numbers. However not all species are of equal conservation value and it is also important to study species overlap, ie. composition, to ensure that all key community species are within reserve areas. Alternatively some conservationists have argued that habitat not species should be the conservation unit (Janzen 1983). This perspective gains further credence given the predicted future climate change. Conservation policy must accommodate the dramatic changes in species' biogeographical ranges predicted over the next century. It is important to recognise that biotic associations are transient entities containing species that respond individualistically to environmental change. The importance of immigration across varied landscapes for the maintenance of species' populations has contributed to the evolution of Metapopulation theory. This new perspective has provided a new medium through which long term conservation policy can be formulated.

This study addresses the following questions:

(1) What are the most significant variables in explaining species richness at a fragment, quadrat and site scale?

(2) Is there a species-area relationship? If so what is its nature? What are the probable mechanisms causing the Species/Area relationship and do they approximate to those proposed by the Equilibrium Theory, Habitat Diversity Hypothesis or the Random Placement theory?

(3) How might habitat subdivision affect species richness?

(4) Do the variables predicting the number of species (i) within different dispersal categories and (ii) with low regional occurrences vary from those predicting total species richness?

(5) Is there a nested species structure across the MLG fragments? Do any particular subsets of species significantly contribute to the nested structure?

(6) What can be learnt from the results which can be applied to regional conservation strategy?

1.7 THE ROLE OF CLIMATE IN DETERMINING SPECIES DISTRIBUTIONS AND THE POTENTIAL IMPACT OF THE PREDICTED FUTURE CLIMATE CHANGE

Variations in climate appear to be of prime importance in determining the composition and distribution of the thirteen different calcareous grassland communities in the British Isles identified by the NVC (Rodwell 1992). Therefore whilst smaller scale factors such as area or habitat may determine the species richness of an individual fragment, it is important to see these factors within a wider context, eg. climate may largely determine the regional species pool. The IPCC's best estimate states that as a result of the doubling of CO_2 by 2030-2050, there will be a rise in global mean temperature of ca. 2.5°C (Houghton 1990,1992). This will be realised by 2100 therefore effecting a rate of change fifteen to forty times faster than past natural change, eg. Quaternary Glacial cycles (Peters 1992). The rapid change in climate predicted for the next century may have dramatic consequences for both the composition and distribution of species within the studied MLG and calcareous grasslands across the British Isles.

Concern regarding the magnitude and rate of the predicted climate change and the impact this might have upon ecosystems has driven the development of a range of predictive models. Environmental response surfaces for individual taxon (a type of static correlative model) are used in this study. It is important to note that this type of modelling depends upon the assumption that the present distribution of the taxon is determined by and in equilibrium with those aspects of the environment to which the correlation is fitted. (In this case the bioclimatic variables: Mean Temperature of the Coldest month (MTCO), the annual temperature sum above 5°C (GDD5) and the ratio of actual to potential evapotranspiration (AET/PET) are used.) This assumption can not readily be tested as the auto ecology of the three species is not sufficiently known. However this study and a variety of others including Prentice et al (1992) and Sykes, Prentice & Cramer (In press) give support to the underlying importance of the three bioclimatic variables used.

Three species were chosen due to their differing biogeographical ranges - *Bromus erectus, Sesleria albicans* and *Thesium humifusum. Bromus erectus* and *Sesleria albicans* are important constituents of the current MLG flora whilst *Thesium humifusum* is currently restricted to South England. The present European distributions for the three species were plotted on a AFE grid with 4419 points each one representing a 50km x 50 km area. For the same grid, values for the three bioclimatic variables were calculated for the geographical midpoint and mean elevation. Using a correlative procedure between the two coverages the climate response surface for each species was created.

The three response surfaces are used to address three questions:

(7) To what extent are the present ranges of the three selected species determined by climate?

(8) How may the potential ranges of the three selected species change under the forecast future climate scenarios?

(9) What are the potential consequences for the studied MLG community and also calcareous grasslands across the British Isles?

It is very important to note that a specific climate response surface is unique to each species and extrapolations can not be made beyond the three species analysed. Therefore this study can not predict the species composition of calcareous grasslands in the British Isles under the predicted scenarios. However it is hoped that it will give an indication of how transient the present is and the dramatic change many species' ranges may undergo if the predictions are realised.

CHAPTER TWO: MATERIALS AND METHODS

2.1 THE STUDY SITES

Three NVC calcareous grassland communities are present in Durham - CG8 (sub communities a,b and c), CG2d and CG6a (Rodwell 1992). Initially forty-two field sites were pinpointed as supporting Magnesian Limestone Grassland (MLG) habitat (see Table 2.1 and Plate 2.1). These included National Nature Reserves (NNRs), Sites of Special Scientific Interest (SSSIs) and County Wildlife Sites (CWS). These 42 sites include all the MLG habitat which is still intact with the exception of the Hart Railway Walk CWS and the coastal strip between Trowpoint and Whitburn SSSI. These sites were excluded as it was impractical to survey them due to their long narrow shape. Furthermore, both are considered to support only marginal MLG habitat within a matrix of varied habitat.

The forty-two sites are dispersed over a triangular area which stretches 30km North to South (from South Shields to Eldon) and 25km West to East (from Eldon to Blackhall Rocks) see Map 2.2. Due to the particular edaphic requirements of calcareous grassland species the sites all occur on shallow outcrops of the Magnesian Limestone and can be classified into three groups: Western Escarpment (which runs from Boldon to Ferryhill), Plateau Reef formations (in the North and East of the region) and Coastal Outcrops (Doody 1980) see Map 2.1.

However from the English Nature Phase 1 Habitat maps it was clear that many of the 42 sites represent a mosaic of habitats. MLG is often interspersed with rank neutral grassland and dense scrub which reflects the seral progressions mediated by soil development and the amount of grazing. Moreover most of the Habitat Surveys completed by English Nature had been undertaken more than 5 years ago or in the case of CWS sites did not exist. Furthermore information on the species present was limited. Therefore existing fragments of MLG habitat had to be delimited from field surveys.

Table 2.1 Summary List of all sites and their fragments

SITE	GRID REF	FRAGMENT	GEOMORPHOLOGY
Bishop Middleham SSSI	NZ 333324	1. Bishop Midd A	Escarpment /Q Floor&Rim
		2. Bishop Midd B	Escarpment / Quarry Rim
Fishburn Grassland SSSI	NZ 363328	1. Fishburn A	Escarpment
		2. Fishburn B	Escarpment
		3. Fishburn C	Escarpment
Cassop Vale NNR	NZ3338	1. Cassop A	Escarpment
		2. Cassop B	Escarpment
		3. Cassop C	Escarpment / Quarry Floor
		4. Cassop Cii	Escarpment / Cutting
		5. Cassop D	Escarpment
		6. Cassop E	Escarp / Q Floor & Rim
Garmondsway Quarry CWS	NZ339334	1. Garm Qu A	Escarpment/ Quarry Rim
		2. Garm Qu B	Escarpment / Quarry Rim
Garmondsway Triangle CWS	NZ335344	1. Garm Tri A	Escarpment / Quarry Infill
		2. Garm Tri B	Escarpment / Quarry Infill
Island Farm CWS	NZ337310	1. Island Farm A	Escarpment / Reclaim
		2. Island Farm B	Escarpment / Knoll
Merryknowle CWS	NZ345320	1.Merryknowle	Escarpment / Quarry Rim
Quarrington Hill CWS	NZ340375	1. Quar Hill A	Escarpment / Reclaim
		2. Quar Hill B	Escarpment / Reclaim
		3. Quar Hill C	Escarpment
Quarrington Quarry CWS	NZ330378	1. Quar Qu A	Escarpment / Q Ledge
		2. Quar Qu B	Escarpment
Coxhoe Plantation CWS	NZ324362	1. Coxhoe A	Escarpment / Road Bank
		2. Coxhoe B	Escarpment / Road Bank
Raisby Hill Grassland SSSI	NZ3335	1. Raisby A	Escarpment
		2. Raisby B	Escarpment / Q Floor
Silent Bank CWS	NZ345396	1. Silent A	Escarpment
		2. Silent B	Escarpment / Road Bank
		3. Silent C	Escarpment / Road Bank
The Carrs SSSI	NZ3032	1. Carrs A	Escarpment
		2. Carrs B	Escarpment / Quarry Floor
		3. Carrs C	Escarpment
Town Kelloe SSSI	NZ359373	1. Town Kelloe A	Escarpment / Glacial Bank
		2. Town Kelloe B	Escarpment / Glacial Bank
		3. Town Kelloe C	Escarpment / Glacial Bank
Thornley Dene CWS	NZ362382	1. Thornely A	Escarpment / Drumlin
		2. Thornley B	Escarpment / Glacial Bank
		3. Thornley C	Escarpment / Glacial Bank
		4. Thornley D	Escarpment / Glacial Bank
Thrislington Plantation NNR	NZ3132	1. Thrislington A	Escarpment / Transplant
		2. Thrislington B	Escarpment
		3. Thrislington C	Escarpment
		4. Thrislington D	Escarpment / Knoll
		5. Thrislington E	Escarpment
Rough Furze Quarry CWS	NZ318324	1. Rough Furze	Escarp / Q Floor & Ledge
Trimdon Quarry SSSI	NZ362353	1. Trimdon	Escarpment / Quarry Floor
Wingate Quarry SSSI	NZ374376	1. Wingate A	Escarp / Q Floor & Rim
		2. Wingate B	Escarpment / Q Rim
Eldon Grassland CWS	NZ247283	1. Eldon A	Escarpment
		2. Eldon B	Escarpment

Table 2.1 continued

SITE	GRID REF	FRAGMENT	GEOMORPHOLOGY
		3. Eldon C	Escarpment
		4. Eldon D	Escarpment
Pittington Hill SSSI	NZ332445	1.Pittington A	Escarpment
		2. Pittington B	Escarp / Q Floor & Ledge
Sherburn Hill SSSI	NZ331417	1. Sherburn A	Escarpment
		2. Sherburn B	Escarpment / Q Infill
		3. Sherburn C	Escarpment
		4. Sherburn D	Escarpment
		5. Sherburn E	Escarpment
Moorsley Banks SSSI	NZ336459	1. Moor Banks A	Escarpment
		2. Moor Banks B	Escarpment
High Moorsley SSSI	NZ334455	1.High Moor A	Escarpment / Q Ledge
		2.High Moor B	Escarpement / Quarry Rim
Houghton Scarp CWS	NZ345504	1. Houghton	Escarpment /Road Cutting
High Haining Hill SSSI	NZ357507	1. High Haining	Escarpment
Castle Eden Dene NNR	NZ413388	1. Castle Eden	Reef / River Bank
Dabble Bank CWS	NZ365434	1.Dabble Bank	Reef Slope
Pig Hill SSSI	NZ364443	1. Pig Hill A	Reef Slope
		2. Pig Hill B	Reef Slope
		3. Pig Hill C	Reef Slope
Tuthill Quarry SSSI	NZ388429	1. Tuthill A	Reef Slope
		2. Tuthill B	Reef Slope
		3. Tuthill C	Reef / Q Infill & Ledge
Field House Farm CWS	NZ405504	1. FH Farm A	Reef / River Bank
		2. FH Farm B	Reef / River Bank
Tunstall Hills SSSI	NZ392547	1. Tunstall A	Reef Slope
		2. Tunstall B	Reef Outcrop
Carley Hill Quarry SSSI	NZ382598	1. F&C Qu A	Reef / Quarry Spoil Slope
		2. F&C Qu B	Reef / Quarry Spoil Slope
		3. F&C Qu C	Reef / Q Floor & Ledge
Herrington Hill SSSI	NZ367528	1. Herring A	Reef Slope
		2. Herring B	Reef / Quarry Infill
Hastings Hill SSSI	NZ353544	1. Hasting	Reef Slope
Claxheugh Rock SSSI	NZ363574	1. Claxheugh A	Reef Slope
		2. Claxheugh B	Reef / Rail Embankment
		3. Claxheugh C	Reef / Quarry Infill
Cleadon Hill SSSI	NZ389631	1. Cleadon A	Reef Outcrop
		2. Cleadon B	Reef Slope
		3. Cleadon C	Reef Slope
Hawthorn Dene SSSI	NZ439460	1. Hawthorn A	Coastal Headland
		2. Hawthorn B	Coastal Bank
Warren House Gill CWS	NZ440426	1. Warren House	Coastal Bank
Marsden Quarry CWS	NZ396645	1. Marsden A	Coastal / Quarry Rim
		2. Marsden B	Coastal / Quarry Rim
		3. Marsden C	Coastal / Spoil Slope
Harton Down Hill SSSI	NZ390655	1. Harton	Coastal Slope
Blackhall Rocks SSSI	NZ4638	1. Blackhall	Coastal Bank / Outcrop

KEY

Q	Quarry
Escarp	Escarpment

Plate 2.1 Photographs of fifteen MLG study sites

Bishop Middleham SSSI

Cassop Vale NNR

Garmondsway Quarry CWS

Quarrington Quarry CWS

Raisby Hill Grassland SSSI

Silent Bank CWS

The Carrs SSSI

Town Kelloe SSSI

Plate 2.1 continued


Thornley Dene CWS


High Moorsley SSSI


Houghton Scarp CWS


Castle Eden Dene SSSI


Pig Hill SSSI


Hastings Hill SSSI


Blackhall Rocks SSSI

2.2 FIELDWORK METHODOLOGY

Field visits took place between 7th May 1995 and 20th June 1995. Six sites visited in early to mid May had a poorly developed flora and were revisited at the end of the field season. This allowed the number of seasonal emissions across the field sites to be both minimised and standardised.

The following fieldwork procedure was followed:

Specific MLG fragments within a site were delimited using the following criterion: the presence of indicator species such as *Sanguisorba minor*, *Briza media*, *Thymus praecox* and locally *Sesleria albicans* which together define "unimproved calcareous grassland" in Habitat Survey Phase I. In general MLG fragments were found on steep slopes and rock outcrops within a site.

Ninety-eight MLG habitat fragments were thus defined (see Maps 2.2 for the location of the wider sites and Appendix I for each fragment's position within the sites). See Table 2.1 for an OS Grid Reference; an indication of the geomorphology and the number of associated fragments for each site.

These measurements were then taken within each fragment:

(i) The precise location and boundaries of the fragment were marked on a 1:10,000 OS Map;

(ii) A list of all vascular plants observed was noted in order to gain a measure of total species richness and composition; (See Table 2.2 for a complete list of the total vascular species found and the number of fragments in they occur and Plate 2.2 for photos of selected species). The keys in Rose (1981) and Hubbard (1980) were used to identify any unknown species. The Nonclemature follows Rose (1981);

(iii) Five 0.5m x 0.5m quadrats were placed randomly in the fragment and the plant species present were noted. This gave a measure of species richness at a smaller scale;

(iv) The length a fragment's boundaries was approximately estimated by pacing. This enabled each fragment's area and perimeter to be subsequently calculated;

(v) Representative measures of slope angle and aspect were taken using a clinometer and compass respectively;

Table 2.2:The Total flora and the number of fragments in which each species occurs

SPECIES	Freq	SPECIES	Freq	SPECIES	Freq
Achillea millefolium	74	Cirsium heterophyllum	5	Holcus lanatus	40
Aegopodium podagraria	7	Cirsium palustre	14	*Hypericum hirsutum	2
Agropyron repens	43	Cirsium vulgare	37	*Hypericum montanum	4
Agrostis capillaris	49	Cochlearia officinalis	1	Hypericum perforatum	11
Agrostis stolonifera	42	Coeloglossum viride	9	Hypericum pulchrum	15
Agrimona eupatoria	8	Conopodium majus	26	Hypochoeris radicata	43
Ajuga reptans	6	Crepis capillaris	2	Juncus articulatus	2
Alchemilla vulgaris	8	Cynosaurus cristatus	34	Knautia arvensis	33
*Anacamptis pyramidal.	5	Dactylis glomerata	79	Koeleria macrantha	34
Anemone nemorosa	2	Dactylorhiza fuchsii	38	Lathyrus pratensis	41
Angelica sylvestris	8	Dactylorhiza purpella	17	Leontodon autumnalis	7
*Antennaria dioica	1	Danthonia decumbens	14	Leontodon hispidus	64
Anthoxanthum odaratum	30	Daucus carota	31	Leucanthemum vulgare	21
Anthriscus sylvatica	14	Deschampia cespitosa	23	Linum catharticum	49
Anthyllis vulneraria	24	Epilobium angustifolium	21	*Linum perenne ang	3
*Aquilegia vulgaris	2	*Epilobium montanum	2	Listera ovata	26
Arabis hirsuta	6	*Epipactis atrorubens	5	Lolium perenne	29
Armeria maritima	4	Epipactis palustris	2	Lotus corniculatus	92
Arrhenatherum elatius	59	Equisetum arvense	8	Luzula campestris	23
Astragalus danicus	5	*Erigeron acer	5	Medicago lupulina	46
Avenula pratensis	65	Eupatorium cannabium	1	Molinia caerula	3
Avenula pubescens	48	Euphrasia officinalis	33	Mysostis arvensis	4
Barberea vulgaris	1	Festuca arundincea	7	Onobrychis viciifolia	1
Bellis perennis	70	Festuca ovina	63	Ononis repens	11
Blackstonia perfoliata	5	Festuca pratensis	27	Ononis spinosa	7
*Brachypodium pinnat.	3	Festuca rubra	92	*Ophrys apifera	4
Brachypodium sylaticum	47	Festuca tenuifolia	5	Orchis mascula	28
Briza media	75	Filipendula ulmaria	7	Origanum vulgare	2
Bromus erectus	30	Fragaria vesca	42	*Parnassia palustris	3
Bromus mollis	10	Galium aparine	9	Pimpinella saxifraga	67
Campanula glomerata	1	Galium cruciata	23	Pinguicula vulgaris	6
Campanula rotundifolia	57	Galium verum	48	Plantago lanceolata	91
Carduus acanthoides	57	Gentianella amarella	26	Plantago major	1
Carduus nutans	24	Geranium molle	3	Plantago maritima	22
Carex caryophyllea	21	Geranium pratense	3	Plantago media	64
Carex flacca	83	Geranium robertianum	14	Poa annua	35
Carex panicea	7	Geranium sanguineum	3	Poa pratensis	29
Carex pulicaris	12	Geranium sylvaticum	2	Poa trivalis	5
Carlina vulgaris	33	Geum rivale	7	Polygala vulgaris	46
Centaurea nigra	97	Gymnadenia conopsea	18	Potentilla anserina	3
Centaurea scabiosa	66	Helianthemum nummul.	39	Potentilla erecta	14
Centaurium erythraea	11	Heracleum sphondylium	80	Potentilla reptans	43
Cerastium fontanum	44	Hieracium spp.	61	Potentilla sterilis	10
Cirsium arvense	27	Hieracium pilosella	60	*Primula farinosa	4

Table 2.2 continued

SPECIES	Freq	SPECIES	Freq	SPECIES	Freq
Primula veris	82	Serratula tinctoria	2	Trifolium medium	24
Primula vulgaris	1	Sesleria albicans	59	Trifolim pratense	86
Prunella vulgaris	48	Silaum silaus	6	Trifolium repens	43
Pyrola rotundifolia	1	Silene alba	1	Trisetum flavescens	28
Ranunculus acris	55	Silene dioica	2	*Trollius europaeus	2
Ranunculus bulbosus	48	Silene vulgare	4	Tussilago farfara	50
Ranunculus ficaria	9	Sonchus asper	22	Valeriana dioica	2
Ranunculus repens	48	Sonchus oleraceus	10	Valeriana officinalis	1
Reseda lutea	10	Stachys officinalis	27	Veronica chamaedrys	45
Rhinanthus minor	27	Stachys sylvatica	3	Veronica officinalis	11
Rumex acetosella	21	Stellaria graminea	11	Vicia cracca	59
Rumex obtusifolius	3	Succisa pratensis	43	Vicia sativa	6
Sanguisorba minor	70	Taraxacum spp.	90	Vicia sepium	15
Sanicula europea	2	Teucrium scorodonia	3	Viola hirta	26
Scabiosa columbaria	48	Thalictrum minus	3	Viola odorata	8
Sedum acre	3	Thymus praecox .	83	Viola reichenbachiana	1
Senecio erucifolius	3	Torilis japonica	1	Viola riviniana	60
Senecio jacobea	58	Tragopogon pratense	4		

KEY

Freq The Number of Fragments (maximum 98) in which each species occurs

* Those MLG species defined as characteristic and rare (see Section 3.3.1)

Plate 2.2 Photographs of fifteen species characteristic of the MLG community

Arabis hirsuta

Carlina vulgaris

Antennaria dioica

Aquilegia vulgaris

Coeloglossum viride

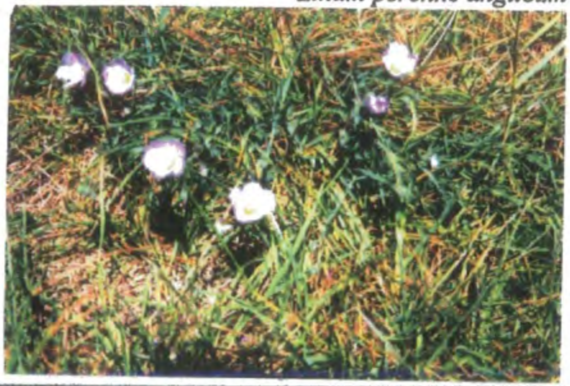
Dactylorhiza fuchsii

Dactylorhiza purpella

Epipactis atrorubens

Plate 2.2 continued


Lotus corniculatus & Polygala vulgaris


Linum perenne anglicum

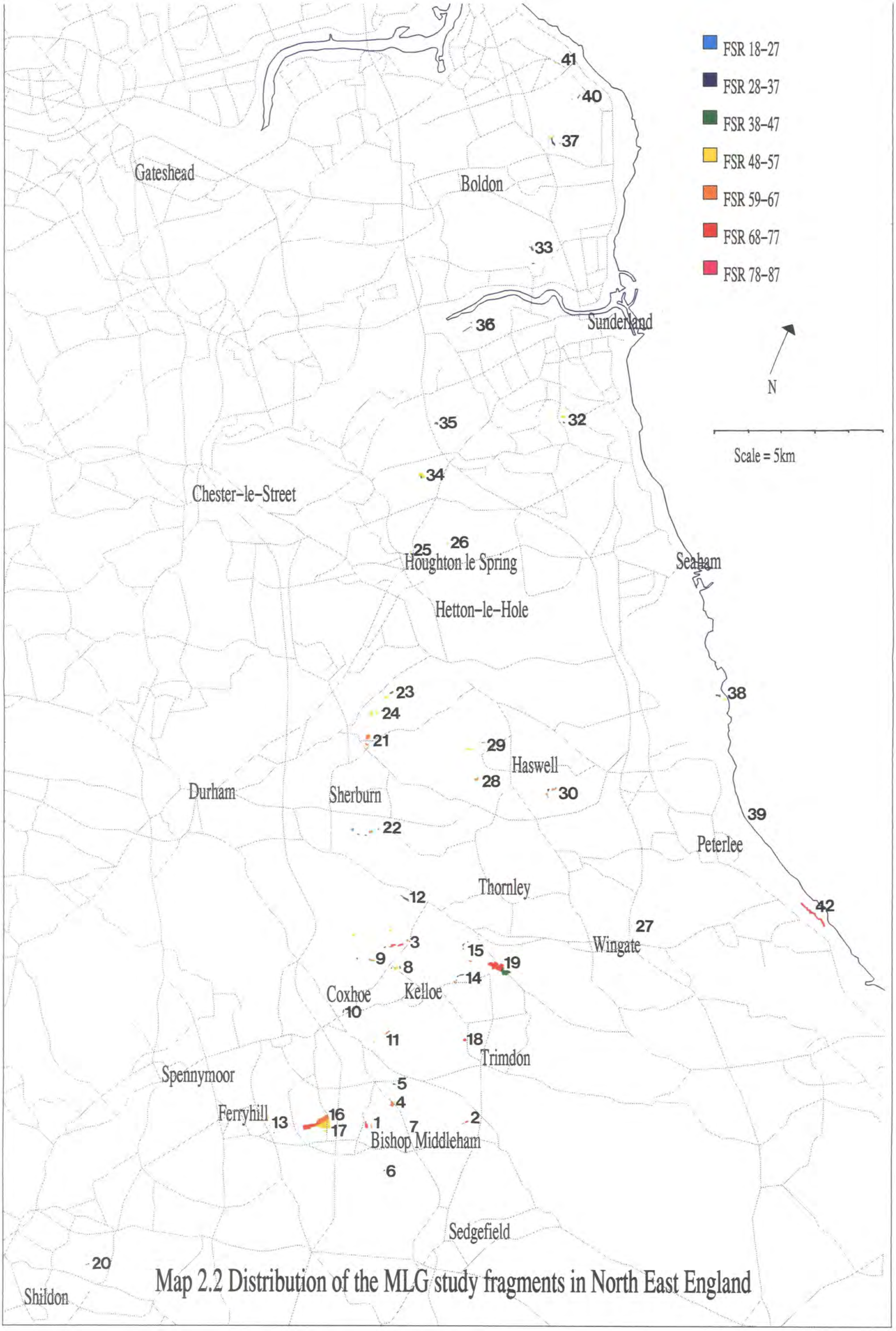

Gymnadenia conopsea


Thymus praecox & Helianthemum


Primula farinosa


Geranium sanguineum & Anthyllis vulneraria


Euphrasia nemorosa



Map 2.2 Distribution of the MLG study fragments in North East England

(vi) After a comprehensive survey of the fragment the overall percentage of bare ground/bare rock was noted along with the number of scrubs (over 0.5 metres high) in a chosen 10m x 10m area. The chosen area was judged to have the least relative scrub cover. Allchin (1993) concluded that scrub density was significant in determining the species composition of MLG;

(vii) Field observations along with documentary evidence, eg. SSSI notifications, were used to decipher the treatment history of the fragment.

A distinction was made between primary habitat of semi-natural origin (areas suffering no major disturbances since historic forest clearance) and secondary habitat effectively of recent origin (which has experienced severe disturbances in the last 200 years, eg. quarrying). Attempts were made to define fragments which were constituted entirely of primary or secondary habitat. However in a few cases this was impossible as primary and secondary habitat were complexly interspersed, eg. at Bishop Middleham. In which case a proportional percentage of each habitat was deciphered.

(viii) In order to assess if any other habitats may influence the species richness of a MLG fragment the presence of any of the following habitats in the adjoining area was noted: Woodland; Neutral Grassland and Acid Grassland. In order to assess whether flushing occurred the presence of a high moss cover or species such as *Juncus articulatus, Carex panicea* or *Carex pulicaris* was used.

Using Comparative Plant Ecology (Grime at al 1988) the dispersal strategy of 164 out of the total 185 species was ascertained. They are all classified in one of three main groups: Wind-Dispersed; Animal-Dispersed and Unspecialised (with morphological dispersal features absent or undetected) see Appendix II. Using this classification the following variables for each fragment were calculated:

(ix) the number of species present which are wind dispersed;

(x) the number of species present which are animal dispersed;

(xi) the number of species present which are unspecialised in their dispersal strategy;

Finally from Graham (1988), the phytogeographic element assigned to each of the 185 species was obtained. Ten elements are present in the total observed flora with 60% of the species placed in the Wide Element (see Appendix II). Wide Element species are characterised by a wide European distribution (inferring broad climatic tolerance and niche space). Many are not exclusively found in calcareous grassland habitat therefore are of less conservational value. In order to gain an indication of the conservation value of each fragment's species the following variable was calculated for each fragment:

(xii) the percentage of observed species which are categorised as Wide Element

Caveat

It was originally intended that the current management regime be recorded for each site. However this was difficult to assess without continual field observations as even at the protected sites the agreed schemes were not followed, especially regarding grazing.

2.3 METHODOLOGY FOR GEOGRAPHICAL INFORMATION SYSTEMS

2.3.1 Obtaining Isolation Parameters

The perimeters of each of the 98 fragments were digitised from a series of 1:10,000 scale maps using a PC (running ARC/INFO Version 3.0). The resulting polygons were labelled and cleaned. These files were then transferred to a workstation running ARC/INFO Version 7.0. Next they were transformed using real world OS co-ordinates and finally built and appended to produce a single coverage of all the fragments. Using the TABLES command the polygon attribute table was unloaded and the area and perimeter of each fragment was obtained. These could be compared with the field estimates to check for inaccuracies in marking the fragments onto the 1:10,000 scale OS map. The command "UNGENERATE" enabled a string of x and y real world co-ordinates for each polygon/fragment to be downloaded into a text file.

Dr. Brian Huntley had written a FORTRAN program which calculated the minimum, mean and maximum distances between all of the 98 fragments from the co-ordinates text file generated by ARC/INFO. The huge data file produced was then processed using a further FORTRAN program. This program used the minimum distance value (thought to be the most ecologically valuable when considering possible interactions between fragments) to list the following parameters for each of the 98 fragments:

xiii) the distance to the nearest neighbour
xiv) the name of the nearest neighbour
xv) the species richness of the nearest neighbour
xvi) the number of fragments within 2.5km*
xvii) the name of the fragments within 2.5km*
xviii) the species richness of each fragment within 2.5km*

By slightly altering the program it could be re-run for a 5km distance to produce additional values for xvi) to xviii).

* The distances 2.5km and 5km were decided on after considering similar studies such as Ouborg (1993). Hanski (1982) suggests that dispersal distances of up to 10km are commonplace for many vascular plant species.

One problem facing this analysis is that no constant mainland pool can be identified within the network of sites. Johnson & Simberloff (1974) suggested that this problem is overcome by calculating the distance from each fragment to an fragment with a flora large enough to act as a significant colonisation source. Therefore the output from both programs was used to calculate:

xix) the minimum distance to a fragment with a species richness of 58 or over (this is the upper inter-quartile value for the species richness of fragments).

Appendix III lists the measured variables for each fragment

In addition to the main analysis which focuses on the fragment- scale, values for i) to viii) and xi) to xix) were then re-calculated for the 42 sites. For example, all the fragments within a site were effectively combined to produce a set of variables for larger scale "site" units. For parameter xix) a species richness of 78 or over was used instead of 58 or over (this is the upper inter-quartile value for the species richness of sites). Appendix IV lists the measured variables for each site.

2.3.2 Producing a map of the study sites (see Map 2.2)

Files containing 1:250,000 Bartholomew map data for the North East of England were imported into the workspace from the server "vega". Three specific attributes were chosen: the coastline; the road network and finally the point-position and names of settlements. In addition a species richness code for each fragment was added to the coverage's polygon attribute file. A macro ".aml" file was then created consisting of a series of commands to apply to the coverage which produces an ".eps" file that can be printed.

Each of the three Bartholomew attributes were superimposed on the coverage and given a colour code. However after viewing the ".eps" file only selected place names were used to prevent the positions of the fragments being concealed. Each fragment was selected according to its species richness (Categories I to VII) and colour coded on a cold to warm spectrum. A key to the species richness scale was then created using a second text file.

2.3.3 Constructing Climate Response Surfaces and simulating future distributions (given the predicted climate change) for three selected species

Sesleria albicans, Bromus erectus and *Thesium humifusum* were selected for this part of the analysis. They were chosen due to their widely differing biogeographic affinities: *Sesleria albicans* is of the Northern Sub-Atlantic element distributed in the North of the UK, West Ireland and Continental Europe's Montane regions (and is close to its UK southern limit in County Durham) see Map 3.5 ; *Bromus erectus* has a Southern Sub-Atlantic element with a wide distribution through Central Europe and is close to its northern limit in County Durham see Map 3.1 ; and lastly *Thesium humifusum* has a current distribution in France, North Spain and South England (it is not currently found in the MLG of N.E England - see Map 3.9).

The distributions of *Sesleria albicans* and *Bromus erectus* have not yet been mapped by Atlas Florae Europaeae (AFE). Therefore maps of their ranges from Meusel, Jäger & Weinert (1965) were transposed onto the 50x50km AFE grid using an ARC/INFO PC program written by Roland Ascroft. The *Thesium humifusum* distribution was obtained from the AFE courtesy of the Botanical Museum Helsinki. For each of these grid cells values for the bioclimate variables : the mean temperature of the coldest month (MTCO-°C); the annual temperature sum >5°C (GDD5-day degrees) and an estimate of the ratio of actual to potential evapotranspiration (AET/PET) were computed for the midpoint and mean elevation (see Huntley et al In Press for full details). By carrying out a locally weighted regression analysis between the species distribution grid and bioclimatic grid a species-specific climate response surface is fitted. The fitted response surfaces can be envisaged as a solid of varying density representing the differing probabilities of the species occurring under any combination of the three variables.

The response surface can be assessed by using it to simulate the current distribution of the species see Maps 3.2, 3.6 and 3.10. As Beerling et al (1995) comment this is analogous to examining a scatter plot to compare a regression line with the data points to which the regression was fitted. However a single comparison of the two maps is impossible as the response surface provides a probability estimate of finding the species under any given combination of bioclimatic values, ie. many different maps can be simulated by choosing different probability thresholds. One hundred alternative simulated distributions were compared with the observed for probability steps of 0.01. Two "descriptors" are calculated for each simulation:

P1 - the proportion of recorded occurrences for which presence was simulated at or above the selected probability threshold.

P2 - the proportion of simulated presences at or above the chosen probability threshold that coincide with recorded occurrences.

The kappa statistic was used to select the best probability threshold for each response surface. The kappa statistic (κ) measures the degree of agreement between the observed and simulated distributions. It can be assessed on a subjective scale (see Montserud 1990 and Prentice at al 1992). The probability threshold which has the maximum κ value is usually very close to that which represents the optimal trade-off between P1 and P2. It must be noted that as the scale of comparison is the individual grid unit (ie. an exact fit was required) all computed values of P1, P2 and κ are conservative compared to those in some studies which use a larger scale of comparison (Prentice et al 1992).

As the simulated distributions for all three species show a significant fit to the observed distributions, the Climate Response Surfaces (CSR) can be used to simulate potential future species ranges under predicted climate scenarios. The Oregon State University (OSU) GCM forecasts that the future doubling of atmospheric CO_2 values and the subsequent radiative forcing will cause a 2.8°C global mean temperature increase along with an 8% increase in global precipitation (Schlesinger & Zhao 1989). In comparison the United Kingdom Meteorological Office (UKMO) predicts that the doubling of CO_2 will result in a 5.2°C global mean temperature rise and a 15% rise in global precipitation (Mitchell 1983). However these global changes obscure strong and consistent regional patterns that amplify or inverse the global changes.

For each GCM cell the predicted control values for mean annual temperature and precipitation are subtracted from the 2 x CO_2 values to gain anomaly values. These values are then smoothed and interpolated for each 50 km x 50 km cell. The interpolated value is added to that observed and the three bioclimatic variables are re-calculated (see Huntley at al, In press). The distribution of each species is then simulated as before given the new bioclimatic variables and mapped using the same probability threshold. As before the degree of fit between the present and simulated distributions for each species can be assessed and described using κ, P1 and P2.

2.4 STATISTICAL METHODS

This section will not detail all the statistical methods used in this study. However it will:

i) state the nature of data transformations used prior to analysis;
ii) describe the procedure used to check that the assumptions imposed by Stepwise Multiple Linear Regression (SMLR) are not violated;
iii) describe a relatively new statistical technique employed - Nested Subset Analysis

2.4.1 Data transformations

Regression analysis assumes that the predictor variables are normally distributed. Therefore the mean and variance of each variable was compared and a histogram drawn. Table 2.3 lists the transformations applied given the nature of any skew and the type of data.

Table 2.3 The transformations applied to the predictor variables relating to fragment and site scales

Variable†	Transformation
(S) Area	Natural Log
(S) Perim	Natural Log
(S) MDNN	Natural Log +1
(S) D58	Natural Log + 1
(S) N5km	Square Root
(S) N2.5km	Square Root
(S) SR2.5km	Square Root
(S)Scrub Density	Square Root
(S) Slope Angle	Square Root
(S)No Adj Hab	Square Root
(S) Aspect	Square Root
(S) % Prim	Arcsin
(S) % BG	Arcsin
(S) % Wide	Arcsin
(S) SRNN	-

† See List of Abbreviations

In order to be consistent the same transformations were applied to variables of the same data type, eg. counts or proportions. Log transformation ensures that any non-linear relationships are transformed to linear relationships. This is important as Multiple Linear Regression only examines for linear relationships between variables.

In any form of regression analysis it is important that data values are standardised to account for differences in scale and measurement units. Otherwise Partial and Beta Coefficients (derived from SMLR) can not be directly compared (Norusis 1993). The calculation for standardising the set of values for each variable is:

(Value - Mean of the Variable) / Standard Deviation of the Variable

If the values have already been transformed then the transformed mean and standard deviation are used.

2.4.2 Stepwise Multiple Linear Regression

SMLR assesses each predictor variable on the unique contribution it makes in explaining the dependent variable (measured by the partial correlation coefficient). Moreover SMLR constructs a model equation which maximises the proportion of variation explained in the dependent variable and minimises the standard error of the estimate. Clearly the ability to produce such results significantly contributes to answering this study's hypotheses.

However James & McCulloch (1990) presented a fierce critique of the use of Multiple Linear Regression and particularly the stepwise selection procedure within ecological studies. This study has taken account of many of their points and adopted many of their recommendations. SMLR should ideally be carried out with predictor variables which are independent, ie. with no inter-correlations. Otherwise a small change in the value of either the predictors or dependent variable could result in a large change in the solution. However the variables which are selected using the stepwise selection procedure tend to be uncorrelated due to the nature of the analysis. Indeed only the selected variables influence the equation. However in order to check that no selected variables are highly correlated two descriptors of co-linearity are checked. The tolerance of each variable must be above 0.50 and no two variables should have high proportions for the same eigenvalue (Norusis 1993).

With regard to James & McCulloch's comments on the stepwise selection procedure, all selection processes (stepwise, forward and backward) choose the same variables as the best predictors of the dependent in this study. Lessons have also been learnt from other studies, Johnson & Simberloff (1974) failed to check for any outlying values which contributed disproportionately to fitting the regression line (McCoy & Connor 1974). In effect all the samples should come from the same population and the removal of any sample should not significantly change the result. In this study this is checked by plotting the covariance ratio, (which estimates the influence of each fragment on the variance of the estimated regression coefficient). Any ratios which exceed 3p/n after 1 is subtracted are examined (p = number of predictor variables in the equation, n = number of observations).

General checks were made by plotting:

(a) the predicted values against the observed dependent values to illustrate the degree to which the variables in the equation predict the dependent;

(b) the residual values against the observed dependent values to gain an indication of the underlying data structure and a histogram of the residuals to determine their distribution;

(c) the partial residuals of the dependent variable against the partial residual of each of the selected independents. This removes the linear effect of other predictor variables from both plotted variables;

Most importantly at no point in this paper will causation be inferred from any of the results or equations produced from SMLR analysis.

2.4.3 Nested Subset Analysis

Species assemblages are said to be nested when the biotas of sites with lower numbers of species tend to be subsets of the biotas at richer sites (Wright and Reeves 1992). This type of analysis has been conducted on both sets of real islands and continental habitat islands. It considers the fate of individual species and the species composition of each "island" in a deterministic manner, ie. interpreting patterns of extinction and survival.

Analysis is performed using the methods of Wright & Reeves (1992), via their *Microsoft*™ BASIC computer program which involves a null hypothesis of equiprobable species. The mathematical details are clearly explained in Wright & Reeves (1992).

Wright & Reeves's "Nc" and "C" are used in preference to the earlier indices "No" and "Ni" as they avoid potential problems posed by "outlier-" and "hole-rich" datasets (Cutler 1991). Further Nc has a clear probability-based interpretation: it counts the number of times that a species presence at a site correctly predicts its presence at richer sites, and sums these counts across species and sites. However "C" is the index which will be used as it is a standardisation of Nc and allows direct comparability between different datasets. Finally Cochran's Q test (a form of χ^2 test) is used to test the significance of any "C" value and z-scores for the difference between values of "C". As the z-scores assume normality a conservative confidence level of 1% will be used to test differences.

CHAPTER THREE: THE RESULTS OF THE ANALYSES

3.1 ANALYSIS OF VARIATION IN SPECIES RICHNESS AT VARYING SCALES

3.1.1 At the Fragment Scale

The first analysis assesses the importance of each measured environmental variable in predicting the variation in species richness across the 98 MLG fragments. Table 3.1 lists the regression values from both the simple and Stepwise Multiple Linear Regression analyses.

Table 3.1: Regression Coefficients (from both simple and multiple analysis) relating each predictor variable to Fragment Species Richness (df=96 and the 5% significance value is +/- 0.17)

Variable †	Simple r value	Signif Level	SMLR Beta Coeff	Signif Level	SMLR Partial R^2 Value
Log Area	0.64	0%	0.53	0%	0.34
SRNN	0.48	0%	0.21	2%	0.08
Log DN	0.10	16%	0.25	1%	0.10
Log D58	-0.47	0%	-0.22	2%	0.04
Log Perimeter	0.60	0%	0.05	N/S	-
Asin Wide	-0.34	0%	-0.05	N/S	-
AVH	-0.29	0%	-0.11	N/S	-
Sqrt N2.5	0.24	1%	-0.02	N/S	-
Sqrt N5	0.24	1%	-0.03	N/S	-
Sqrt SD	-0.20	3%	-0.01	N/S	-
Sqrt SR2.5	0.16	N/S	-0.05	N/S	-
Sqrt H	0.16	N/S	0.05	N/S	-
Asin Prim	0.10	N/S	0.05	N/S	-
Asin BG	-0.08	N/S	0.01	N/S	-
Sqrt A	0.04	N/S	-0.02	N/S	-
Sqrt SA	0.00	N/S	0.00	N/S	-

† All variables were transformed (except AVH and SRNN) and then standardised prior to analysis (see Section 2.4.1 and the List of Abbreviations)

‡ These Beta Coefficients are obtained after the final variable has been selected.

If one compares the two analyses, 9 variables are significantly related in the simple analysis whilst only 4 variables are significant in the multiple analysis. This is due to the fact that SMLR controls for inter-correlations between any predictor variables, ie. duplicated information in the explanation of FSR. This is particularly evident with Log Area and Log Perimeter which are strongly correlated, with a simple "r" value of 0.96. SMLR selects Log Area first as it has the highest coefficient. This causes the beta coefficient of Log Perimeter to decrease dramatically. This also occurs among the closely related "isolation" variables. The selection of SRNN and Log D58 significantly reduces the beta coefficients of Sqrt N2.5 and Sqrt N5.

Figure 3.2: The Relationship between the residuals and observed FSR.

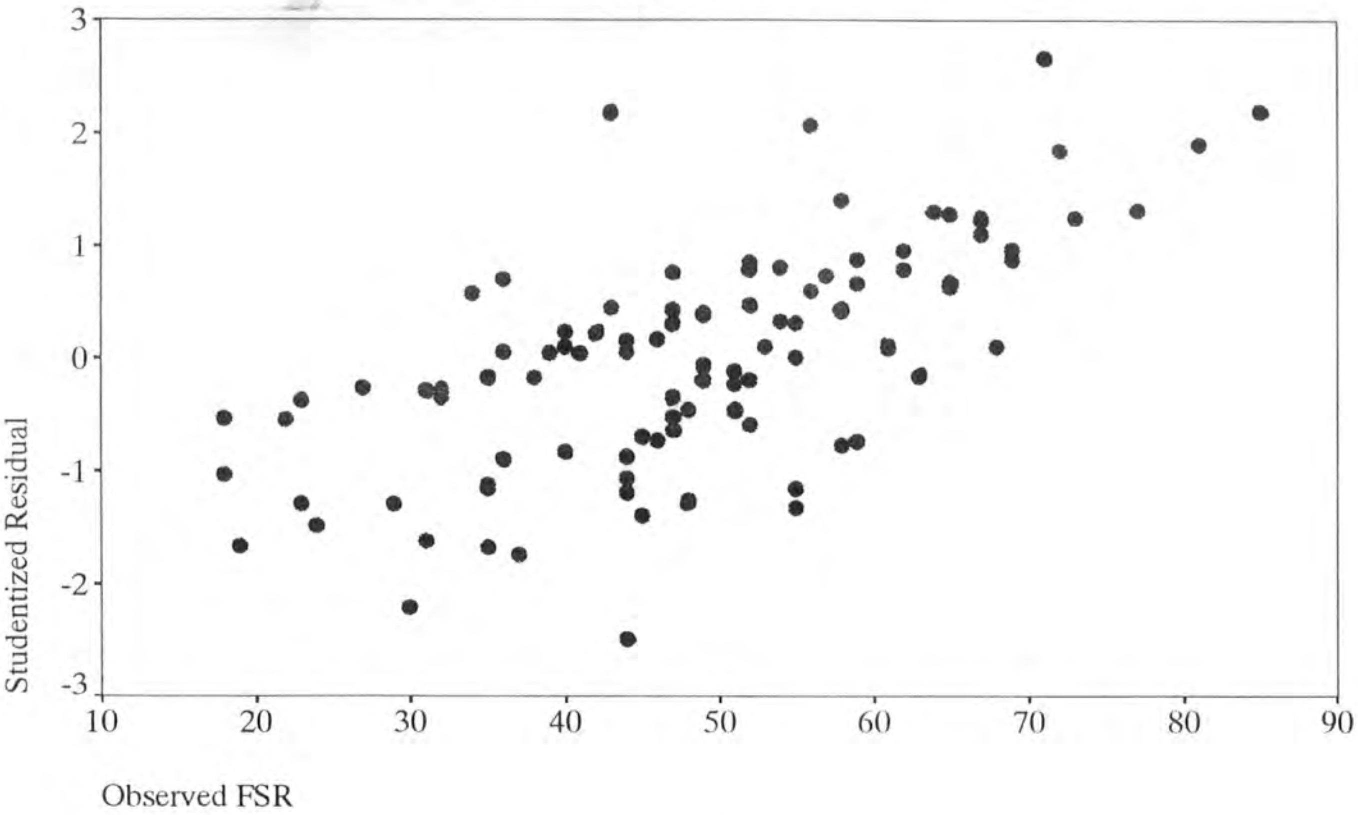
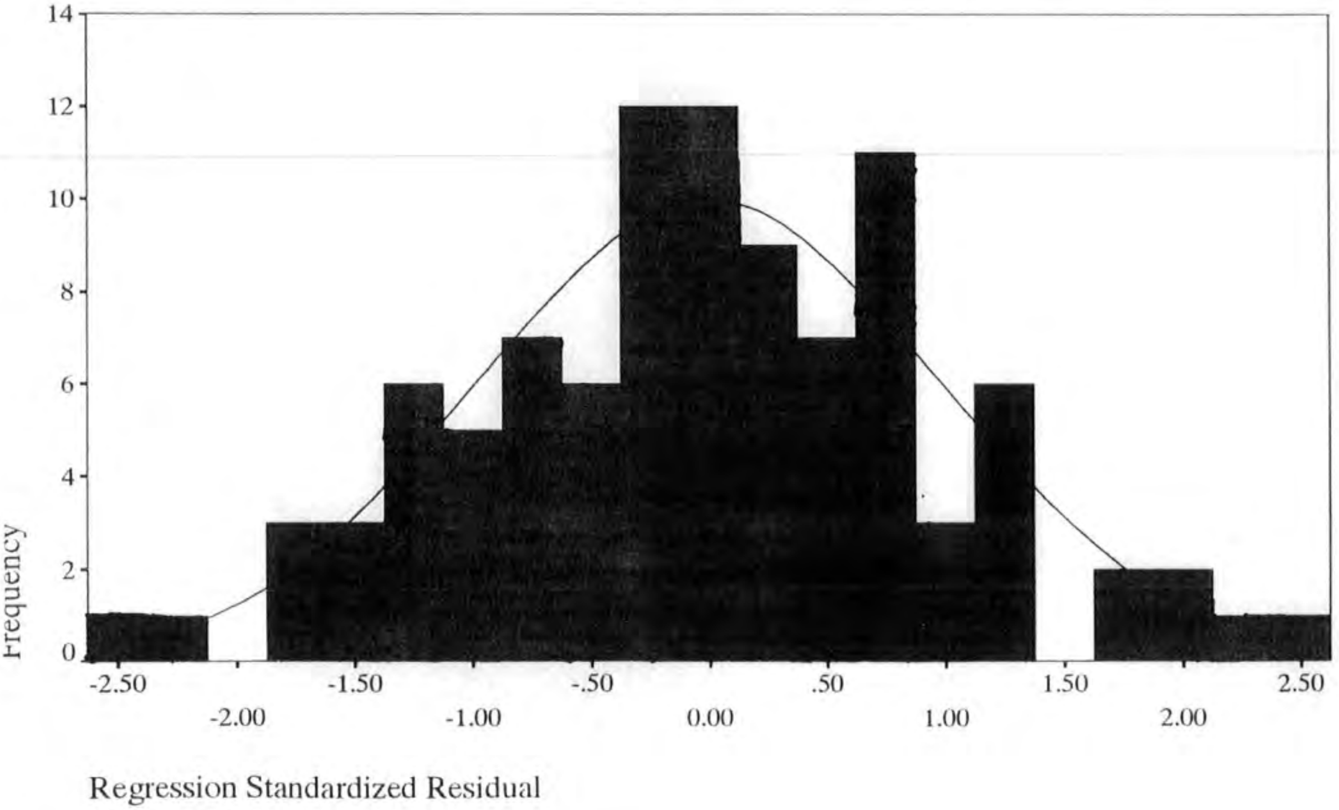


Figure 3.3: The Distribution of the residual values from Equation One



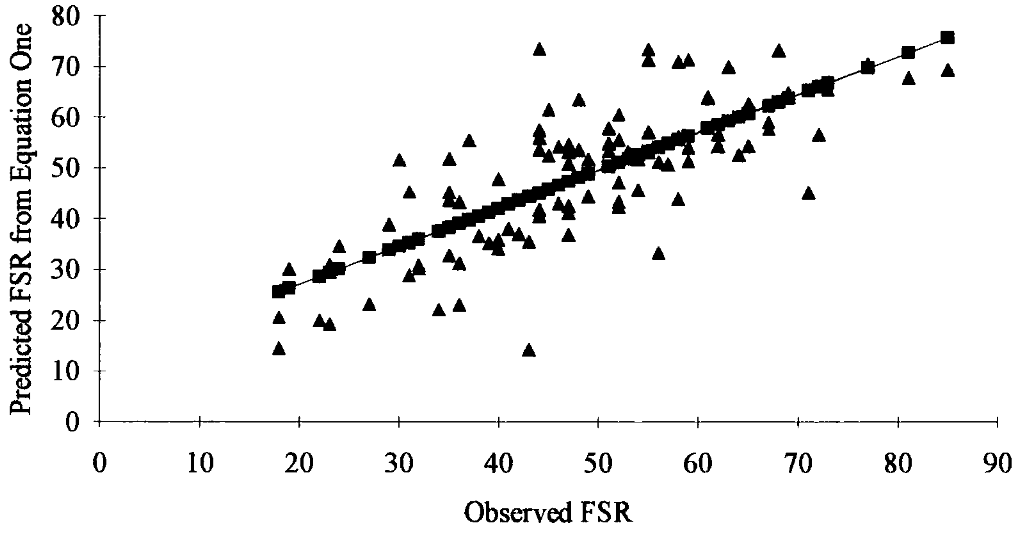
If the above inter-correlations are taken into consideration the results from the simple and multiple analyses are roughly comparable with the exception of Log DN. In the simple analysis this variable has a low, insignificant "r" value whilst in SMLR it is selected to be in the equation. Therefore this particular result must be viewed with caution. Stepwise selection procedure can inflate the importance of variables which to some extent uniquely explain the dependent variable.

The model equation obtained from SMLR analysis for Fragment Species Richness is as follows:

EQUATION ONE: $FSR = 0.53 Log Area + 0.25 LogDN - 0.22 Log D58 + 0.21 SRNN$

The ANOVA F statistic which tests whether there is a linear relationship between FSR and the predictor variables in the equation is significant at a 0% level. The R^2 value for the equation is 0.56 indicating that 56% of the variation in fragment species richness is predicted. Figure 3.1 below illustrates the relationship between predicted and observed FSR.

Figure 3.1: The Regression line for the predicted FSR values against the observed FSR values



However as mentioned in Section 2.4.2 it is important to check that the assumptions associated with SMLR have not been violated. Figure 3.2 shows that there is no distinct pattern in the distribution of the points therefore the underlying data structure is normally distributed. Figure 3.3 indicates that the residuals values, ie. (the predicted FSR values - the observed FSR values) are normally distributed further fulfilling the assumptions made by SMLR.

Figure 3.4 checks for any outlying values which contribute disproportionately to fitting the regression line, in other words constructing the equation. Given the accepted range of $1 \pm 3p/r$ for the covariance (Belsey 1980), the seven circled points are clearly outside this range.

Figure 3.4: Covariance ratio plot for Equation One

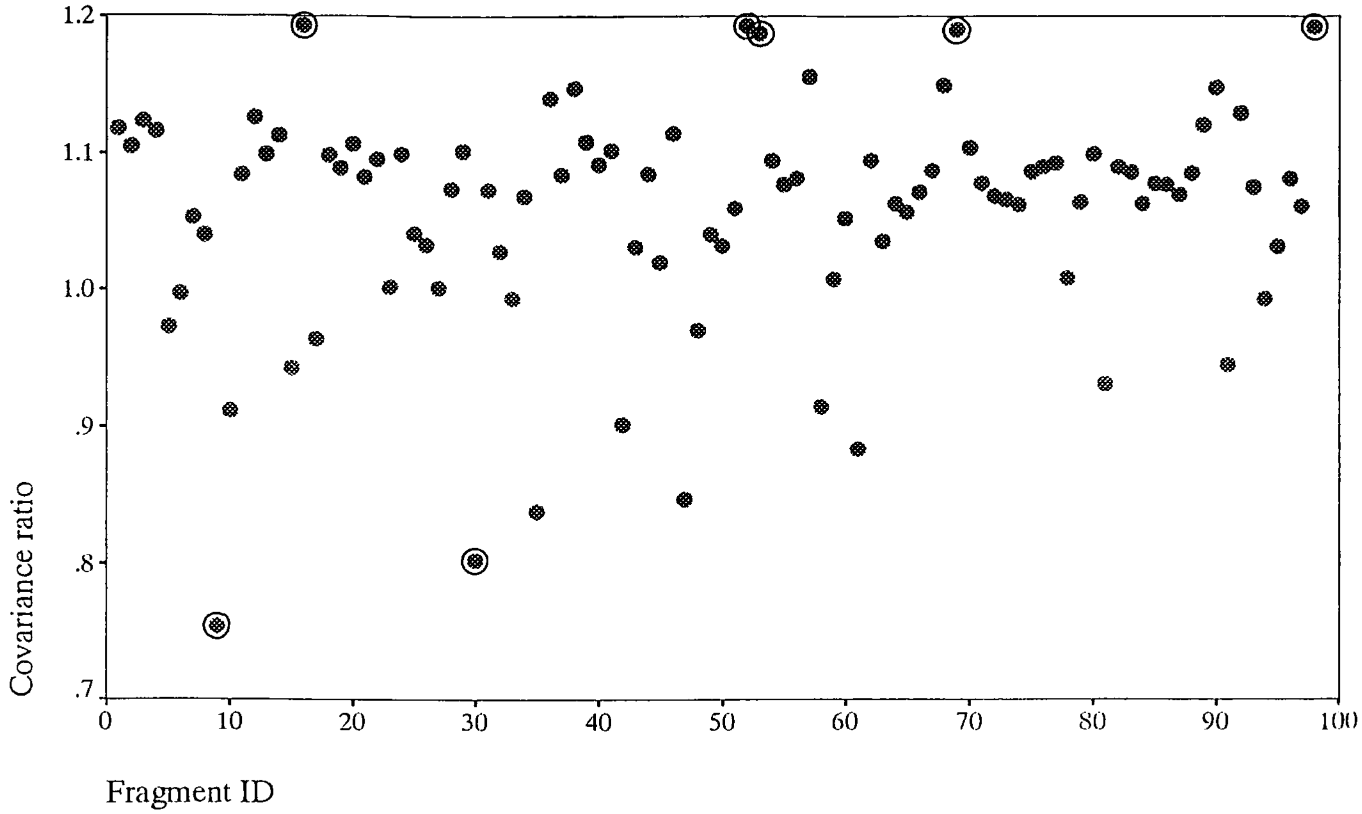


Table 3.2 explores why these seven fragments are clear outliers. This is important as these outlying fragments have a disproportionate role in the fitting of the regression line.

Table 3.2: Listing the values of the equation variables for each of the outlying fragments

Fragment	FSR	Rel FSR†	Area m^2	Rel Area†	DN	Rel DN†	D58 m	Rel D58†	SRNN	Rel SRNN†
Typical		High		High		High ?		Low		High
Typical		Low		Low		Low ?		High		Low
Fishburn B	71	High	482	Low	16	Low	6	V Low	58	High
Blackhall	68	High	33565	V High	3337	High	8374	High	53	Mod
Thris B	59	Mod	21645	High	0	V Low	0	V Low	71	High
Herring A	49	Mod	15317	High	0	V Low	8431	High	38	Low
Wingate B	44	Low	34508	V High	3	Low	3	Low	69	High
Herring B	38	Low	2827	Mod	0	V Low	8471	High	49	Mod
Cleadon B	33	V Low	8093	Mod	0	V Low	19546	V High	56	High

† Means and Variances for all the variables are given in Appendix III

Figure 3.5: Partial Regression Plot of the dependent variable FSR against the most important predictor variable Log Area.

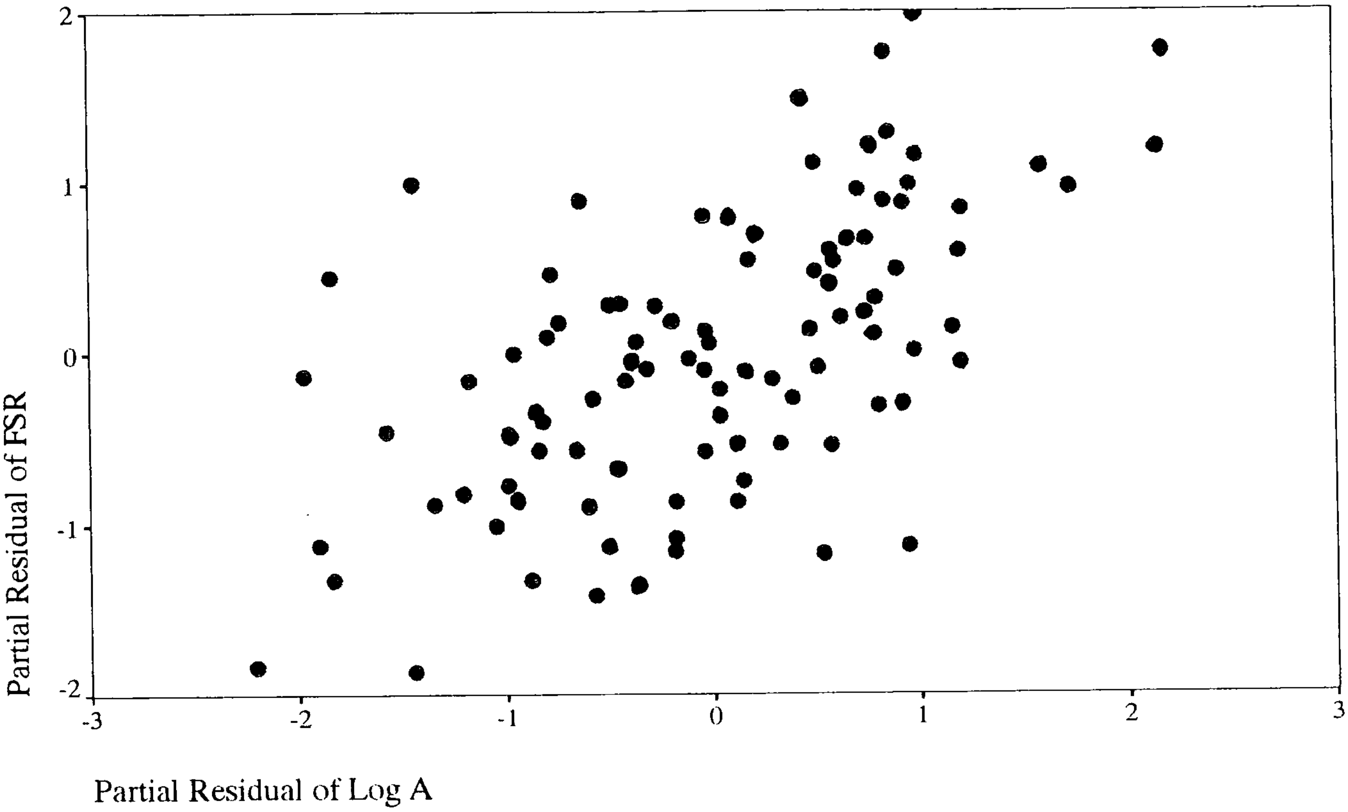
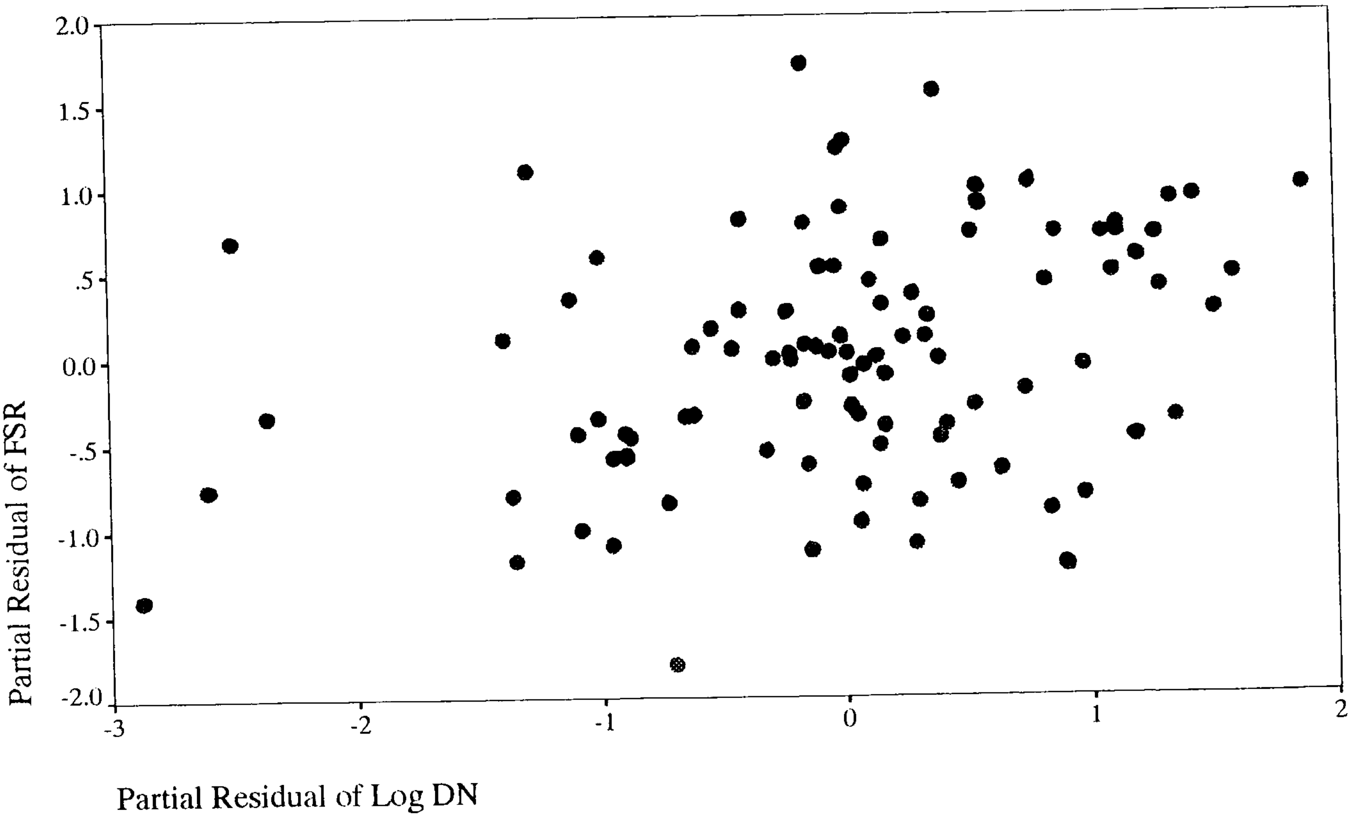


Figure 3.6: Partial Regression Plot of the dependent FSR variable against the anomalous Log DN



Further checks reveal no evidence to suggest that there is a high degree of co-linearity among the selected equation variables. None of the equation variables have a tolerance of below 0.5 or share high values for any one eigenvalue. (This occurred for all of the SMLR analyses included in this paper, eg all QSR tolerances were above 0.75 and all SSR above 0.90 see Sections 3.1.2 and 3.1.3.)

Only after these comprehensive checks are conducted in relation to the SMLR results can inferences be drawn or the findings investigated further. Partial regression plots are a useful tool as they remove the linear effect of other predictor variables from both plotted variables. Therefore by calculating the R^2 value for each Partial regression plot the relative importance of each variable in the equation can be more clearly assessed. (Beta coefficients values are influenced by the other variables in the equation.) In Figure 3.5 the R^2 value between the two variables is equal to 0.34 which is the proportion of the FSR variation not predicted by any other variable but Log Area. This is to be compared to lower Partial R^2 values of (SRNN), (Log D58) and (Log DN) (See Table 3.1). All four Partial regressions lines fit significantly at a 5% level using ANOVA F values.

From both Equation 1 and the calculated Partial R^2 values, Area has by far the most important role in explaining variation in fragment species richness (followed by three variables associated with the degree of isolation of the fragment). However from Figure 3.6 it is evident that several "outliers" play a disproportionate role in determining the regression equation. Furthermore the total R^2 value for the equation is 0.56 leaving a significant proportion of the variation in FSR unexplained. No habitat variables as such are significant at this scale.

3.1.2 At a Quadrat Scale (0.25m^2)

The part of the analysis uses species richness within a 0.5m x 0.5m area as the dependent variable. It must be noted that values of the predictor variables are identical to those used for the FSR regression analysis, ie. they do not specifically relate to the quadrat scale. Table 3.3 lists the results for this scale of analysis.

Table 3.3: Regression Coefficients (from both simple and multiple analysis) relating each predictor variable to quadrat species richness (df =96 and the 5% significance value is +/- 0.17)

Variable †	Simple r value	Signif Level	SMLR Beta Coeff‡	Signif Level	SMLR Partial R^2 Value
Log Area	0.55	0%	0.38	0%	0.17
AVH	-0.39	0%	-0.32	0%	0.13
Asin BG	-0.20	3%	-0.21	2%	0.07
Log D58	-0.45	0%	-0.20	3%	0.05
Log Perimeter	0.50	0%	0.07	N/S	-
SRNN	0.38	0%	0.12	N/S	-
Sqrt N2.5	0.24	1%	0.00	N/S	-
Asin Wide	0.24	1%	0.03	N/S	-
Sqrt SR2.5	0.23	1%	0.03	N/S	-
Sqrt SD	-0.21	2%	-0.12	N/S	-
Sqrt A	0.20	2%	0.10	N/S	-
Asin Prim	0.20	3%	0.10	N/S	-
Sqrt N5	0.14	N/S	-0.03	N/S	-
Sqrt H	0.14	N/S	0.09	N/S	-
Sqrt SA	0.09	N/S	0.10	N/S	-
Log DN	-0.05	N/S	0.12	N/S	-

† See Table 3.1
‡ See Table 3.1

Twelve variables are significantly correlated in the simple analysis whilst only 4 variables are significant in the multiple analysis (presuming a 5% level). As before the explanation for this difference hinges on a number of inter-correlations between the predictor variables. With the exception of Asin BG, the variables which are significant in the multiple analysis are amongst the top four most significant values for the simple analysis. Two more significant inter-correlations are evident (in addition to those mentioned in Section 3.1.1): Asin BG and Asin Prim ($r = -0.38$); Log A and Asin Wide ($r = 0.37$). Therefore primary habitats are associated with low levels of bare ground and larger fragments lower percentages of Wide Element species.

Figure 3.8: The Distribution of the Residual values from Equation Two

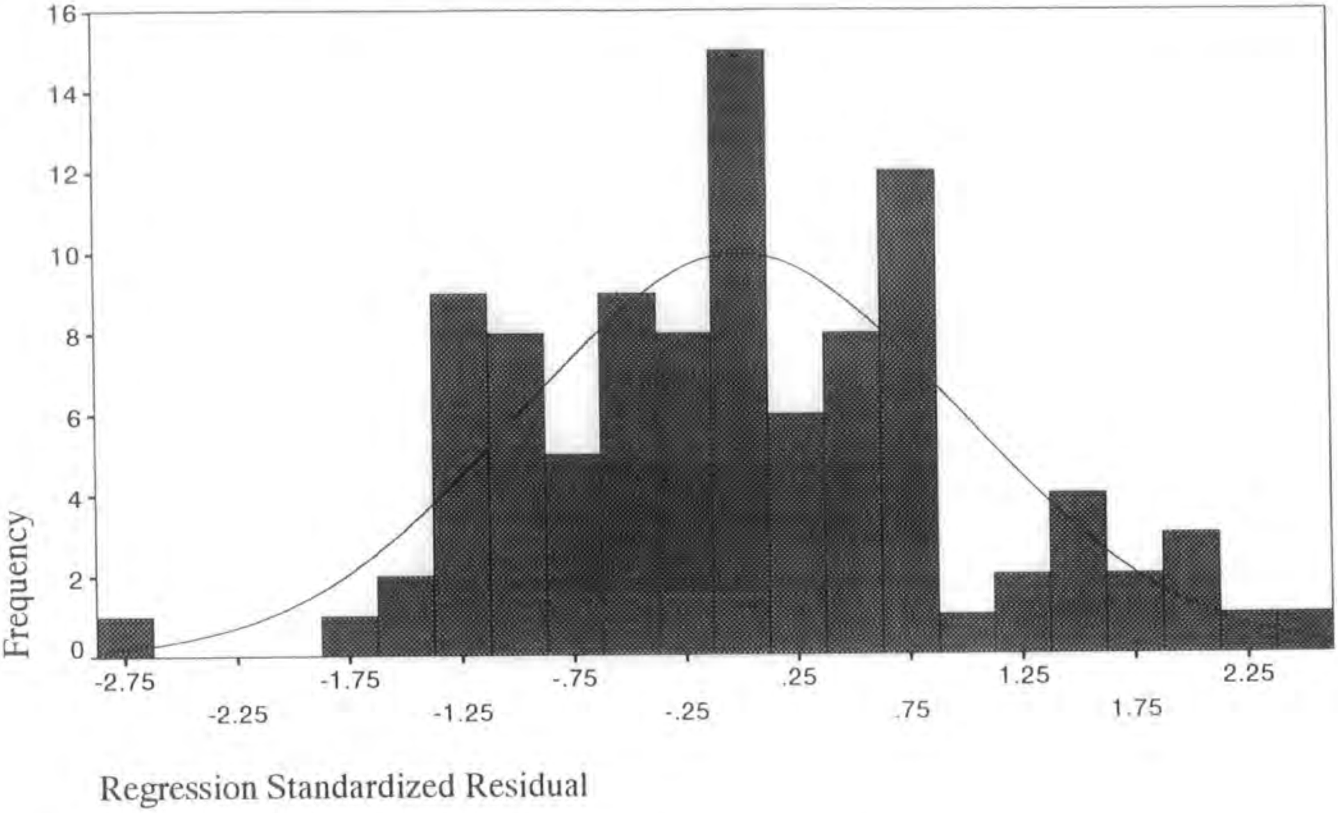
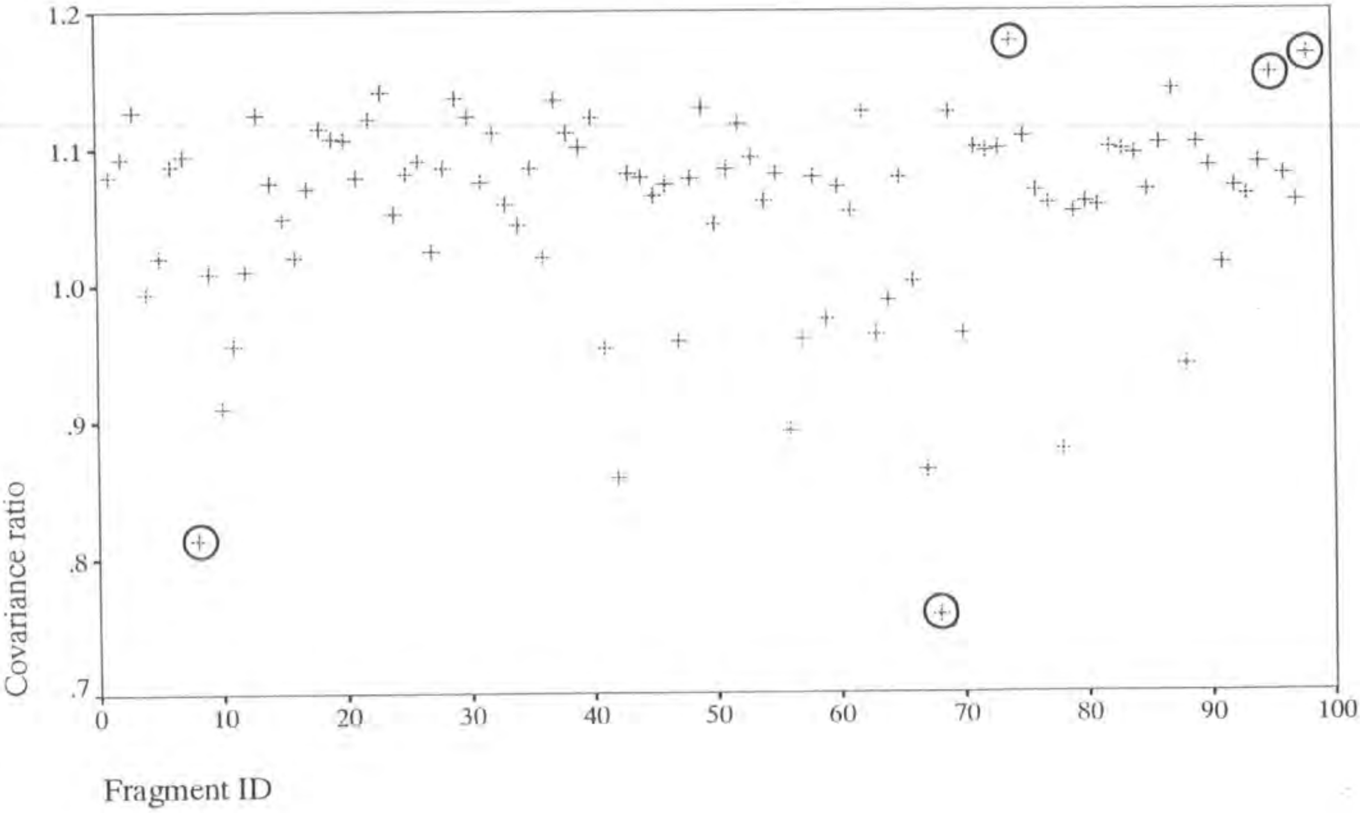


Figure 3.9: Covariance ratio plot for Equation Two



The model equation obtained from the SMLR analysis for Quadrat Species Richness within each fragment is as follows:

EQUATION TWO: $QSR = 0.38 \, Log\, A - 0.32\, AVH - 0.21\, Asin\, BG - 0.20\, Log\, D58$

The F-statistic for the regression equation is 20.00 which is significant at a 5% level, ie. there is a significant linear relationship between QSR and the predicted values calculated from Equation Two (see Figure 3.7). The R^2 value for the equation is 0.46.

Figure 3.7: The Regression line for the relationship between predicted QSR values against those observed in the field

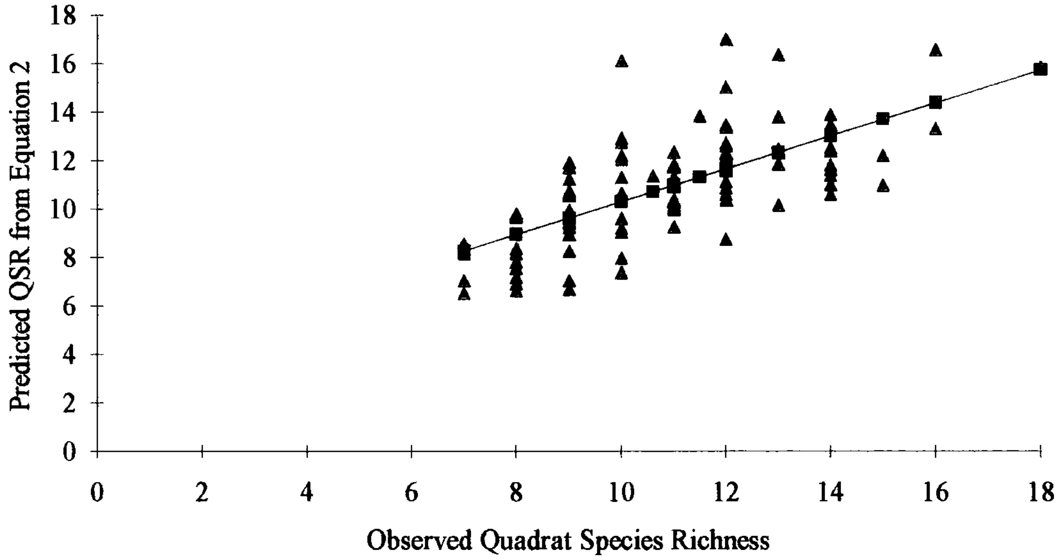


Figure 3.8 adjacent indicates that the SMLR regression residuals are distributed approximately normally.

Figure 3.9 adjacent shows that there are five clear outliers (they are circled). These points disproportionally influence the fitting of the regression line. The reasons why these fragments may be "atypical" are explored in Table 3.4 overleaf and discussed in Section 3.1.3.

In order to assess the relative importance of each variable in Equation 2 the R^2 values for each partial regression plot are calculated. (The plots are not illustrated to save space). The R^2 values for the partial regressions of the equation variables against QSR are listed in Table 3.3.

Table 3.4: Values for each Equation variable for the five outlying fragments identified in Figure 3.9

Fragment	QS R	Rel QSR†	Area m^2	Rel Area†	AV Hcm	Rel AVH†	BG %	Rel %BG†	D58 m	Rel D58†
Typical		High		High		Low		Low		
Typical		Low		Low		High		High		
Fishburn A	15	High	229	V Low	13	High	5	Low	16	Low
Thornley B	12	High	815	Low	7	V Low	50	V High	472	Low
Blackhall	11	Low	33565	V High	20	High	15	Mod	8374	High
Thris B	10	V Low	21644	High	9	Low	5	Low	0	V Low
Isl Farm A	9	V Low	925	Low	22	V High	40	High	1357	Mod

† Means and Variances for all the variables are given in Appendix III.

3.1.3 At a Site Scale

As in Sections 3.1.1 and 3.1.2 simple and multiple linear regression analyses were used in order to assess how well the predictor variables explain species richness at a site scale (see to Table 3.5 below). However there is a notable difference from the two previous analyses, new values for the predictor variables have been calculated to correspond to the larger spatial scale (see Appendix IV for the raw data values corresponding to each of the 42 sites)

Table 3.5: Regression Coefficients (from both single and multiple analysis) relating each predictor variable to Site Species Richness (df = 40, the 5% significance value is +/- 0.27)

Variable†	Simple r value	Signif Level	SMLR Beta Coeff‡	Signif Level	SMLR Partial R^2 Values
S Log Perim	0.61	0%	0.55	0%	0.26
S Sqrt N2.5	0.41	0%	0.29	3%	0.13
S Log Area	0.60	0%	0.03	N/S	-
S AVH	-0.37	1%	-0.22	N/S	-
S Sqrt N5	0.34	2%	0.05	N/S	-
S Log D78	-0.33	2%	-0.11	N/S	-
S SqrtSR2.5	0.30	3%	-0.21	N/S	-
S Log DN	-0.28	4%	0.22	N/S	-
S Asin Prim	-0.14	N/S	0.01	N/S	-
S Asin Wide	-0.09	N/S	0.04	N/S	-
S Sqrt H	0.08	N/S	0.14	N/S	-
S SRNN	0.06	N/S	0.04	N/S	-
S Sqrt SA	0.04	N/S	-0.04	N/S	-
S Sqrt SD	0.04	N/S	0.11	N/S	-
S Asin BG	0.01	N/S	-0.05	N/S	-

† See the List of Abbreviations
‡ See Table 3.1

Figure 3.11: The Distribution of the Residual Values from Equation Three

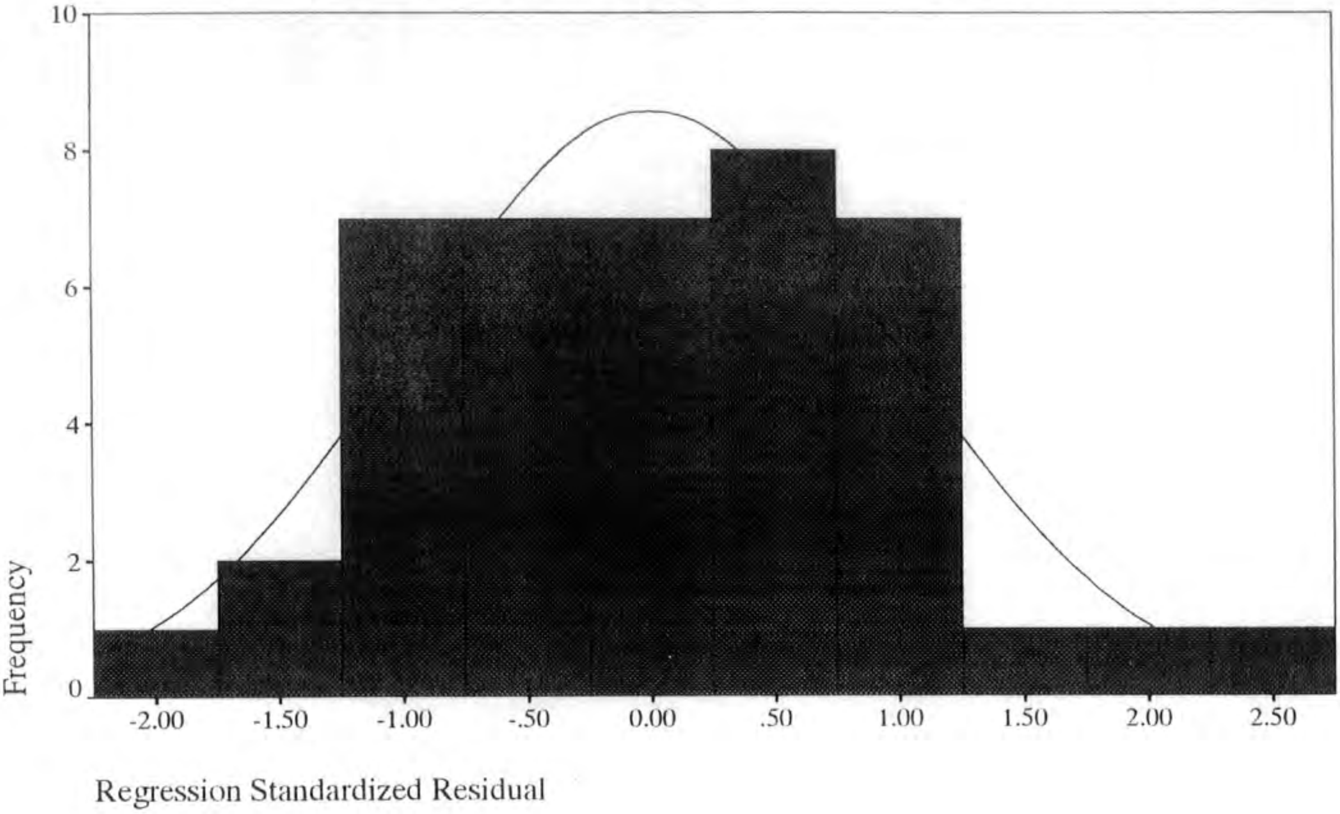
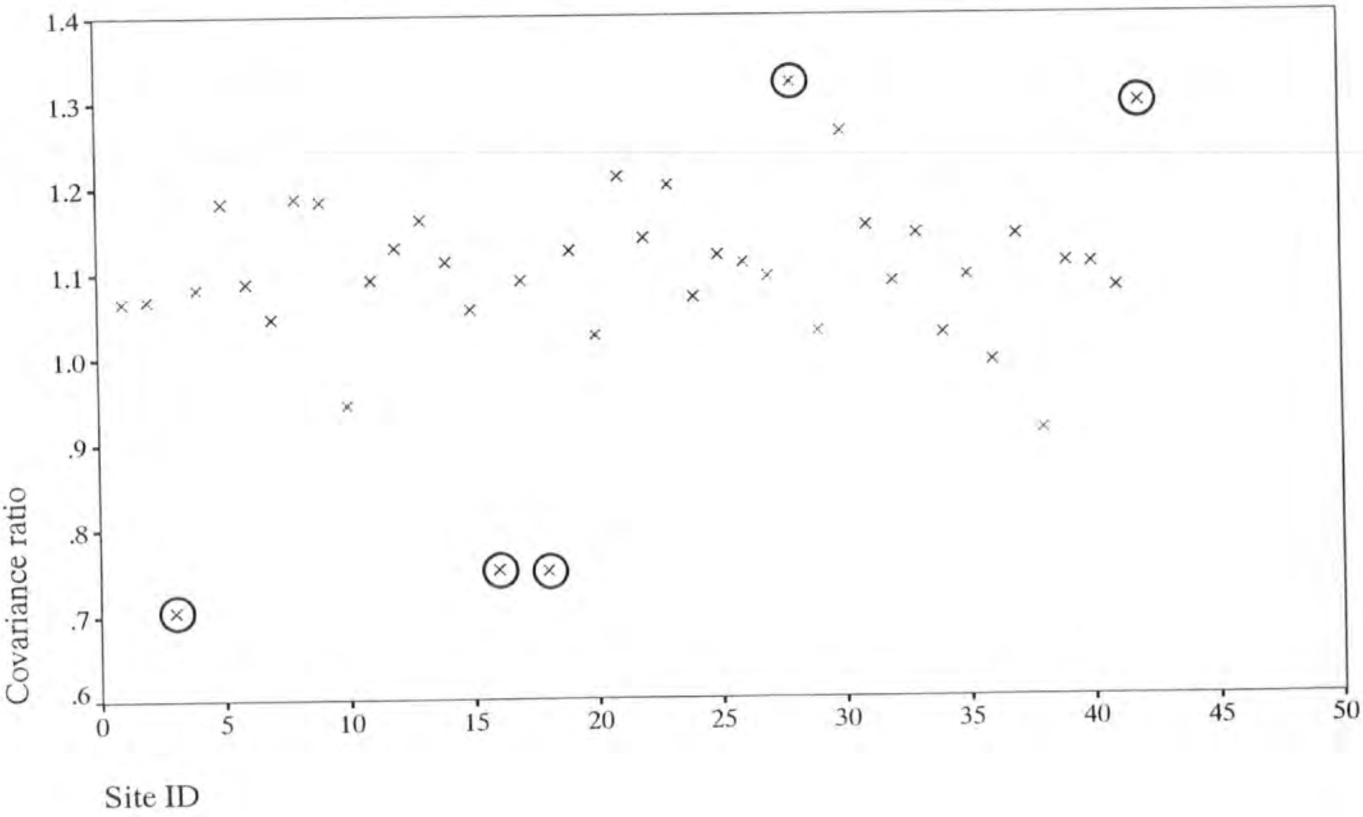


Figure 3.12: Covariance Ratio Plot for Equation Three



If one compares the simple and multiple analyses, 8 variables are significantly correlated in the simple analysis whilst only 2 are significant at a 5% level in the multiple analysis. This can be explained by the inter-correlations between Log Area and Log Perimeter and the six isolation variables, detailed previously. Aside from Log Area, the two variables selected by SMLR as the most significant in predicting SSR, also have the highest simple "r" values.

The model equation obtained from SMLR analysis for SSR is as follows:

EQUATION THREE: = *0.55 Log Perimeter + 0.29 Sqrt N2.5*

The F-statistic is significant at a 5% level and the R^2 value of the equation is 0.45. Figure 3.10 illustrates the relationship between predicted and observed SSR.

Figure 3.10: The Regression line for the predicted SSR values against those observed.

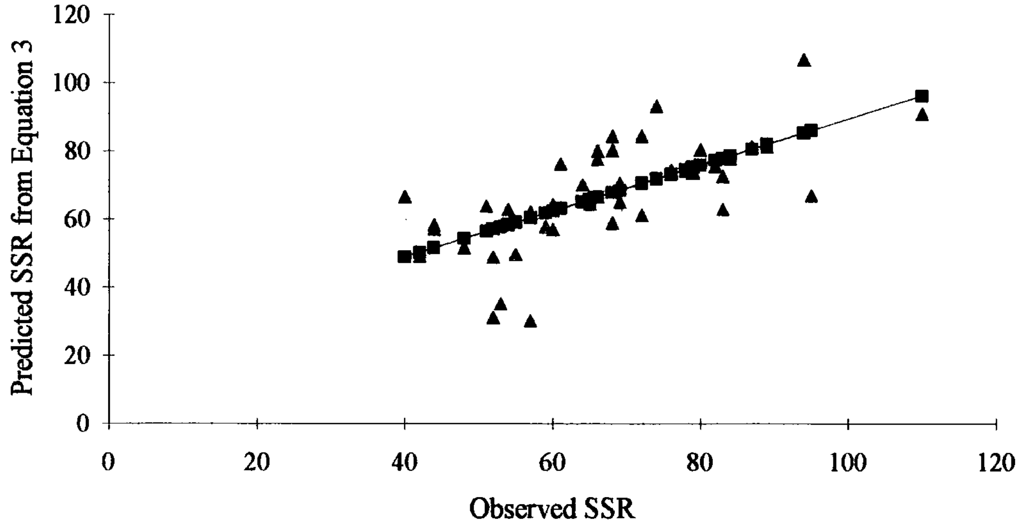


Figure 3.11 adjacent illustrates that the residual values have an approximate normal distribution. Secondly the covariance value for each study site is plotted in Figure 3.12 adjacent. The five outlying values are circled

The reasons why these sites have atypical covariance ratios are explored in Table 3.6

Table 3.6: The values of the Equation 3 variables for each of the five outlying sites

Site	SSR	Rel SSR†	Perim (m)	Rel Perim†	N 2.5	Rel N2.5†
Typical		High		High		High
Typical		Low		Low		Low
Cassop	110	V High	1524.10	Mod	17	V High
Fishburn	95	V High	374.27	Low	6	Low
Thrislington	94	High	4386.43	High	12	High
Blackhall	68	Mod	2414.96	High	0	V Low
Garmond Tri	40	V Low	264.89	V Low	15	V High

† Means and Variances of each variable are listed in Appendix IV

Three of the above sites include fragments which have been identified as outliers in both the previous regression analyses: Fishburn; Thrislington; and Blackhall (see Tables 3.2 and 3.4). Blackhall appears to have a depauperate species richness at all three scales given the equations produced. In contrast the Fishburn site seems to have an over-saturated species richness at all three scales. Finally Thrislington has an over-saturated species richness at a site scale. However one of its fragments "B" has a depauperate species richness at a quadrat and fragment scale.

The relative importance of each variable in Equation Three can be assessed from the Partial R^2 values shown in Table 3.5.

Comparison of the FSR, QSR and SSR Regression Results

The simple correlation coefficients between the three scales are as follow: FSR / Sqrt QSR equals 0.69; FSR / SSR equals 0.54 and Sqrt QSR / SSR equals 0.50 (all are significant at both a 1% and 5% level). It is of no surprise that Sqrt QSR / SSR has the lowest coefficient, ie. weakest relationship, as QSR and SSR are at either end of this scale spectrum. However what is interesting is that FSR is more highly correlated with small scale QSR as opposed to the larger scale SSR.

The SMLR results differ quite markedly between the scales. Log Area is obtained as the most important variable in predicting the variation in FSR and QSR however Log Perimter is obtained for SSR. This may be a result of the way perimeter was calculated for each site - it may have been overestimated. This aside there are still significant differences, Log Area has a much higher beta and Partial R^2 value in the FSR regression as opposed to the QSR, eg. 0.34 compared with 0.17. This is logical since the quadrat data is for such a small scale and the size of the larger fragment has a reduced influence on smaller scale species richness. Secondly different "isolation" variables are significant in Equation Three (Sqrt N2.5) as opposed to Equations One and Two (Log D58/Log DN/SRNN). Though all isolation variables are of secondary importance to either Log Area or Log Perimeter in predicting SSR.

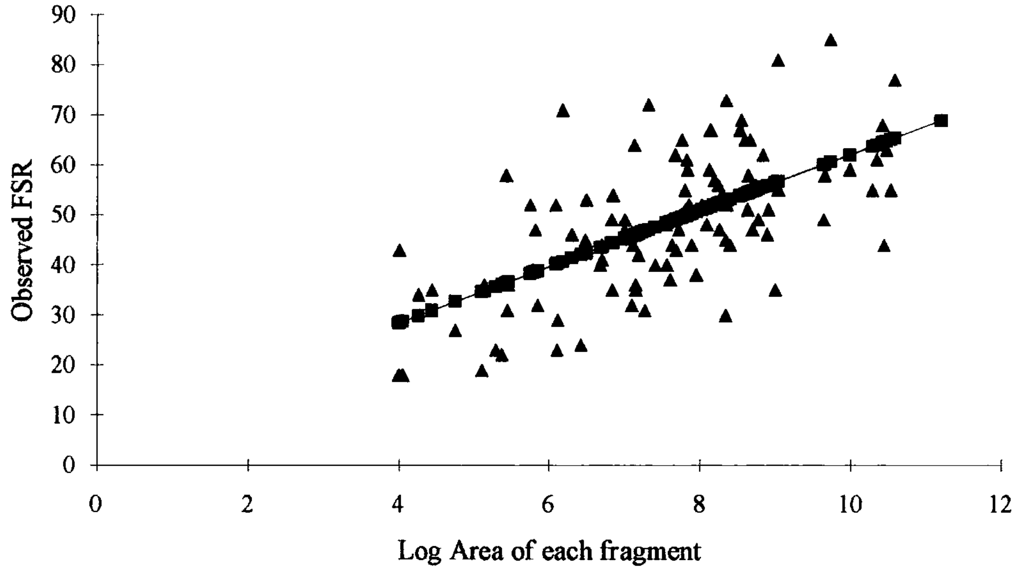
Perhaps the most interesting difference is the fact that a large number of "habitat variables" are significant in the QSR regression, ie. Percentage of Primary Habitat. Furthermore two "habitat" variables (%BG and AVH) are included in Equation Two and have Partial R^2 values of 0.13 and 0.07 both of which are not much less than Log Area. Indeed the variable %BG does not even have a significant simple correlation coefficient with FSR.

Finally, it must be noted that the total R^2 value (ie. the percentage of variation of the dependent variable predicted) is lower for Equation Two (0.46) and Equation Three (0.45) than for Equation One (0.56). This suggests that the measured variables predict the greatest proportion of the variation in species richness at the fragment scale. This supports the choice made to focus on FSR as the dominant scale in this study.

3.2 ANALYSIS OF THE SPECIES/AREA RELATIONSHIP

In order to explore the relationship between area and species richness at a fragment scale several further analyses are performed. In this study it appears that the relationship between species richness and area is not a classic Power Function relationship but of exponential form (SR = C + ZLog A) (McGuiness 1984) see Figure 3.13. The regression residuals were plotted against Log Area and showed no identifiable pattern hence the underlying dataset can be assumed to be normally distributed.

Figure 3.13: Simple Regression line between FSR and Log Area



The R^2 value is 0.40 which is significant at a 5% level as it has a high F-statistic of 64.87.

The predicted values calculated for the simple regression between Fragment Species Richness and Log Area can be used to produce what Reed (1981) terms the Saturation Values for each fragment. The calculation is as follows:

Saturation Value ={Actual Species Number/Predicted Species Number x 100} -100

This indicates if a fragment has either a higher (SV=1 to 100) or lower (-1 to -100) species richness given its Log Area. A value of zero indicates that the a fragment's observed species richness is equal to that predicted by Log Area. The Saturation Values for each fragment are illustrated in Figure 3.14 overleaf.

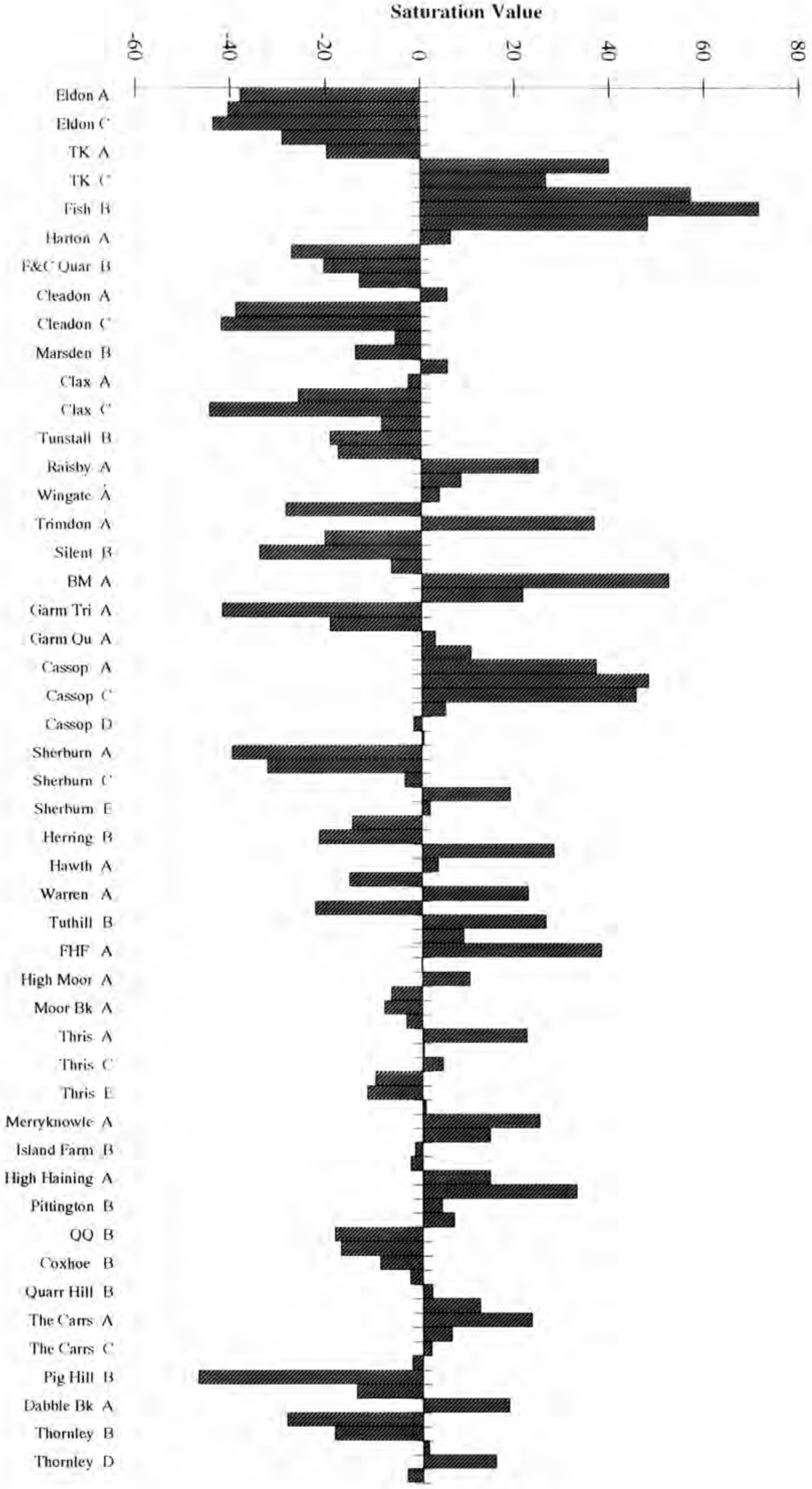


Figure 3.14 : The Saturation Values for each fragment

The following fragments are either over-saturated or under-saturated by more than 30%:

Over-Saturated	Under-Saturated
Town Kelloe B	Eldon A, B&C
Fishburn A, B&C	Cleadon B&C
Trimdon	Claxheugh C
Bishop Middleham A	Silent Bank B
Cassop A, B&C	Garmondsway Triangle A
Field House Farm A	Sherburn A&B
Pittington A	Pig Hill B

Secondary sites which have been severely disturbed in the last 150 years may be expected to have depauperate floras for several reasons: colonisation and succession are still in their early stages; as a consequence of disturbance soil chemistry may have changed to favour competitive ruderal species which quickly become dominant, eg. *Epilobium angustifolium* (Doody 1977). However there is no significant relationship between the Saturation Value and the %Prim.

Finally in this section, two cumulative species-area curve are drawn (see Figure 3.15 overlaef) which represent: (i) the number of cumulative species on the most subdivided subset of habitat patches (largest number with smallest average area) with (2) the cumulative number on the least subdivided subset (smallest number and largest average size) (Quinn & Harrison 1988). If the spatial structure of the habitat sampled did not affect species richness the two curves would be identical. However as can be seen below, the small to large curve (representing (i)) rises at a quicker rate than the large to small (representing (ii)) and is consistently above it. This would appear to suggest that many small fragments are likely to have a greater total species richness than a few large ones.

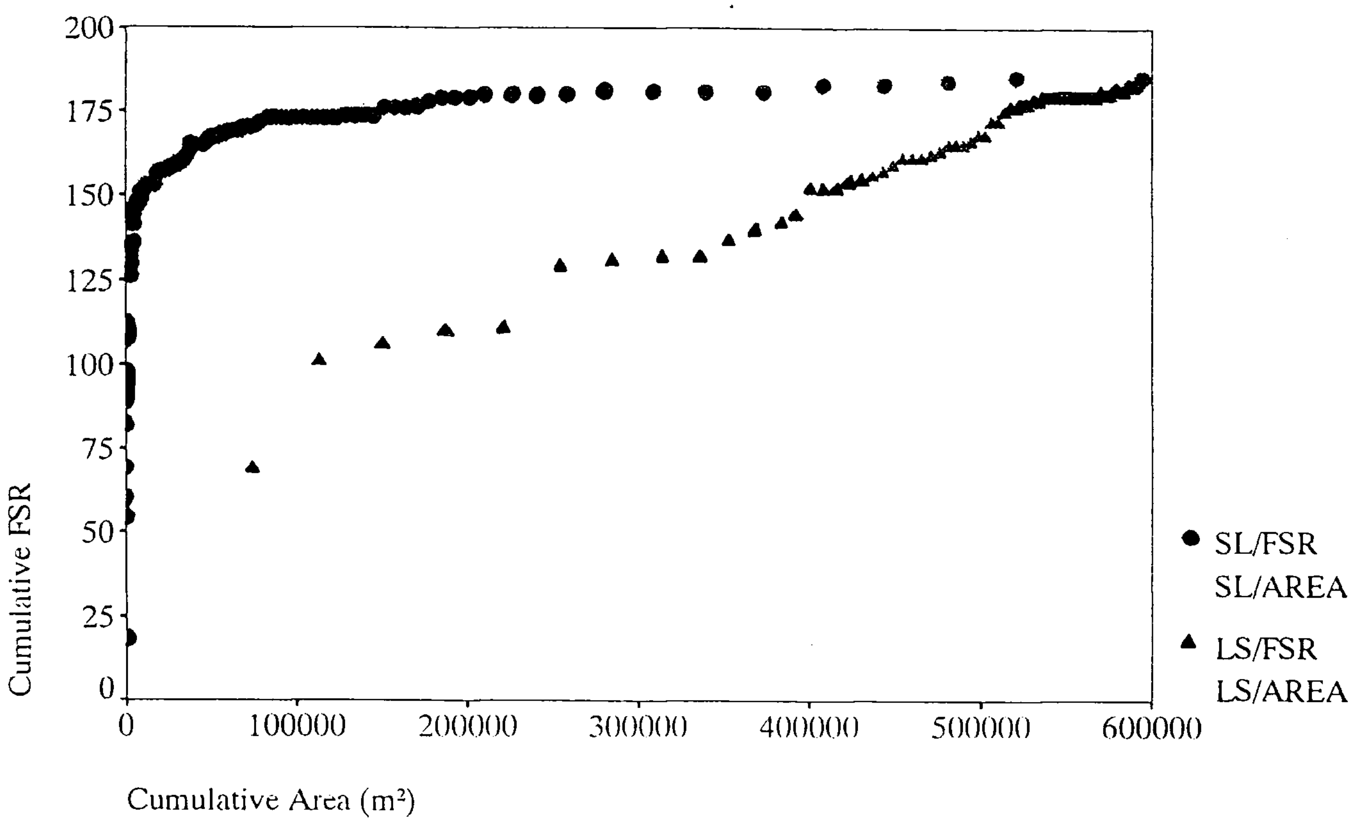
However there are 24 species which do not occur in any fragment with an area less than 2000m^2. (Approximately half the studied MLG fragments have an area of less than 2000m^2). The names of these species are as follows:

**Antennaria dioica*
**Aquilegia vulgaris*
**Arabis hirsuta*
Barbarea vulgaris
Campanula glomerata
Cochlearia officinalis
Crepis capillaris
**Epilobium montanum*
**Linum perenne anglicum*
**Parnassia palustris*
**Pinguicula vulgaris*
Plantago major
Poa trivalis
**Primula farinosa*
Pyrola rotundifolia
Tragopogon pratensis agg.

**Epipactis palustris*
**Erigeron acer*
Festuca tenuifolia
Geranium sanguineum
**Trollius europaeus*
**Valeriana dioica*
Valeriana officinalis
Viola reichenbachiana

The starred species are restricted to MLG habitat in the lowlands of County Durham and Tyne & Wear (Graham 1988).

Figure 3.15: Two Cumulative Species/Area Curves



3.3 ANALYSIS OF SPECIES RICHNESS WITHIN SUBSETS OF THE TOTAL FLORA

3.3.1 Regression results for different species subsets subdivided by dispersal mechanism and low regional occurrence

As mentioned in Section 2.2, 164 species out of a total flora of 185 were subdivided into one of three categories: Animal-Dispersed ; Wind-Dispersed (WD) and Unspecialised. For each fragment, the number of species animal-dispersed (ADSR); wind-dispersed (WDSR) and unspecialised (UDSR) was calculated. Three separate simple regression analyses were then conducted with the dependent variable as one of the three categories and the same predictor variables in FSR and QSR. Table 3.7 lists which predictor variables are significantly related to species richness within each dispersal subset.

Table 3.7: Regression Values relating each predictor variable to species richness within different dispersal categories (df = 96, the significance level at 5% is +/- 0.17)

Variable	UDSR- R	UDSR - R^2†	ADSR- R	ADSR - R^2†	WDSR - R	WDSR - R^2†
Log Area	0.54	0.29	0.58	0.34	0.54	0.29
Log Perim	0.54	0.29	0.53	0.28	0.49	0.24
Asin Wide	-0.35	0.12	-0.31	0.10	N/S	-
SRNN	0.33	0.11	0.46	0.21	0.45	0.20
Log D58	-0.29	0.08	-0.57	0.32	-0.36	0.13
Sqrt SD	-0.25	0.06	N/S	-	N/S	-
Log DN	0.19	0.04	N/S	-	N/S	-
Sqrt H	0.17	0.03	0.22	0.05	N/S	-
AVH	N/S	-	-0.36	0.13	-0.28	0.08
Sqrt N2.5	N/S	-	0.32	0.10	0.24	0.06
Sqrt N5	N/S	-	0.31	0.10	0.20	0.04
Asin Prim	N/S	-	0.31	0.10	N/S	-
Asin BG	N/S	-	-0.23	0.05	N/S	-
Sqrt SR2.5	N/S	-	0.18	0.03	N/S	-

† All Regression lines fit significantly at a 5% level. This was tested using the ANOVA F-statistic.

The UDSR subset can be used as the control to ensure that any noted differences are due to mode of dispersal as opposed to any other factors. With the exception of Log DN, ADSR has a higher R^2 value than WDSR and UDSR for every "isolation" variable. In fact the variable Log D58 has the second strongest relationship with ADSR (r = -0.57). This "r" value almost rivals Log Area which has taken the top position in most of the simple and SMLR regressions undertaken. Moreover ADSR is significantly related to more variables than either other category (or as a matter of fact FSR, QSR or SSR). This suggests that a greater proportion of the variation in ADSR is predicted by the measured variables. ADSR is the only dispersal category to have a significant relationship with either Asin Prim and Asin BG.

A similar analysis was carried out comparing the R^2 values for total FSR and the Number of Rare Species found in each fragment (RSR). Rare species were defined as occurring in no more than 5 out of the 98 fragments and also must be characteristic calcareous grassland species. (The species defined as rare are starred in Table 2.2). In general, the R^2 values for RSR are low (the highest being 0.37 for Log Perimeter). It therefore appears that much of the variation is unexplained by the measured variables. The only significant variable which has a higher R^2 value for RSR (0.05) than FSR (0.04) is Scrub Density.

3.4 ANALYSIS OF REGIONAL MLG SPECIES DISTRIBUTION

3.4.1 Chi-Squared tests to see if the phytogeographical element of a species effects its regional distribution

Two hypotheses were tested using the χ^2 test:

i) Is there any difference between the number of species with a Southern Distribution found in MLG quarry floor habitats and MLG primary habitats?

ii) Is there any difference between the number of species with a Northern Distribution inhabiting Flushed MLG and Non-Flushed MLG habitat.

The first hypothesis was proposed by Dalby (1991) and the second was suggested by Doody (1980). However in this study both tests showed that there was no significant difference at the 5% level. Whilst undoubtedly there are several southern distributed species found exclusively on quarry floors, eg. *Erigeron acer*, many more are widespread across the region including the coast, where the local climatic gradient creates warmer conditions, eg. *Bromus erectus*.

3.4.2 Analysis of the regional species structure across the habitat fragments

Nestedness analysis tests if there is a structure in the distribution of the each species across the sampled habitat fragments (see Section 2.4.3). The standardised C statistic is listed for the full dataset (A) and a variety of Habitat (B & C) and Species Subdivisions (D, E &F) in Table 3.8. All the computed C values are above 0.40 which according to Wright & Reeves's (1992) subjective classification indicates a medium degree of Nestedness. (A "C" value of 0 indicates equiprobability whilst a value of 1 indicates perfect nestedness with a value exceeding 0.60 considered high.) Every computed C statistic was tested for significance using Cochran's Q test.

Table 3.8: The Standardised Nestedness values for different datasets (The Cochrane's Q values are calculated by the computer program for each separate analysis and compared with the χ^2 critical value of 3.84 at 5% significance level and for 1 df)

Dataset	**C Value (4dp)**	**Significance Level**
A: Fragment Species Richness (Total)	0.4447	<0.0001
B: Primary Habitats	0.4373	<0.0001
C: Secondary Habitats	0.4210	<0.0001
D: Unspecialised Dispersal	0.4300	<0.0001
E: Animal - Dispersed	0.4462	<0.0001
F: Wind-Dispersed	0.4219	<0.0001

These results were then tested for significant difference from the overall or control value using the z score at a 5% level and the results are shown in Table 3.9 below.

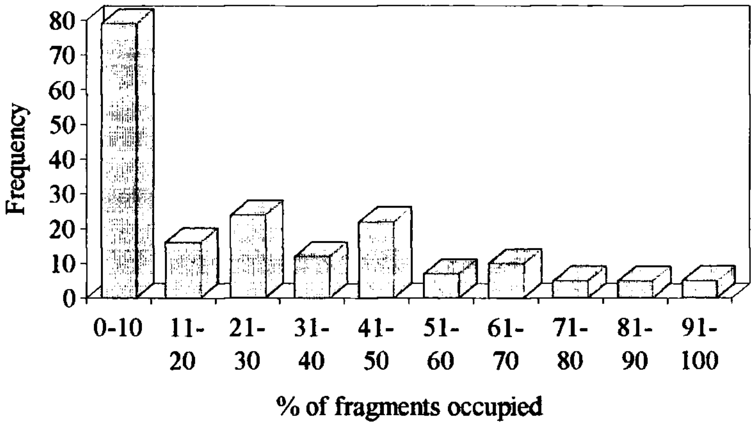
Table 3.9: Summary of the results testing differences between C values (A "z" value of 1.64 is significant at the 5% level)

Dataset Subdivision	**Significantly greater than the overall FSR**	**Not Significantly different from the overall**	**Significantly less than the overall FSR**
Habitat Type		Primary	Secondary
Species Dispersal		Animal-Dispersed	Unspecialised Wind-Dispersed
	Significantly greater than USR	**Not Significantly different from USR**	**Significantly less than USR**
Species Dispersal	Animal-Dispersed		Wind-Dispersed

In addition to these results the C values for primary and secondary habitat were proven to be significantly different. Therefore whilst no subsets proved to have significantly higher nestedness than the overall FSR dataset, distinct differences have been identified in the contribution of each subset to the overall nested structure.

An additional way of analysing the structure of the species distribution across the studied MLG fragments is to plot the overall frequency distribution of each species (see Figure 3.16 overleaf).

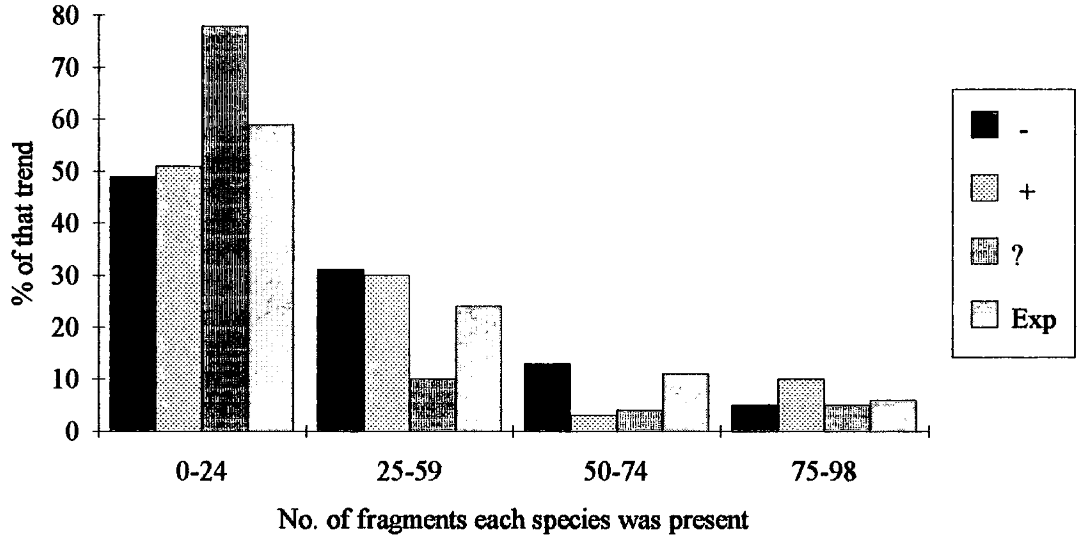
Figure 3.16: The Distribution of species across the sample fragments



As can be seen from the diagram above the distribution is highly skewed with a large number of species present in between 1% and 10% of fragments. This distribution does not match that proposed by Hanski (1982) which demonstrates bimodality at either end of the spectrum with peripheral and core species. However the large number of species with a low number of occurrences may result from the inclusion of species which are not typically associated with calcareous grassland, eg. *Sanicula europea.* In addition the low number of species occurring in 80% or over of fragments is significant.

Using Grime et al (1988), 164 species (out of the total 185) were classified according to the extent which their abundance is changing in response to modern methods of landuse. Three classes exist: "+" indicating that the species is increasing; "-" indicating that the species is decreasing and "?" uncertain. However the "-" class has by far the largest number of species, approximately 50%. This information is further subdivided according to a species frequency to determine whether it is the rarest or more common species at greatest threat. As can be seen from Figure 3.17, it is in the middle categories (species occurring in between 25 to 74 fragments) that the highest proportions of "-" status species occur. Moreover these classes include the majority of the characteristic MLG species, eg. *Sesleria albicans, Helianthemum nummularium.* Those occurring in over 74 sites tend to be generalists, eg. *Centaurea nigra.*

Figure 3.17: A Comparison of the proportions of each status category in relation to the number of occurrences



3.5 PREDICTING FUTURE CHANGES IN THE SPECIES COMPOSITION OF MLG IN NORTH EAST ENGLAND

In order to indicate the magnitude and direction of potential change, two dominant MLG species and one found to the south of the study area were used. (Details of the methods employed are given in Section 2.3.4.). For this part of the analysis a European scale is used though discussion of the results is focused on the consequences for the UK.

The Climate Response Surfaces (CRS) illustrated (Figures 3.18, 3.19 and 3.20) can be envisaged as solids of varying density (according to probability of the species occurring) and are illustrated as a series of slices with respect to the AET/PET axis, each slice having GDD5 as its horizontal and MTCO as its vertical axis. The Dark Green areas represent the area of available climate space in Europe. Table 3.10 summarises for each species: the threshold values for each bioclimatic, the degree of fit between the simulated and observed distributions (κ) and finally the value for the P1 and P2 descriptors.

Figure 3.18: Climate Response Surface for *Bromus erectus* in Europe. Three dimensional response surface fitted to present distribution and bioclimate for the 50km AFE grid. Each panel shows a cross-section of the surface at a different value of AET/PET. The x axis represents GDD5 (units are 10^3 degree-days) and the y axis represents the MTCO in °C

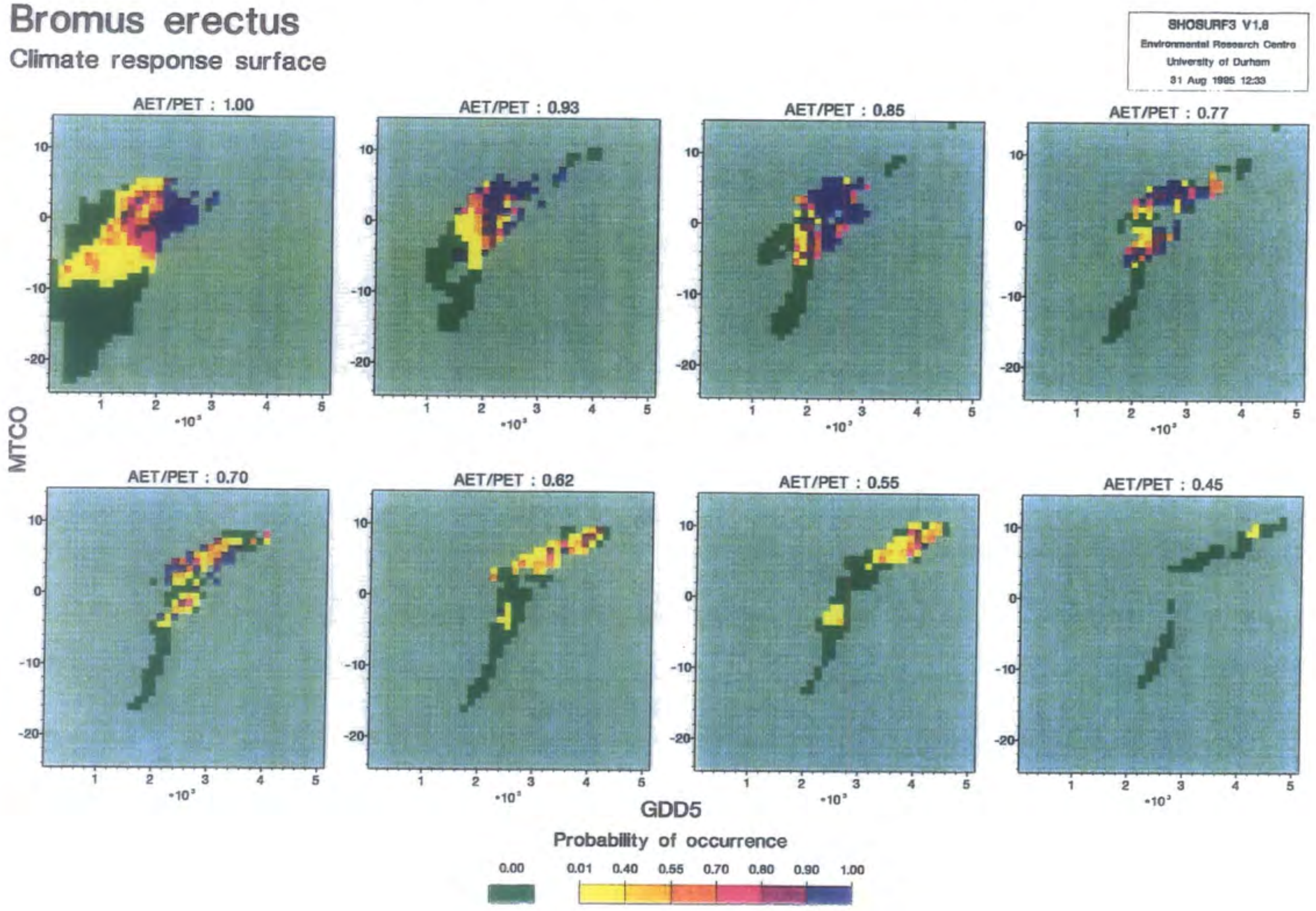
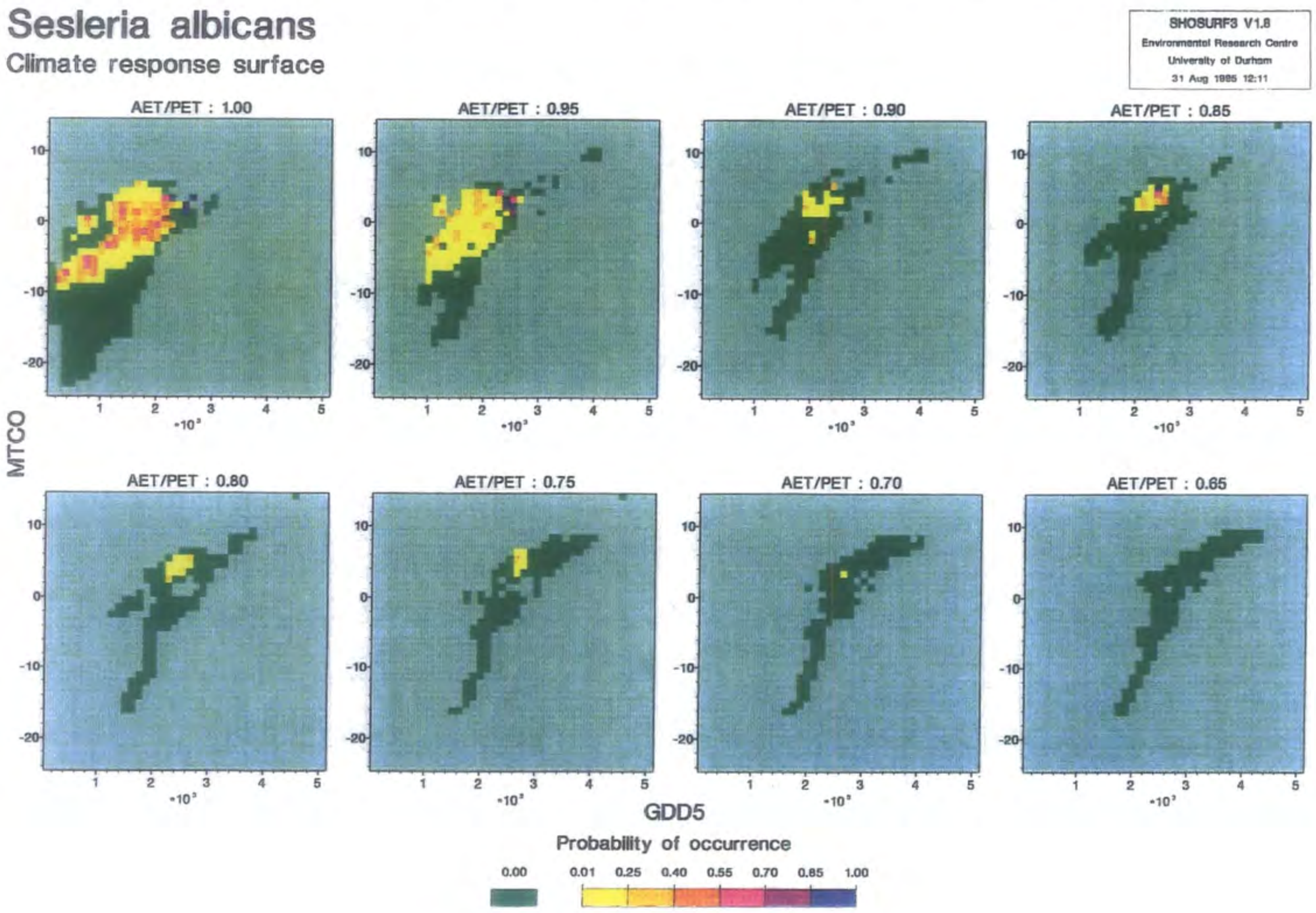


Figure 3.19: Climate Response Surface for *Sesleria albicans* in Europe. Three dimensional response surface fitted to present distribution and bioclimate for the 50km AFE grid. Each panel shows a cross-section of the surface at a different value of AET/PET. The x axis represents GDD5 (units are 10^3 degree-days) and the y axis represents the MTCO in °C



Thesium humifusum

Climate response surface

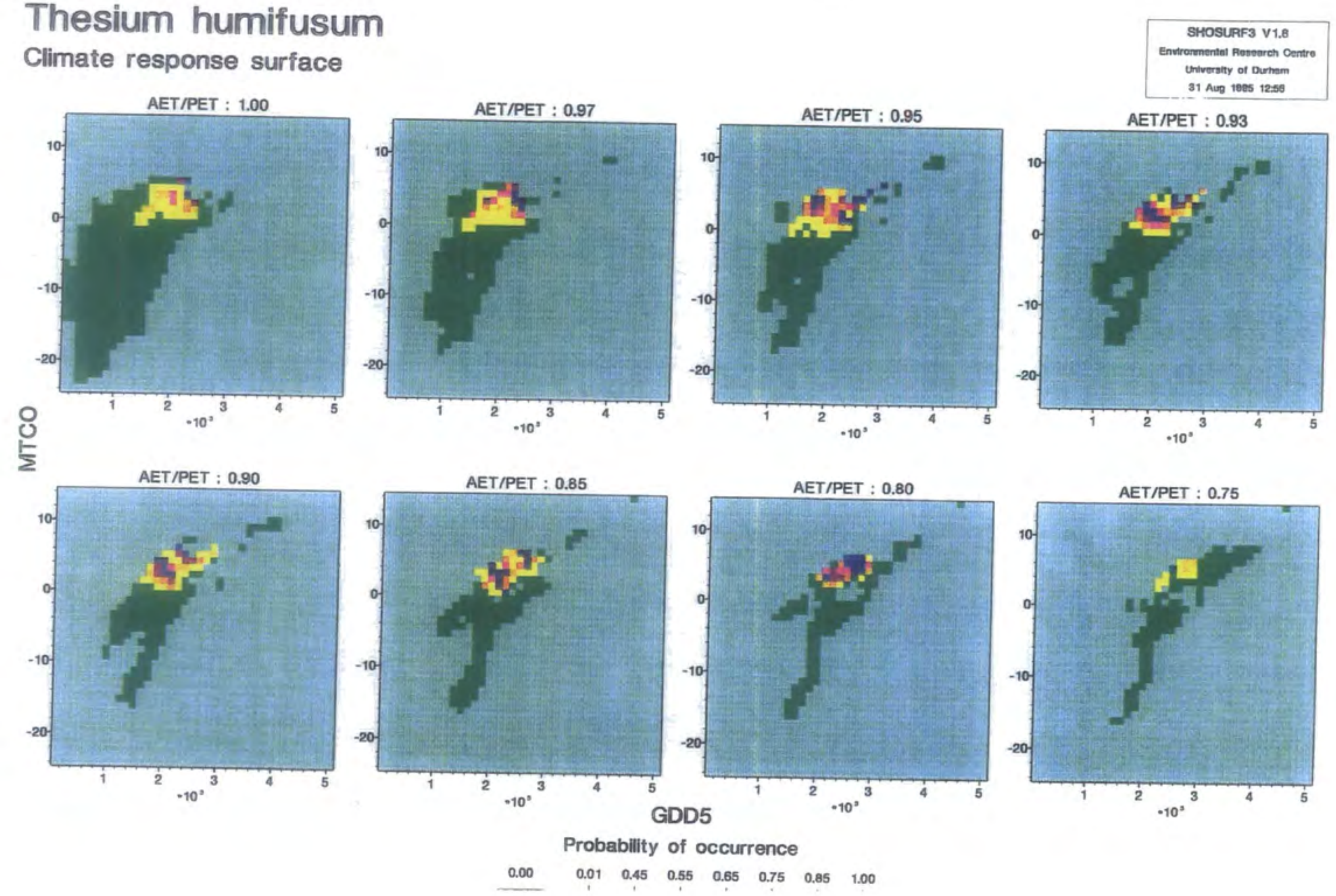


Table 3.10: Summary of the bioclimate thresholds and the goodness of fit descriptors for the three species

Species	MTCO Threshold	GDD5 Threshold	AET/PET Threshold	Prob Threshold	Max Kappa	P1	P2
Bromus erectus	-9° to 9°	200-4500	0.50	0.40	0.75	80%	77%
Sesleria albicans	-9° to 6°	200-2700	0.74	0.24	0.45	58%	41%
Thesium humifusum	0° to 7°	1600-3000	0.70	0.45	0.77	79%	76%

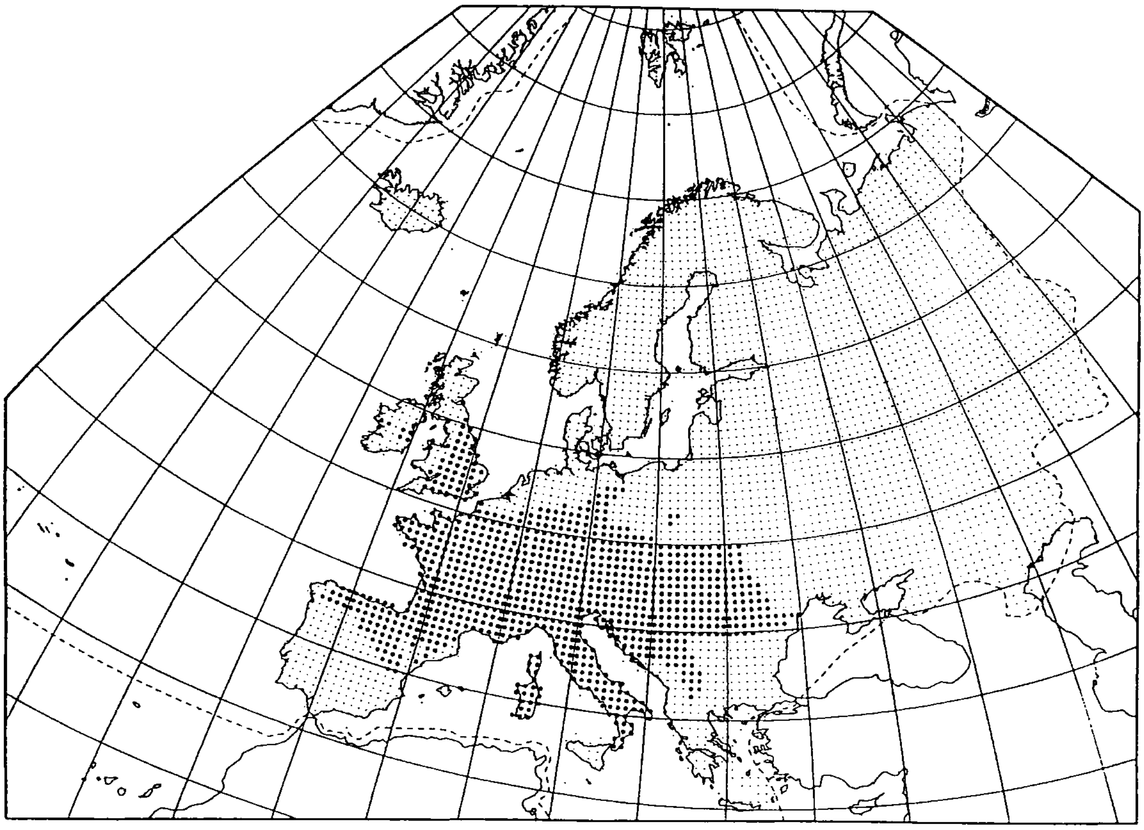
The bioclimatic ranges relate to the climate space where the species occurs at a probability above its threshold and are limited to the climate space found in Europe
The AET/PET threshold is the lower limit for each species

Firstly the CRS for *Bromus erectus* shows that the species has a marked lower MTCO threshold that increases as AET/PET decreases, ie. at the lowest AET/PET value (ca. 0.50) the MTCO threshold rises to -4° C. However the bioclimatic variable which restricts *Bromus erectus* in its UK range (see Map 3.1) is GDD5. Though the species can tolerate a broad range of GDD5 values, it has a distinct optimum between 1600 and 3400. This is outside of the range found in Scotland and North-West England. Finally the species threshold for soil moisture availability is relatively low (ca 0.50) compared to *Sesleria albicans* and *Thesium humifusum* which exhibit a more Westerly/Sub-Atlantic distribution. The CSR of *Bromus erectus* simulates a present distribution (see Map 3.2) which closely matches that observed. The maximum κ statistic is considered a very good fit according to Monserud (1990). Furthermore the simulated distribution shows a significant κ for a large range of probabilities - 0.02 to 0.82. The P1 and P2 descriptors are such that 80% of the observed occurrences are simulated whilst 77% of the simulated occurrences match observed occurrences.

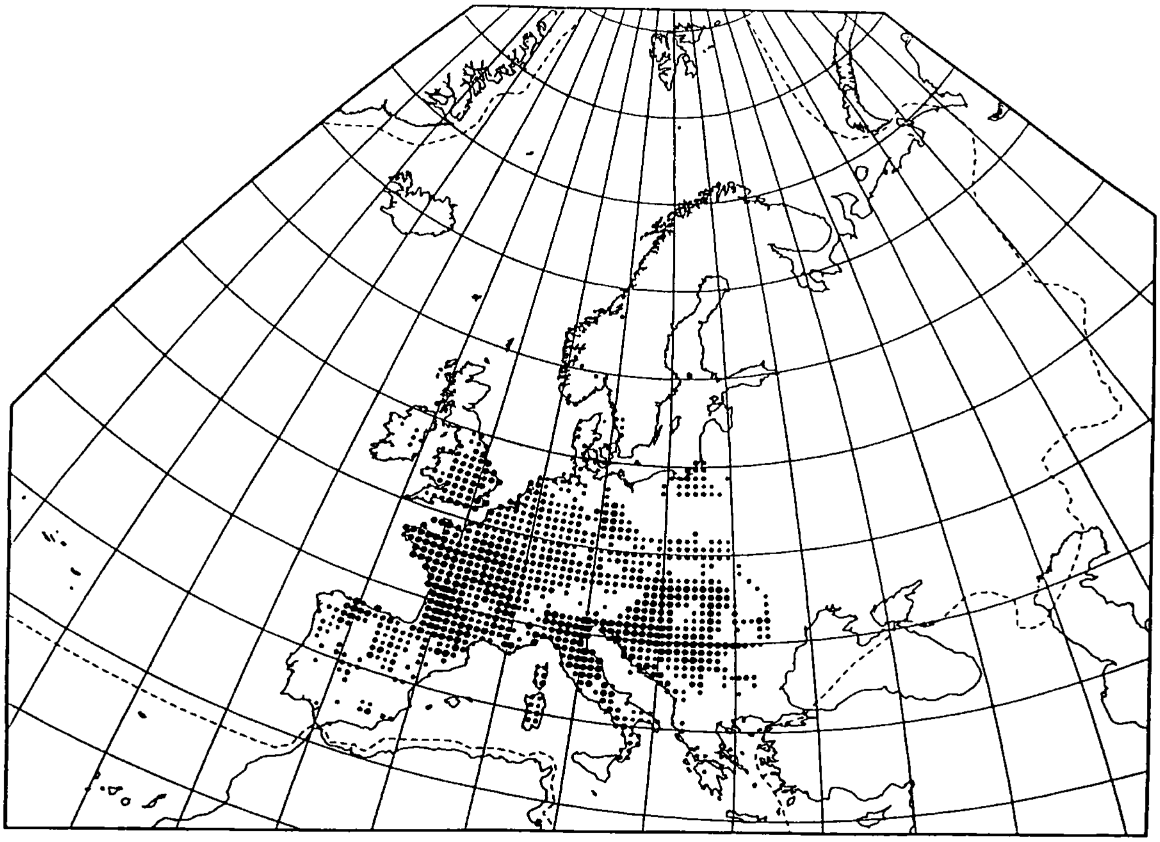
However this is in contrast with the results for *Sesleria albicans*. The CSR (see Figure 3.19) is flat with very few areas of climate space where it has a high probability of occurrence. In fact the maximum κ statistic can be interpreted as showing only a fair fit between the simulated and observed distributions Monserud (1990). Moreover only 58% of occurrences are simulated whilst 41% of the simulated occurrences match observed occurrences. However perhaps the most striking feature of the CSR is the very high soil moisture availability threshold (see Table 3.10). Together with its restricted GDD5 range, this would appear to explain its North-West and montane distribution in Europe and the UK (see Map 3.5).

Thesium humifusum has a very compact CSR, hence its narrow observed distribution, which shows greater similarity to *Sesleria albicans* than *Bromus erectus* (see Figure 3.20). *Thesium humifusum* has a very high soil moisture availability threshold (see

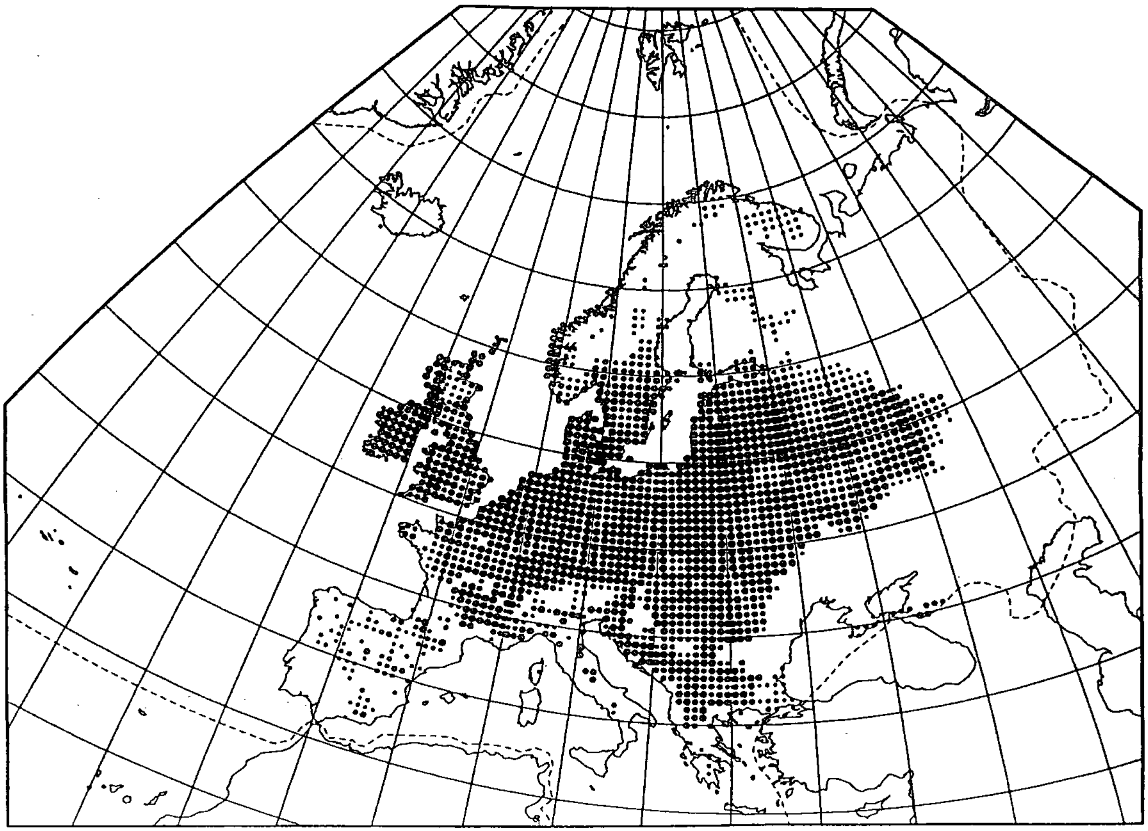
Map 3.1 Recorded distribution of *Bromus erectus* in Europe. Presence/absence on a 50km AFE grid; redrawn from Meusel, Jäger & Weinert (1965)



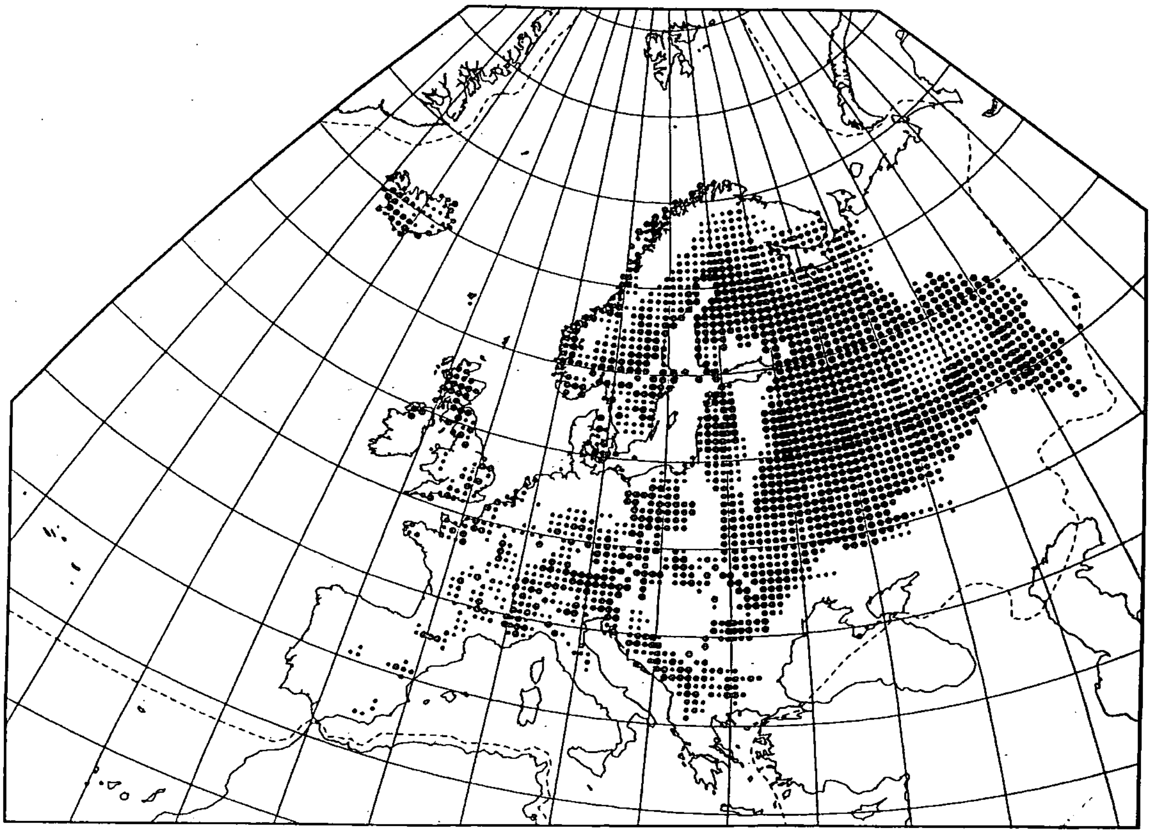
Map 3.2 Simulated distribution of *Bromus erectus* in Europe. Distribution on a 50km AFE grid simulated using the response surface. Dot size indicates the relative probability of occurrence with the smallest dots representing the threshold probability of 0.40.



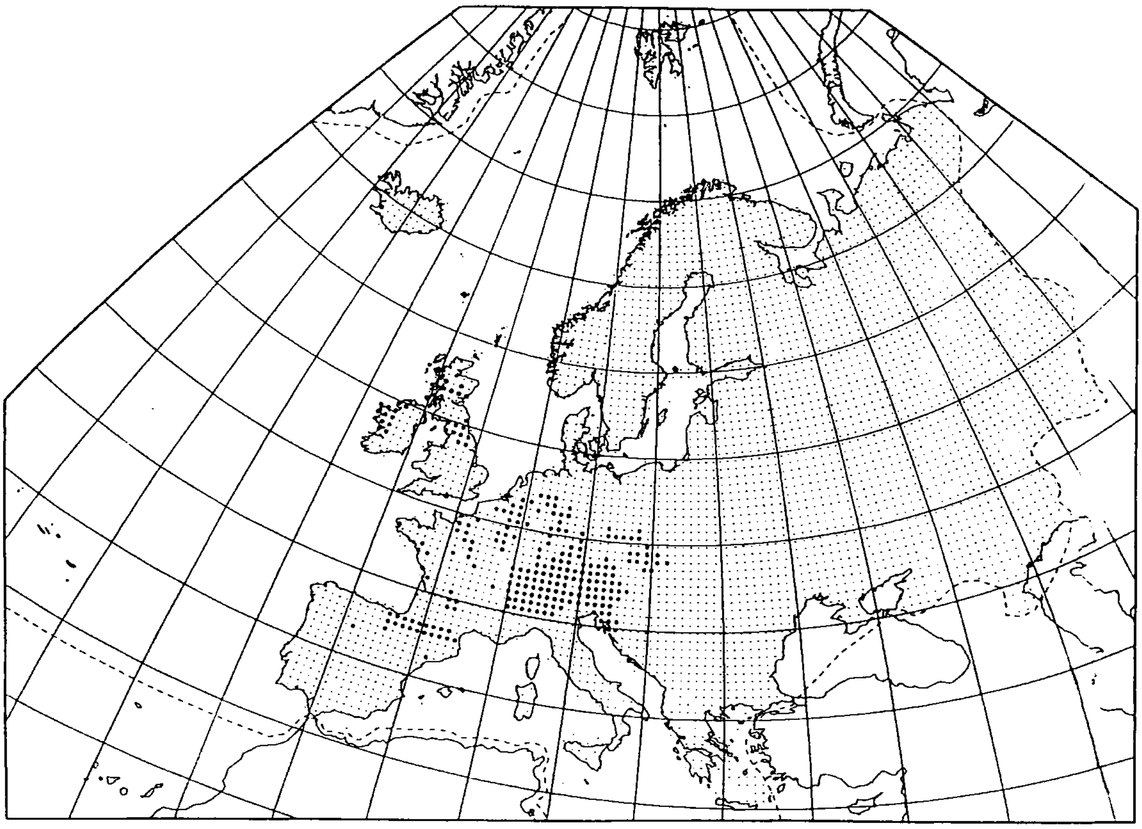
Map 3.3 Simulated potential distribution of *Bromus erectus* in Europe for the OSU 2 x CO_2 scenario. Distribution on a 50km AFE grid simulated using the response surface and the 2 x CO_2 scenario forecast by the OSU GCM. Dot size as Map 3.2



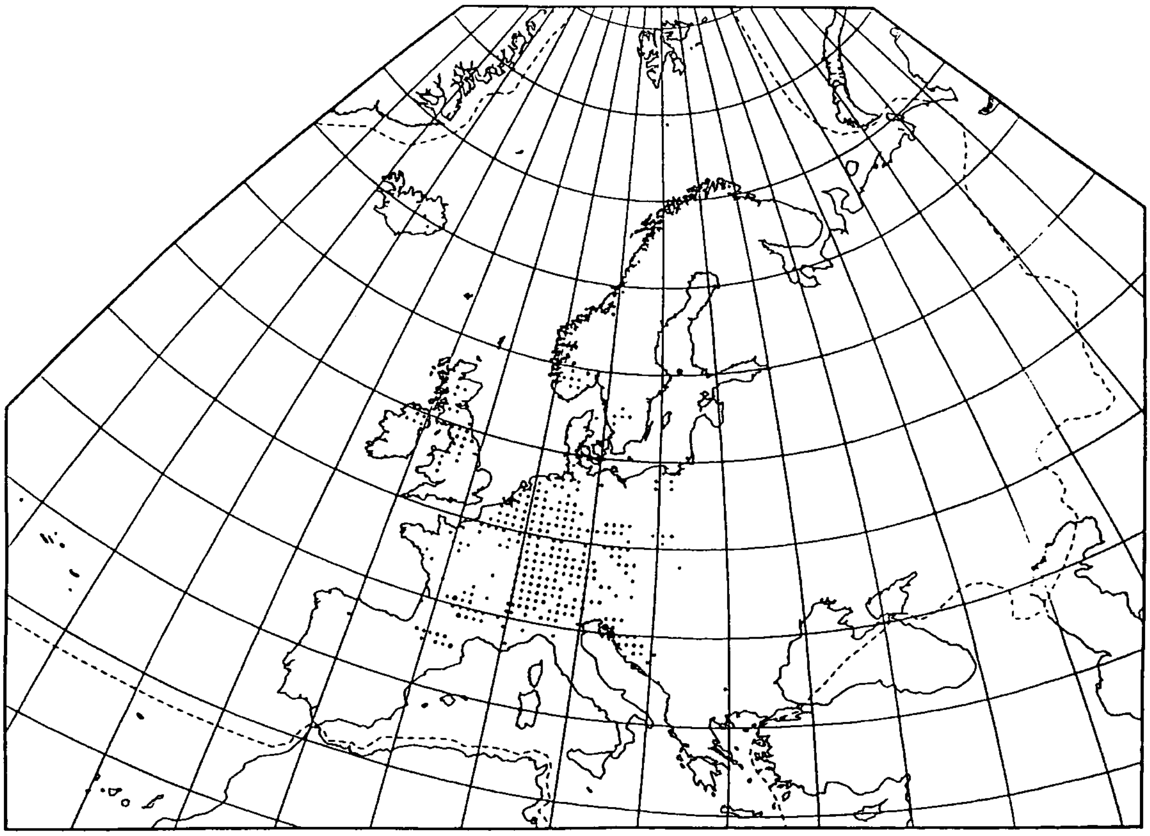
Map 3.4 Simulated potential distribution of *Bromus erectus* in Europe for the UKMO 2 x CO_2 scenario. Distribution on a 50km AFE grid simulated using the response surface and the 2 x CO_2 scenario forecast by the UKMO GCM. Dot size as Map 3.2



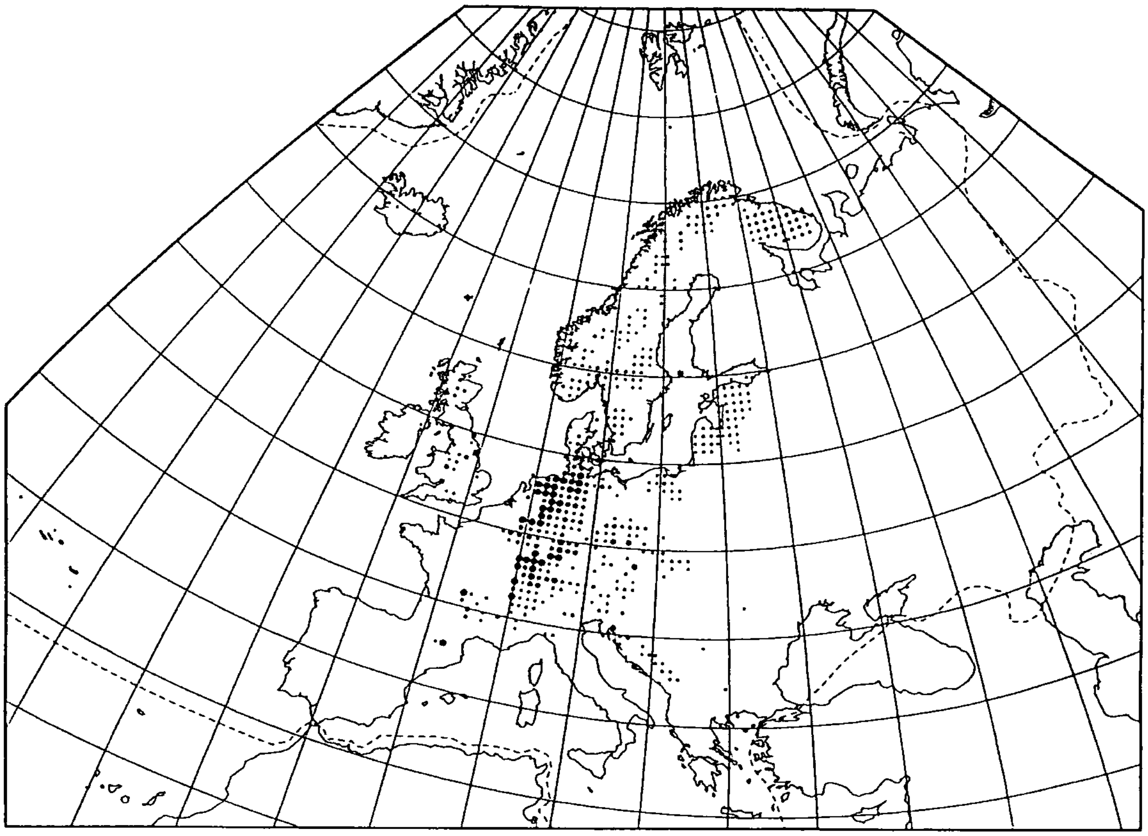
Map 3.5 Recorded distribution of *Sesleria albicans* in Europe. Presence/absence on a 50km AFE grid; redrawn from Meusel, Jäger & Weinert (1965)



Map 3.6 Simulated distribution of *Sesleria albicans* in Europe. Distribution on a 50km AFE grid simulated using the response surface. Dot size indicates the relative probability of occurrence with the smallest dots representing the threshold probability of 0.24.



Map 3.7 Simulated potential distribution of *Sesleria albicans* in Europe for the OSU 2 x CO_2 scenario. Distribution on a 50km AFE grid simulated using the response surface and the 2 x CO_2 scenario forecast by the OSU GCM. Dot size as Map 3.6



Map 3.8 Simulated potential distribution of *Sesleria albicans* in Europe for the UKMO 2 x CO_2 scenario. Distribution on a 50km AFE grid simulated using the response surface and the 2 x CO_2 scenario forecast by the UKMO GCM. Dot size as Map 3.6

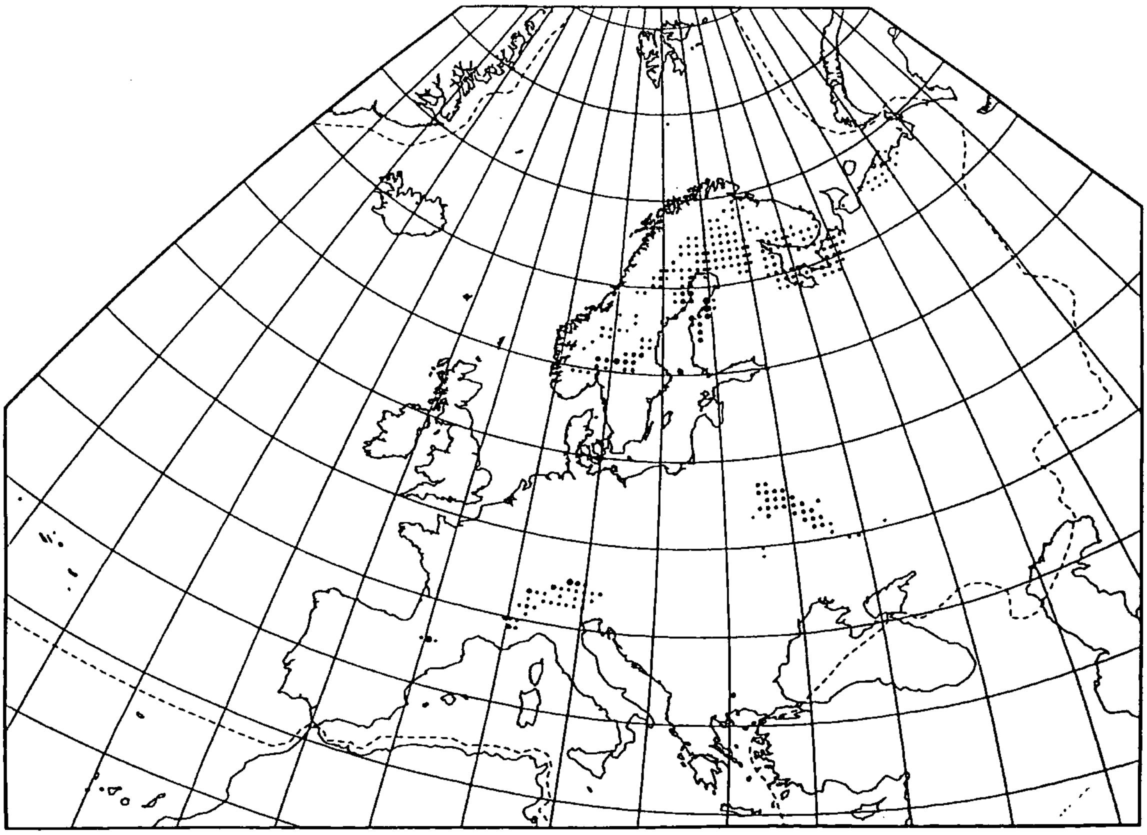


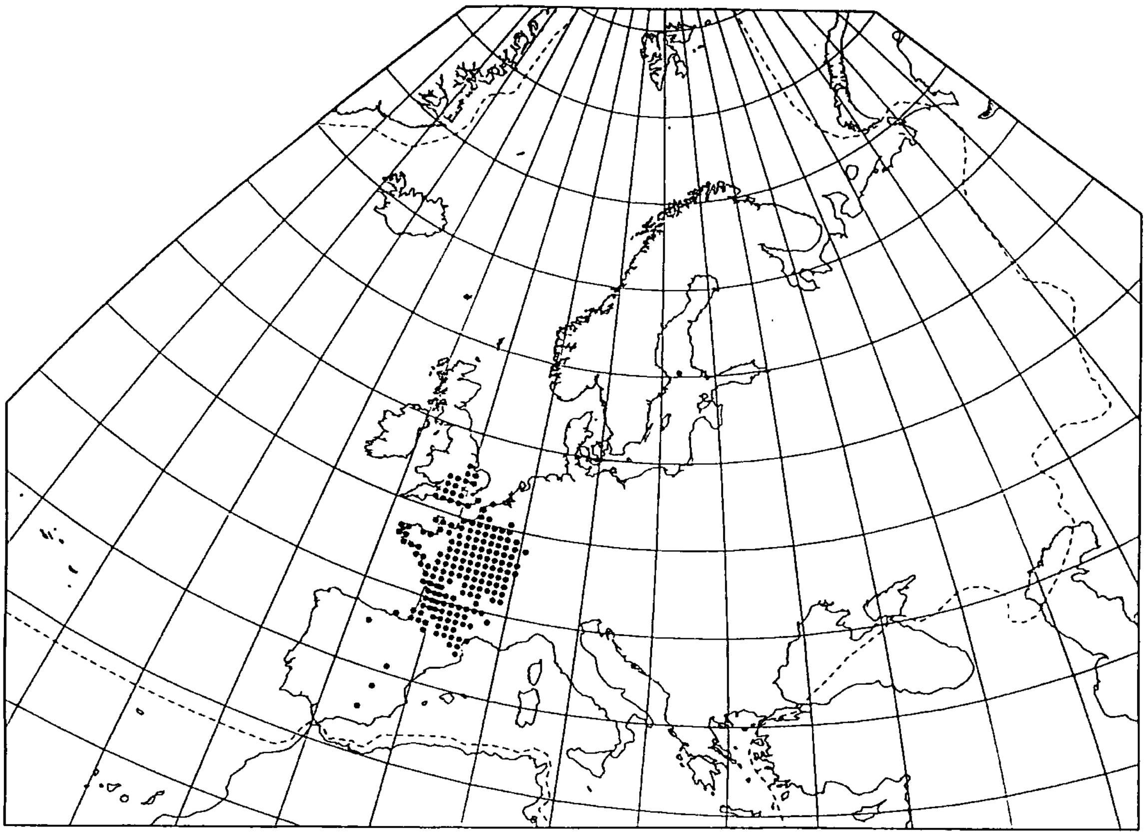
Table 3.10) therefore it is restricted to Western Europe. However it is has a much lower northern limit in the British Isles (Lincolnshire) than *Sesleria albicans* (see Map 3.9). This is a result of its higher MTCO and GDD5 thresholds particular at the lower end The simulated distribution (see Map 3.10) has the highest κ degree of fit to its observed distribution of any of the three species (see Table 3.10). Furthermore 79% of occurrences are simulated whilst 76% of the simulated occurrences match observed occurrences.

It can be concluded therefore that the broadscale features of the distributions of *Bromus erectus, Thesium humifusum* and more tentatively *Sesleria albicans* are correlated with the three bioclimate variables used to fit the CSR and are probably mechanistically determined by them. If therefore the simulated distributions (Maps 3.2, 3.6 and to 3.10) are re-examined as maps of the potential distribution of the species under present climate conditions, the species appear to be close to achieving equilibrium with the present climate particularly in the British Isles. The only possible exception is *Sesleria albicans* which has only relatively moderate probabilities of occurrence in the UK and is simulated to be in the Welsh mountains which is outside the present distribution. (The absence of *Bromus erectus* from the Alps in the simulated distribution is an sampling artefact caused by using the mean altitude for each grid square.)

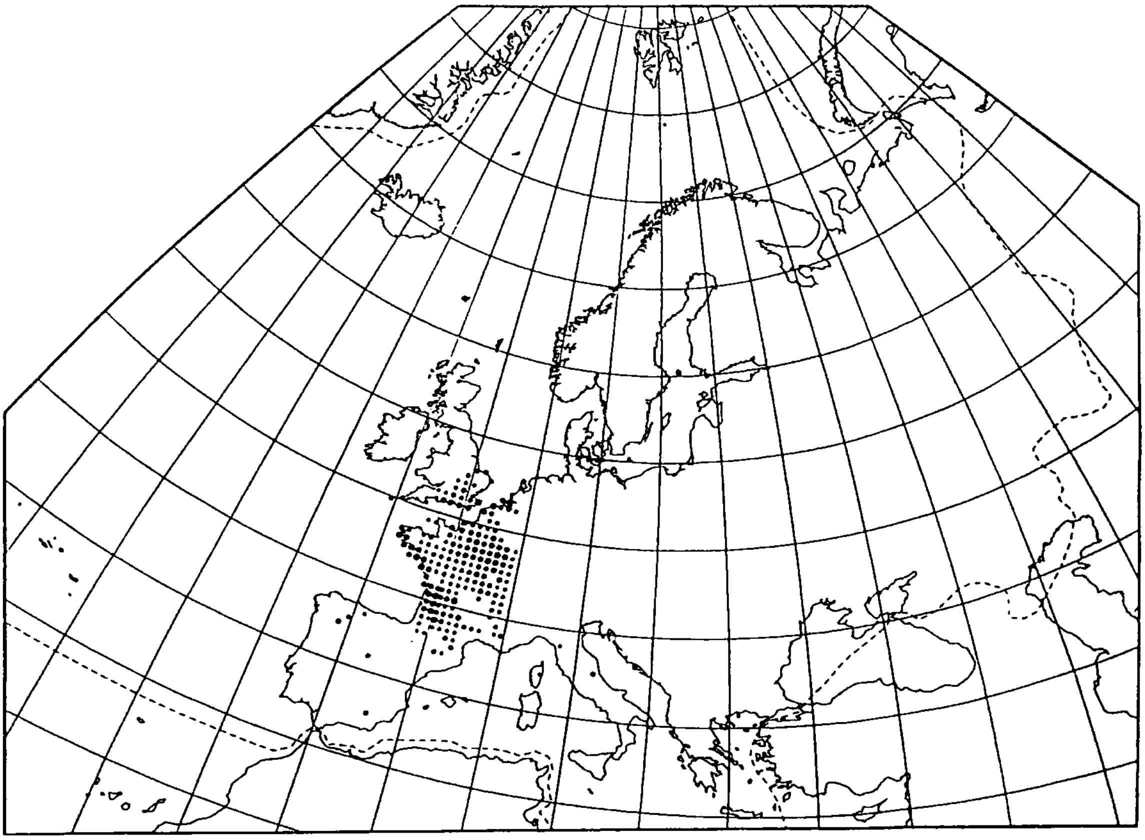
Given that the distributions of *Bromus erectus* and *Thesium humifusum* (and to some extent *Sesleria albicans)* are primarily determined by climate the CSR can be used to simulate potential future ranges under predicted climate scenarios. For a description of the methods employed and details relating to the two GCMs refer to Section 2.3.4. For each species two simulated potential future distributions are mapped on the same AFE 50km grid. Dot size indicates the relative probability of occurrence with the smallest dots representing the specific threshold probability.

The OSU scenario for *Bromus erectus* (see Map 3.3) shows the species occurring across most of the British Isles at high probabilities. North-East England is nearer the centre of its range as the distributional limit shifts markedly North into Scandinavia and East into the Baltic States and Russia. These changes reflect the year-round warming predicted in the mid latitudes. Also in the east, the amplified temperature increases simulated at high latitudes in the winter months. The UKMO scenario (see Map 3.4) results in a more accentuated shift of particularly the eastward limit. The centre of the species' range is firmly based in Russia with North East England at the periphery and the highest UK probabilities in North Scotland.

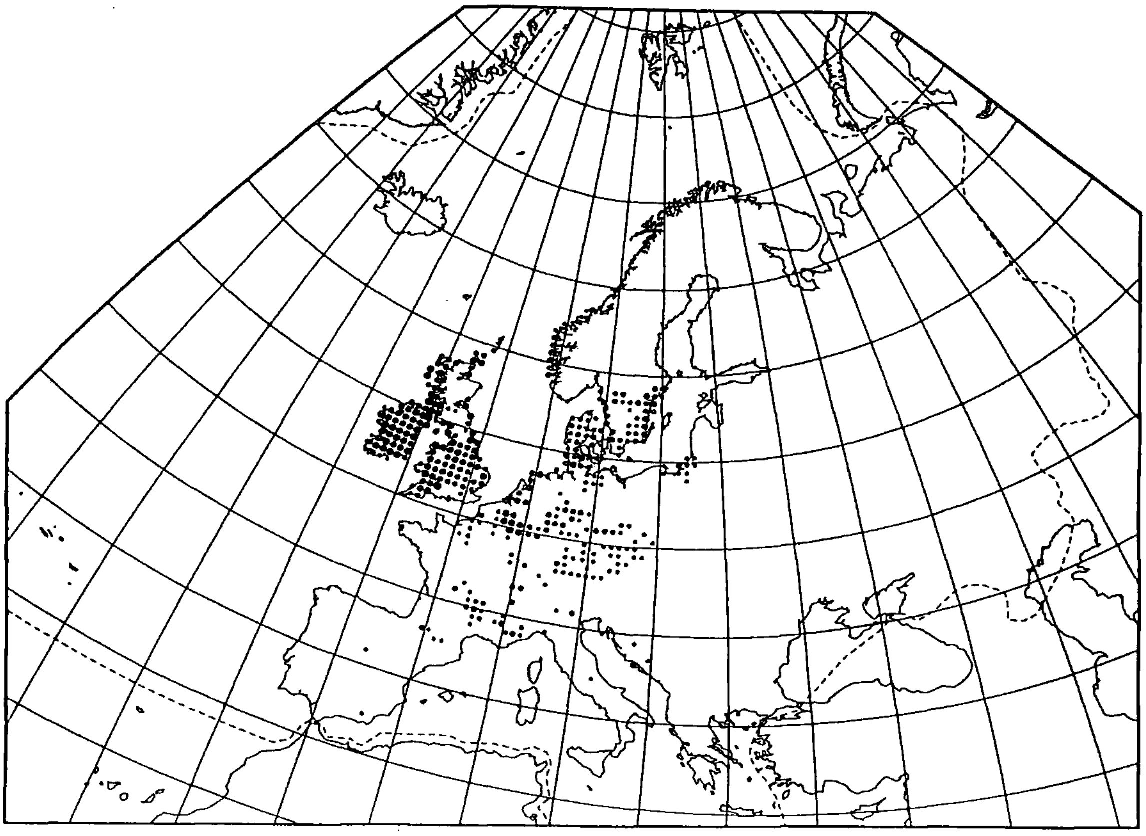
Map 3.9 Recorded distribution of *Thesium humifusum* in Europe. Presence/absence on a 50km AFE grid; machine readable copy from the Botanical Museum, Helsinki.



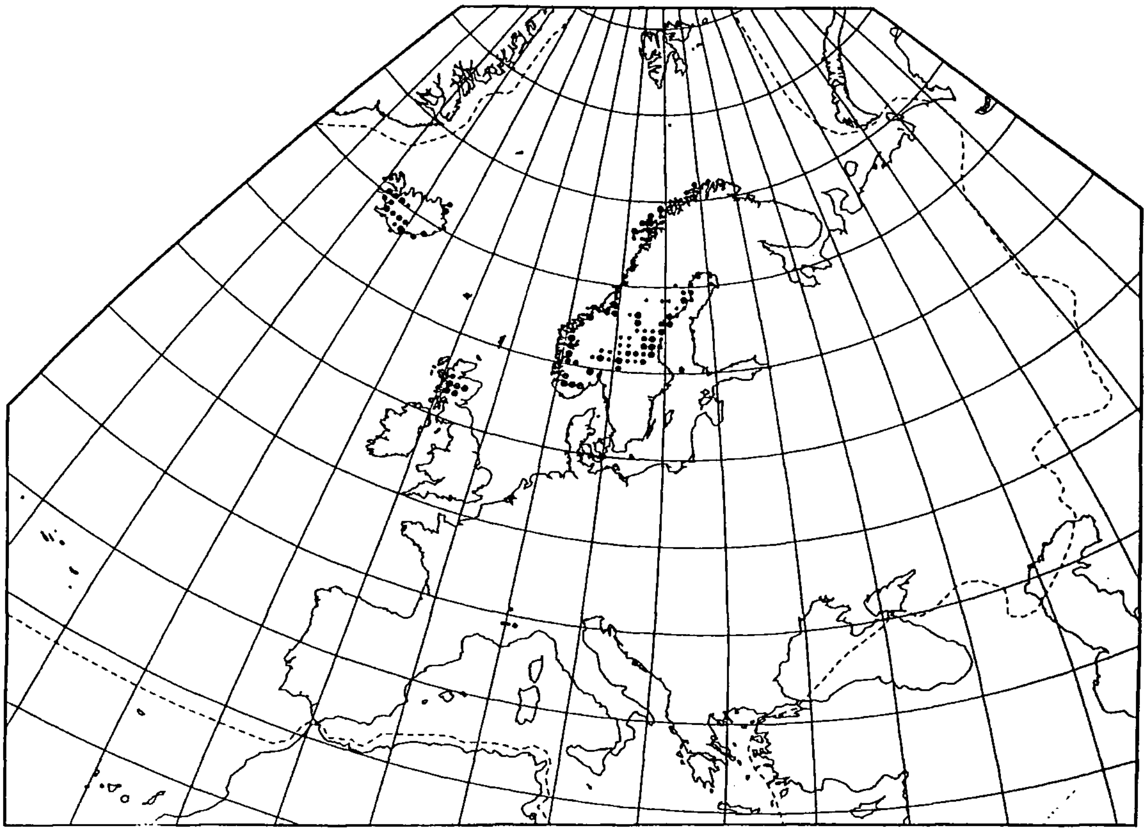
Map 3.10 Simulated distribution of *Thesium humifusum* in Europe. Distribution on a 50km AFE grid simulated using the response surface. Dot size indicates the relative probability of occurrence with the smallest dots representing the threshold probability of 0.45.



Map 3.11 Simulated potential distribution of *Thesium humifusum* in Europe for the OSU 2 x CO_2 scenario. Distribution on a 50km AFE grid simulated using the response surface and the 2 x CO_2 scenario forecast by the OSU GCM. Dot size as Map 3.10



Map 3.12 Simulated potential distribution of *Thesium humifusum* in Europe for the UKMO 2 x CO_2 scenario. Distribution on a 50km AFE grid simulated using the response surface and the 2 x CO_2 scenario forecast by the UKMO GCM. Dot size as Map 3.10.



The OSU scenario predicts that *Thesium humifusum* (see Map 3.11) will expand its range north and east and largely retreat from France. Ireland and Central England will become its heartland with a high probability of occurrence in the present MLG area. Though is it able to expand east due the predicted rise in winter temperatures, it is still restricted to those area with high AET/PET, ie. those with a strong maritime influence. The UKMO scenario (see Map 3.12) results in a potential distribution that might be characterised as Arctic-Alpine. *Thesium humifusum's* southern limit would be north of the MLG region if the UKMO scenario was realised.

Finally tentative inferences will be made with regard to the potential future distribution of *Sesleria albicans*, given that climate may not be the only important factor in determining its distribution. According to the OSU scenario (see Map 3.7) its distribution expands in a North-Easterly direction into Scandinavia and the Baltic states and retracting from Ireland and much of the UK (but it still has a relatively high probability of occurrence in the MLG area). Though it has a high soil moisture availability threshold it differs from *Thesium* as it can tolerate lower MTCO and requires lower GDD5 values. Hence under the OSU scenario Germany becomes an optimal location. The UKMO scenario (see Map 3.8) predicts that the species will disappear from all its current locations with the exception of the Alps. This is probably occurs as a result of the winters becoming too warm in North West Europe. *Sesleria albicans* has a MTCO upper threshold of 6°C (see Table 3.10). Therefore its distribution shifts eastwards where winter temperatures though warmer than at present are still within its tolerance range. However it is still restricted to those areas with high AET/PET, ie. those with a strong maritime influence. Therefore the centre of the range is in the Baltic states and North coast of Siberia where precipitation totals will markedly increase.

CHAPTER FOUR: THE DISCUSSION

4.1 FACTORS PREDICTING MLG SPECIES RICHNESS AT THREE CONTRASTING SCALES

The variables which predict species richness differ quite markedly between the three scales : quadrat; fragment and site. However for all scales either Log Area or Log Perimeter is the most significant predictor of species richness, ie, it has the highest R^2 value. (The Species Richness / Area relationship is further discussed in Section 5.2.) Though Perimeter is closely connected to area, it is also dependent on shape. Merriam & Wegner (1992) concluded that the shape of a habitat patch is the dominant factor in determining the size of the ecotonal edge. Furthermore ecotones usually support very different species (eg. species from the adjacent habitats or generalists) compared to the interior of the patch therefore potentially boosting the total number of species. A significant number of MLG patches have elongated and non-compact shapes therefore probably have high proportions of ecotonal habitat.

At least one isolation variable is found in all three equations. Therefore it is possible to infer that degree of isolation is significant in predicting species richness at all three scales. However due to the inter-correlations between many of the isolation variables it is very difficult to state the precise nature of this relationship, at the three scales. However what is evident is that the 26 Tyne & Wear fragments all have relatively low FSR and QSR values (a mean FSR of 42.31 as opposed to an overall mean FSR of 48.41) and a relatively high degree of isolation from fragments with a high number of species. This doubtless contributes to the negative beta coefficient for Log D58 in both Equation One and Two and the positive coefficient of SRNN in Equation One. However at a site scale, SRNN is not significantly correlated with species richness and instead the most significant isolation variable is number of sites within 2.5 km. This suggests that at a larger scale a higher number of potential colonist pools close by is more important in explaining species richness than the number of species occurring in the single nearest site.

From the results in Section 3.1 it is quite clear that habitat variables, such as Average Vegetation Height and Percentage Bare Ground, are much more significant in determining species richness at a small scale. Furthermore this is the only scale at which Percentage of Primary habitat is significantly correlated with species richness. Primary habitat fragments support more species in a small area ($0.25m^2$) than secondary habitat fragments.

Caveat

The fragment scale was selected for further analysis as the SMLR Equation predicted the highest percentage of variation in species richness.

4.2 THE SPECIES / AREA RELATIONSHIP

At the fragment scale there is a strong relationship between species richness and Log Area (with Log A accounting for 41% of variation in the simple analysis and 34% of variation in the multiple analysis). However as can be seen from Figure 3.13 this relationship does not fit the classic Power Function relationship ($SR=CA^{z}$ - Preston 1962). Instead it has an exponential form ($SR = C + Z\text{Log } A$) with species number rising at an exponential rate between $1m^2$ and $8000m^2$ area and then levelling off. In this respect this MLG dataset does not appear to support the Equilibrium Theory of Island Biogeography (MacArthur & Wilson 1967). Furthermore this result lends support to the argument that it is not appropriate to apply the Equilibrium theory to continental habitat isolates. Continental habitat "islands" are not as effectively isolated as true islands therefore many transient species occur. This acts to reduce the overall slope of the Species/Area relationship and exaggerate the role of Immigration.

However this aside it is still important to assess the mechanisms which may account for the existence of a Species/Area relationship within this particular dataset. The null hypothesis of Random Placement (Arrhenius 1921) states that the relationship occurs merely due to a sampling phenomenon. This hypothesis can not be tested rigorously without the construction of an expected Species/Area curve. Simberloff (1976) suggests this is achieved by sampling successively smaller areas from several islands of similar size. However this was not undertaken for this particular dataset therefore no firm conclusion can be made. It is of note though that the exponential shape of the Species/Area curve in this study is of the same form as that usually taken by the expected curve, ie. indicating the Species/Area relationship may have no biological significance (McGuiness 1984).

The Habitat hypothesis (Williams 1943) predicts that for "islands" ranging between $10cm^2$ to 1 ha in size (this encompasses 86 out of the 98 studied MLG fragments) the Species/Area relationship bests fits the exponential model as a result of the Random Placement Hypothesis. In other words habitat variation is thought not to significant in determining species richness in areas below 1 hectare in size. However for areas greater than 1 hectare, area is presumed to act via the addition of new ecological conditions resulting in a Power Function relationship. However there is no evidence (see Figure 3.13) that the nature of the relationship changes after the 1 hectare threshold. But the MLG data does appear to conform with the prediction that habitat diversity is not significant at small spatial scales. This may be accentuated as a result of the strict physio-chemical requirements of MLG species. Moreover habitat diversity across the whole sample is low. An indication of this is the very low β- diversity of 0.04 (if the dependence on sample size is corrected). Beta diversity measures for heterogeneity of species composition across sites and usually reflects habitat diversity (Whittaker 1972).

However some variation in micro-habitat exists and this appears to be particularly important in predicting species richness within a $0.25m^2$ area. Furthermore it is unlikely that all significant micro-habitat variation was captured by the measured variables. However even at this small scale, the Log Area of the wider fragment is the strongest correlated variable with species richness. This suggests that area's role in determining species richness at this small scale is direct, ie. it is not an indirect result of micro-habitat variation (Kohn & Walsh 1994).

From the evidence so far it seems that the Species/Area relationship is simply a sampling effect with no biological significance. There is no suggestion that area directly controls population size and thus extinction rate as proposed by MacArthur & Wilson (1967). However by investigating the dataset using alternative methods further insights are gained. Using a method devised by Reed (1981) fragments were assigned a Saturation Value which measured whether each fragment had fewer or more species than expected given its area. The fragments which are over-saturated by 30% or more (see Section 3.2), with the exception of one, are all protected, managed and occur on the West Durham escarpment. They include both primary and secondary fragments. Five out of eleven of the fragments under-saturated by 30% or more are not managed or protected and occur in stressful environments, eg a road central reservation or are relatively isolated, eg. Eldon A,B & C (See Map 2.2).

"Ecological theory makes no clear predictions on how the distribution of habitat among partially correlated sub-habitats should affect species richness on a regional scale" (Quinn & Harrison 1988). Indeed the Equilibrium theory makes no explicit prediction but implies that habitat subdivision depresses species richness. However this outcome assumes a relatively high species overlap between smaller fragments. From Figure 3.14 it can be seen that the most subdivided set of MLG fragments has a consistently higher cumulative species number than the least divided. In effect, a collection of smaller islands maintains a higher number of different species than a few large fragments. This result agrees with over 90% of those produced by Quinn & Harrison (1988) for both habitat isolates and oceanic islands. Many different causal mechanisms may cause this pattern. However given this particular dataset I believe the following are important:

- * Edge Effect: The most subdivided fragments will have higher proportions of ecotonal habitat relative to their areas. Ecotones tend to support additional non-characteristic species.
- * Colonisation Species Pool: This is of particular consequence for secondary habitat. If there are many small fragments there is a larger effective colonisation pool which reduces the probability that the same species will colonise each fragment.
- * Historical Factors: Small fragments which were once part of larger habitat units may be super-saturated given their current situation and the number of species they can support will inevitable decline through time.

There is certainly no evidence that there is a deterministic order of extinction in relation to MLG fragment area.

It should be noted however that 24 MLG species occur exclusively in fragments with a area of over 2000m². They are listed in Section 3.2 and include: two rare species characteristic of MLG (and particularly associated with the CG8 community) - *Linum perenne anglicum* and *Primula farinosa* and two rare species found on the northern edge of their range *Erigeron acer* and *Arabis hirsuta.* However the list also includes non-characteristic species such as *Poa trivalis.* As a result of random placement some species will inevitable occur in only large fragments. However it is possible that for a few species area may determine extinction risk. This may be masked within the complex overall dataset.

4.3 FACTORS INFLUENCING THE NUMBER OF SPECIES, (i) WITH A PARTICULAR DISPERSAL MECHANISM AND (ii) WITH A LOW REGIONAL OCCURRENCE, IN AN INDIVIDUAL FRAGMENT.

Patterns found in the overall dataset may obscure those specifically related to subsets of species. Therefore by analysing subsets separately an indication of the degree of heterogeneity within the MLG community is gained. When species richness within subsets representing different dispersal mechanisms were regressed separately with the predictor variables, the Animal-Dispersed subset were shown to have higher significant R^2 values for the isolation variables. Therefore there appears to be a reduction in the number of Animal-Dispersed species found in a fragment as the distance to another fragment with species richness of 58 or over increases. A differential between species with different dispersal mechanisms was also found in a study carried out by Kadmon & Pulliman (1995).

Animal-Dispersed species include: *Sesleria albicans*, *Scabiosa columbaria* and *Helianthemum nummularium* all of which are dominant species in the MLG community. Moreover this subset of species is the only dispersal category to have a significant correlation with Percentage Primary habitat and Bare Ground. In that ADSR tends to increase as the proportion of primary habitat increases and percentage of bare ground decreases. It appears that habitat variables become more important when studying either small spatial scales or for the subsection of species which are animal-dispersed.

In relation to those characteristic MLG species which are regionally rare (see Table 2.2 for names), the only variable which has a higher R^2 regression value with this species subset, as opposed to the total flora, is Scrub Density. Scrub invasion is a successional process which through time creates environmental conditions which appear to be particularly adverse for rarer MLG species, eg. the calcium content of the soil is reduced. Sixty percent of sites suffer from scrub invasion (Pritchard 1989).

4.4 THE REGIONAL DISTRIBUTION OF SPECIES ACROSS THE STUDIED FRAGMENTS

A significant nested structure is present across the MLG habitat studied. This suggests that to some extent species are distributed across the MLG fragments such that biotas with lower numbers of species tend to be subsets of the biotas at richer sites. Though the overall Nestedness score is only moderate, the result implies that to some extent the species are distributed non-randomly. For example rare species tend to be found in the same MLG fragments. Therefore the Random Placement theory which states that species are randomly distributed through space appears to be weakened. However as yet research has not been able to pinpoint the exact processes and mechanisms which cause a Nested structure to develop. Theoretically nested patterns can be generated by either or both of the principal processes governing community change: Immigration and Extinction. However both these factors are highly inter-correlated and can offset each other (Wright & Reeves 1992).

Systems which are extinction-dominated, eg. landbridge archipelagos, have been shown to have the highest measures of Nestedness. One reason proposed for this is that species exhibit a graded series of extinction risks. This is created by the fact that the variance of stochastic processes changes inversely with population size, therefore extinction-driven systems may behave deterministically (Patterson 1990). However the results from the cumulative species curves showed that there was unlikely to be a significant graded series of extinction risks across MLG species as subdivision increases. It is possible however that graded extinctions patterns exist for a few rare characteristic MLG species. But they are obscured by the immigration of non-characteristic species, for example, ecotonal species. Furthermore it is possible that some species are doomed to extinction in the long term as a result of habitat loss (see the later example of *Linum perenne anglicum*). This will probably lead to the development of a stronger nested structure in the future.

By analysing species and habitat subsets separately for a Nested structure, insights are gained on which types of species or habitats contribute significantly to nestedness. It appears that MLG secondary habitats (which are expected to be influenced by Immigration to a greater extent) are not significant contributors to the overall nested structure. Therefore there is no evidence of consistent ordering during species colonisation certainly in the long term (most sites were abandoned over 50 years ago). Out of the three dispersal mechanism categories, animal-dispersed species (which are relatively lacking in adaptations for long range dispersal) show the strongest nested structure. This has also been shown by Kadmon (1995). It appears to suggest that if these species become extinct in a patch there is lower probability that individuals from a different population will recolonise. (Brown & Kodric-Brown (1977) term this the Rescue Effect).

As discussed previously non-characteristic species occur across the MLG habitat fragments and may act to distort species richness values. Figure 3.16 shows their effect on the overall distribution of species across the sampled fragments. The number of species occupying between 1-10% of fragments is accentuated. This may also be a result of the fact that several species in the MLG flora are on the edge of their biogeographical range. However even if these factors were controlled the distribution would probably not match that proposed by Hanski (1982) which predicts a bi-modal pattern with two primary groups; core species occurring at >90% of all fragments and satellite species occurring at <10% of all sites. (See Hanski 1982 for details). The main difference between the model and this distribution is that there are very few core species. In fact the few core species tend to be generalists as opposed to species characteristic of MLG, eg. *Centaurea nigra.* Characteristic species such as *Sesleria albicans* occurs in only sixty percent of sites. Figure 3.17 demonstrates that many of the species characteristic of MLG are categorised as decreasing due to modern landuse methods (Grime et al 1988). In effect the amount of habitat which coincides with their particular niche space is decreasing. This suggests that this community is particularly vulnerable to environmental change and is a conservation priority.

4.5 IMPLICATIONS FOR CONSERVATION POLICY

4.5.1 SLOSS debate (Single Large or Several Small)

There are a number of factors to be taken into account when discussing SLOSS in relation to a particular habitat. The critical factors are: the overlap in species composition between sites and the number of species per unit area in the different sites. The Cumulative Curve analysis showed that several smaller fragments (the most subdivided area) had a consistently higher cumulative species total than a few larger fragments (the least sub-divided area), ie. species overlap was low amongst smaller fragments. This implies that many small MLG reserves would protect a higher number of species as a opposed to a few large reserves. However neither of these analyses takes account of actual species composition. Needless to say not all the species found in the MLG fragments have equal conservation value. Those species which are of least value are generalists, ie. those found in many habitats - *Taraxacum spp.* Many of these species are members of the Wide Element. Moreover, there is a significant negative correlation between Percentage of Wide Element Species and Area of a fragment. This suggests that small areas are likely to have higher proportions of species with less conservational value. This is supported by Merriam & Wegner (1992) who found that smaller patches contain a larger proportion of ecotonal habitat which tends to support a mix of generalists and ruderals.

The case to protect large fragments is further advanced by the fact that over 23 species (listed in Section 3.2) do not occur in any of the 45 fragments which have an area of less than 2000m^2. Moreover this group of species contains several which are regarded as core CG8 species (Rodwell 1992). Furthermore there is also a possibility that smaller fragments may be in historical disequilibria. This means that the number of species supported will inevitably reduce over the long term as adjustments are made to past external changes, eg. increased isolation. A further argument favouring the protection and management of large fragments is the view that ecological relationships and habitat systems should be conserved as opposed to non-contextual species (Janzen 1983). If dramatic environmental change occurs, the chances of successful range migration by calcareous species not currently present are increased if the habitat area is maximised. In addition by maximising the amount of protected habitat, a greater range of micro-habitats are maintained which may support both remnant populations and new colonising species.

There are actually very few large MLG fragments left (only 12 are above one hectare). One of the largest remaining fragments is at Blackhall. Though the community has some of the species found on the inland fragments many others are absent particularly *Sesleria albicans*. I would therefore argue that whilst this site has conservational valuable it can not be considered true MLG habitat. In addition, the Thrislington site, which supports by far the largest area of MLG habitat in the study region, has an uncertain long term future. Though it is designated an NNR it may still be threatened by quarrying operations.

However it is possible that the area of MLG habitat may be increased if scrub is removed at approximately 60% of the fragments. But there remains uncertainty whether a MLG community could re-establish as soil chemistry may have been indelibly altered (Pritchard 1989). It is of note that in this study a significant negative relationship was found between the number of rare characteristic MLG species and scrub density. Therefore it appears optimal to protect and carefully manage all the existing large MLG fragments and as many small ones as possible. At present 65 out of the 98 fragments have either NNR or SSSI status but many of the small fragments are poorly managed, eg. under- or over-grazed. If choices have to be made regarding management priorities not only should a fragment's species richness and species overlap with other protected sites (termed "complementarity" by Vane-Wright, Humphries & Williams 1990) be considered but also the habitat extent.

Caveat

Much scientific attention has been focused on whether, in the long term, secondary sites can support MLG communities similar to those found on the primary sites, eg. Richardson, Davis & Evans (1980). (Most of the secondary sites have been recolonising for at least 50 years). Results from this study suggest that in general secondary fragments are not significantly under-saturated, ie. they do not contain fewer species than expected given the Species/Area relationship for all MLG fragments. In fact Bishop Middleham "A" has the highest fragment species richness. From their relatively low nested structure there does not appear to be any evidence of an ordered re-colonisation. Instead this appears to largely depend on the surrounding species pool, eg. undisturbed quarry rims. There is no significant relationship between the percentage of Wide element species and Secondary fragments. The only scale at which species richness appears to be significantly higher for primary sites is at the smallest quadrat scale.

4.5.2 Population Interactions between fragments

This study has shown that degree of isolation is significantly negatively correlated with species richness at all scales. Furthermore when species were divided according to their dispersal mechanism, those that are least adapted to long distance dispersal, eg. Animal-Dispersed, showed a stronger negative relationship with the degree of isolation. The negative relationship is most significant when degree of isolation is measured to a fragments with a high species richness. Therefore as a fragment becomes more isolated from others with a high species richness, the number of Animal-dispersed species decreases. It is possible that species populations in close proximity may interact to some extent, ie. individual fragment populations may be parts of wider metapopulations. This would suggest that fragment extinction rates may be related to the Immigration rate. However the distance threshold for population interactions is species-specific and requires detailed examination of a species' autoecology.

From the data collected in this study it is possible to draw some inferences from calculated Mean Interpopulation Distances (MIPD) (see Quinn et al 1994). For example it is unlikely that there is any interaction between the three populations of *Linum perenne anglicum* found across the study area as their MIPD is 23.3km. This suggests that the small existing populations are relicts and may well be doomed to extinction in the long term. In contrast *Epipactis atrorubens* is almost as rare with five populations but they are all concentrated on the Escarpment with a MIPD of 4.1km. Therefore they may interact and be viable long term populations.

In order to preserve the regional distribution of MLG species (and possibly increase abundance levels) particular attention should be given to conserving a close network of MLG sites. From within the study area I would choose the West Durham Escarpment sites where many of the most characteristic MLG communities exist (Doody 1977). Garmondsway Quarry and Quarrington Hill fragments both contain valuable MLG habitat and vegetation communities but as they are not protected or managed, are in danger of losing their wildlife interest. This would inevitably cause the Escarpment network to be weakened. The MLG fragments in Tyne & Wear tend to have a lower species richness. This produces an approximate North-South species-richness gradient. It is possible that there are a variety of causal factors including: isolation from species rich fragments ; Tyne & Wear is more heavily urbanised which reduces the extent of adjacent habitats which may source ecotonal species and imposes greater recreational use. The gradient may also be partly due to larger scale factors, such as climate, which work in synthesis with local agents to determine species' wider distributions (Ricklefs 1987).

4.6 THE ROLE OF CLIMATE IN DETERMINING SPECIES' BIOGEOGRAPHICAL RANGES

There is ample evidence that most autotrophs are highly effected by climatic variables (Woodward 1992). This assumption is further explored in relation to three species and their specific relationships with three bioclimatic variables (MTCO, GDD5 and AET/PET).

Due to the high degree of fit between the observed species distribution and that simulated from the three bioclimatic variables, it can be concluded that the distributions of *Bromus erectus* and *Thesium humifusum* over a 50km by 50km grid scale are correlated and probably mechanistically determined by climate. *Sesleria albicans's* distribution is only however partially correlated with the three bioclimatic variables as the degree of fit between the two distributions is only moderate. Though the climate response surface model predicts its range fairly accurately the probability of occurrence is generally low. One possible explanation may be that soil chemistry or historical factors are significant in determining *Sesleria albicans's* distribution. For example there is no climatic explanation why *Sesleria albicans* is absent from the South-East of England yet present on the Normandy Chalk (Rodwell 1992).

On a smaller scale, Doody (1980) notes that *Sesleria albicans* is not present on the Magnesian Limestone habitat on the North-East coast. From its Climate Response Surface the species has a very restricted GDD5 range particularly at the higher end. This would appear to be the specific limiting bioclimatic variable at the coast where accumulated temperatures are higher than on the Magnesian plateau (Mean Annual Temperature is 11.5°C for the coastal areas and 10.5°C for inland areas - Elmes & Free 1994). Conversely *Bromus erectus* is absent from inland MLG habitat North of Moorsley Banks (see Map 2.2). From its climate response surface it appears that GDD5 again is the limiting factor, except that *Bromus erectus* is restricted as GDD5 values are too low rather than too high. Furthermore it is possibly the same variable, GDD5, which prevents the further northward spread of *Thesium humifusum* in the British Isles. Its current northerly limit is in Lincolnshire. However these conclusions are tentative as they are of relatively fine resolution compared with the grid scale used to determine the Climate Response Surfaces.

In general the species appear to be in equilibrium with the present climate as there are no major areas of discrepancy between the observed and simulated distributions, ie. all suitable climate space is occupied. However *Sesleria albicans* only achieves low probabilities of occurrence across its observed range.

4.7 THE PREDICTION OF FUTURE SPECIES' DISTRIBUTIONS GIVEN THE OSU AND UKMO CLIMATE CHANGE SCENARIOS

Simulations of the distributions of the three species under the two contrasting 2 x CO_2 climate scenarios show major shifts of potential range (see Maps 3.1 to 3.12). In relation to the studied MLG area the predictions are as follows: under both scenarios *Bromus erectus* occurs in the MLG region, it is particularly prevalent under the OSU scenario with the studied area becoming close to the centre of its range; *Thesium humifusum* is predicted by OSU to expand northwards through England reaching the present MLG area, however the UKMO predicts a more extreme range shift such that its southern limit is north of North-East England; *Sesleria albicans* is predicted under the OSU to remain in the MLG area at the periphery of its range whereas the UKMO predicts a complete disappearance from the British Isles.

The potential consequences of the predicted climate change are therefore dramatic. Table 4.1 summarises the percentage correspondence between the simulated distributions from the climate change scenarios and those observed at present. From these results it is evident that *Thesium humifusum* with the most restricted present distribution is predicted to undergo an almost complete range shift under both scenarios. As species' migration rates are restricted it would appear that all species but particularly *Thesium humifusum* may be endangered as a consequence of climate change

Table 4.1 The Percentage Correspondence Values between the future simulated distributions and the present distributions for each species

Climate Change Scenario	*Bromus erectus*	*Thesium humifusum*	*Sesleria albicans*
OSU	0.34	0.09	0.19
UKMO	0.20	0.00	0.10

The most recent IPCC report (Houghton 1992) concludes that the best estimate of climate change is closer to that of the OSU with the UKMO now considered to represent an extreme scenario (see Section 2.3.4 for further details). Under a "Business as Usual scenario" doubling of carbon dioxide may occur by 2030-2050 however this may not be fully realised until the turn of the C21. There still exists a great degree of uncertainty regarding both the rate and magnitude of change particularly with regard to the degree to which cloud at different altitudes, atmospheric sulphate aerosols and sea plankton may act to reduce either radiative forcing or carbon dioxide levels.

There are several further reasons why the simulated species distributions under the scenarios may be unrealistic. Firstly, in the model, climatic change is applied "all at once" whilst in reality the change will be more gradual. However even considering this, it is unlikely that species such as those modelled will be able to achieve migration rates fast enough in order to be able to keep in contact with their rapidly shifting "bioclimatic envelope". Migration will be further perturbed by natural barriers such as expanses of water and mountain ranges. The UKMO scenario predicts a complete shift of *Thesium humifusum's* range across the Baltic Sea into Scandinavia. Furthermore no account has been made of human alteration of the natural environment which has reduced the amount of potentially available habitat which species could use as "stepping stones". At the very least it appears many species may undergo rapid range contraction. The only species identified as yet that may be able to achieve the necessary rates of migration (eg. >100km in 100 years - Peters 1992) to keep up with its shifting climatic optimum is *Fallopia japonica* (Beerling et al 1995). Finally the modelling techniques used take no account of the direct effects of CO_2 and its interaction with a species' physiological response to climate.

It has been argued that static correlative models such as climate response surfaces can not produce robust predictions of changes in plant distribution (Woodward & Smith 1994). However as more accurate mechanistic process based models are still on the drawing board. Static correlative models are the only practical tool at present which can be used to predict changing distributions. Moreover the palaeoecological record has revealed historic Temperate zone shifts of similar magnitude to those predicted here for analogous conditions. Furthermore different methods used in static correlative modelling produce very similar predictions. For example Huntley at al (In press) and Sykes, Prentice & Cramer (1994) who predicted very similar changes in the distributions of tree taxa via different methods.

Map 4.1: The distribution of calcareous exposures in the British Isles. Redrawn from Rodwell (1992)

KEY

a	Durness
b	Inchnadamph
c	Skye
d	Caenlochan-Glen Clova
e	Breadalbane
f	Upper Teesdale
g	Yorkshire Dales - Craven
h	Morecambe Bay
i	Great Orme
j	Derbyshire Dales
k	Durham - Yorkshire Magnesian
l	North York Moors
m	Yorkshire Wolds
n	Chilterns
o	Cotswolds
p	Breckland
q	Gower
r	Mendips
s	North Downs
t	South Downs
u	Hampshire & Dorset
v	Torbay

Those underlined are mentioned in the text

4.8 THE CONSEQUENCES FOR MAGNESIAN LIMESTONE GRASSLANDS

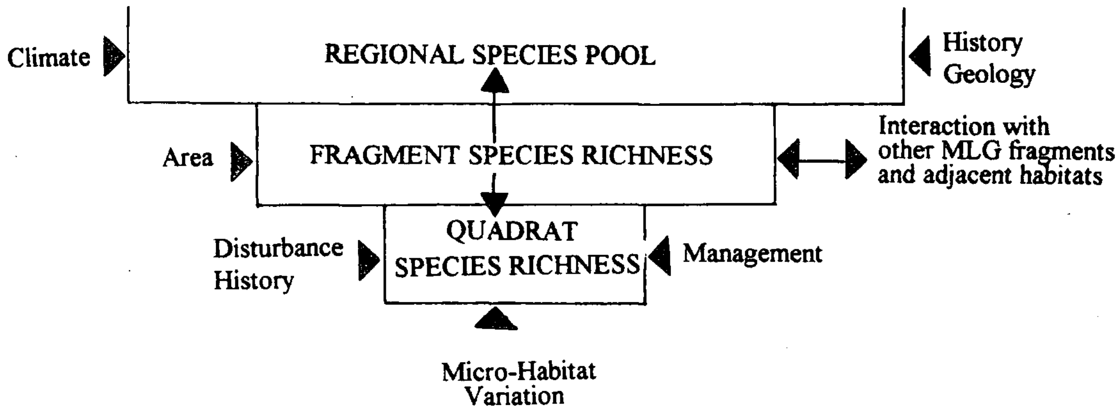
This part of the analysis has only involved three species and as the palaeoecological record shows species respond individualistically to climate change (Huntley 1991). Therefore it is impossible to extrapolate the findings beyond generalities, eg. ranges tend to expand in a northerly and easterly direction as a result of the predicted climate change. If the OSU scenario is realised the MLG community at present will change significantly as present species' ranges migrate and other species expand their distributional limits into the Magnesian Limestone area. A new association of species will arise and new ecological relationships/community dynamics will become established making prediction at the relatively small regional scale more difficult. It is probable however that the core community associated with MLG will not be dominated by *Sesleria albicans.* However *Bromus erectus* may become more important. Furthermore it is probable that species which currently have their southern limit in MLG, eg. *Primula farinosa* and *Epipactis atrorubens* will disappear shifting their range limits much further North. Elmes & Free (1994) predict that species which are stress tolerator strategists or niche specialists, (eg. *Primula farinosa* and *Epipactis atrorubens* and many other species which are found exclusively in calcareous grasslands) will be relatively disadvantaged as a result of climate change. In comparison strategists such as competitive-ruderals, who can tolerate a wide range of environmental conditions, will be advantaged.

It may be futile for conservationists to focus long term policies on particular species and especially those which are on the edge of their biogeographic range. In order to accommodate the predicted range shifts within conservation policy it is important to view sites and species from a national perspective. Map 4.1 shows the restricted spatial distribution of calcareous grassland in the British Isles. Magnesian Limestone outcrops extend sporadically into Nottinghamshire and are also in close proximity to the Carboniferous Limestone found in the Yorkshire Dales. However the Magnesian Limestone outcrops are relatively isolated from the linear bands of Limestone found in the South of England, eg. the Chilterns and Cotswolds. This is likely to be of significance for the future migration of species between regions as climate change occurs.

If the predicted rate of change is realised it is unlikely that the regional or local species richness of MLG habitat will be maintained due to limitations on species' migration rates. Migration rates of calcareous species may be further slowed by their specific habitat requirements. The MLG flora of North East England would no longer be the meeting point between the Arctic Alpine grasslands of the North and the Lowland thermophilous grasslands of the South which at present affords much of the botanical interest. Furthermore unless present sites are sufficiently protected they may become under increasing pressure from agriculture, as changing climate shifts crop belts, yield potentials and hence financial returns. However an initial study predicts that for County Durham and Tyne & Wear the proportion of land under cereal crops will not change dramatically (Parry et al In Press).

4.9 IN CONCLUSION

The schematic diagram below shows the variety of processes determining species richness at the quadrat, fragment and regional scale and also how the different spatial scales are inter-related.



Given the questions proposed at the outset of this study and the ensuing results each question is addressed briefly.

i) Multiple Linear Regression analysis showed Area or Perimeter to be the most significant variable predicting species richness at each of the three scales. At least one variable representing degree of isolation of the habitat is negatively correlated with species richness at all three scales. Micro-habitat variation is of most importance in determining species richness at the smallest scale.

ii) There is a strong exponential Species/Area relationship across the studied MLG fragments. The high number of ecotonal species in smaller fragments causes the curve to rise initially at an exponential rate. Several mechanisms contribute to the Species/Area relationship including a random sampling effect. However whilst the relationship is not maintained by an Equilibrium between Immigration and Extinction (as stated by MacArthur & Wilson (1967)), it is possible that a subset of rarer species may have a graded extinction risk which may be determined directly by area.

iii) It appears that a higher number of different species are supported in several small fragments compared to a few large ones. The low overlap in species composition between the small fragments may also be the result of the higher proportion of ecotonal habitat and historical disequilibrium. There are however several core MLG species which do not occur in fragments less than 2000m^2 in size.

iv) When species are divided according to dispersal mechanism or frequency of occurrence different combinations of variables predict species richness within these subsets.

v) There is a moderate nested structure suggesting that a proportion of species are not distributed randomly across the MLG fragments. Animal-Dispersed species show the strongest nested structure possibly suggesting that their limited dispersal ability in some way enhances the probability of extinction.

vi) Few characteristic MLG species occur in a high percentage of fragments. All existing MLG habitat should be protected and managed effectively. In the short term this allows the largest number of species to be protected and in the long term maximises the chance that suitable habitat will be available for migrating calcareous species. Self supporting metapopulations should be encouraged by regarding the individual fragment as part of a wider network.

vii) The distributional ranges of *Bromus erectus* and *Thesium humifusum* are highly correlated with MTCO, GDD5 and AET/PET. *Sesleria albican's* distribution whilst correlated with these bioclimatic variables appears also to be determined by additional variables.

viii) The distributional ranges of all three species change dramatically under the two scenarios. The degree of difference between the present and future simulated distributions is between 66% to 100%.

ix) The present MLG association will dissolve as species respond individualistically to climate change. It is likely that *Sesleria albicans* will no longer be the dominant grassland species. The regional migration of calcareous grassland species across the British Isles is likely to be further limited due to their specific habitat requirements.

4.10 RECOMMENDATIONS FOR FUTURE WORK

This study takes little account of treatment history or succession which is believed to be very important in maintaining the species richness of this type of grassland (Rodwell 1992). The specific effect of grazing, scrub removal and seral succession on fragment species richness and composition is very important when formulating local conservation policy for the Magnesian Limestone Grasslands. In addition it would of further value to investigate and quantify micro-habitat gradients in order to fully understand their contribution to small scale species richness.

If this study were to be repeated it would be of great value if the relative abundance of species and species overlap between fragments could be empirically quantified. This would facilitate the use of modern diversity indices which overcome some of the limitations faced when only using species richness values (Magurran 1988).This would also allow the role of transients in increasing species richness to be assessed.

In order to gain a comprehensive understanding of the MLG community and be able to predict its future with more certainty long term monitoring of species' populations and distributions is needed. This would allow information to be gathered on the factors influencing persistence times and extinction risks of specific MLG species. Furthermore in the future, it may be possible to quantify dispersal abilities of individual species in relation to a specific landscape with the use of Geographical Information Systems. This could be used both at a local scale for present distributions and at a national or international scale for those predicted by the climate change scenarios.

In addition more studies are required which study the potential consequences of future climate change on the community dynamics of calcareous grasslands, eg. the ongoing study at Aston Rowant, Oxfordshire which studies the effects on recruitment and inter-specific interactions from winter warming and changing summer precipitation on calcareous grasslands. Ideally these studies should transplant species not currently present but whose climatic range may potentially include the study area. Due to the magnitude of the predicted change future studies must incorporate a national perspective and view all calcareous grasslands as one disjointed species pool.

APPENDICES

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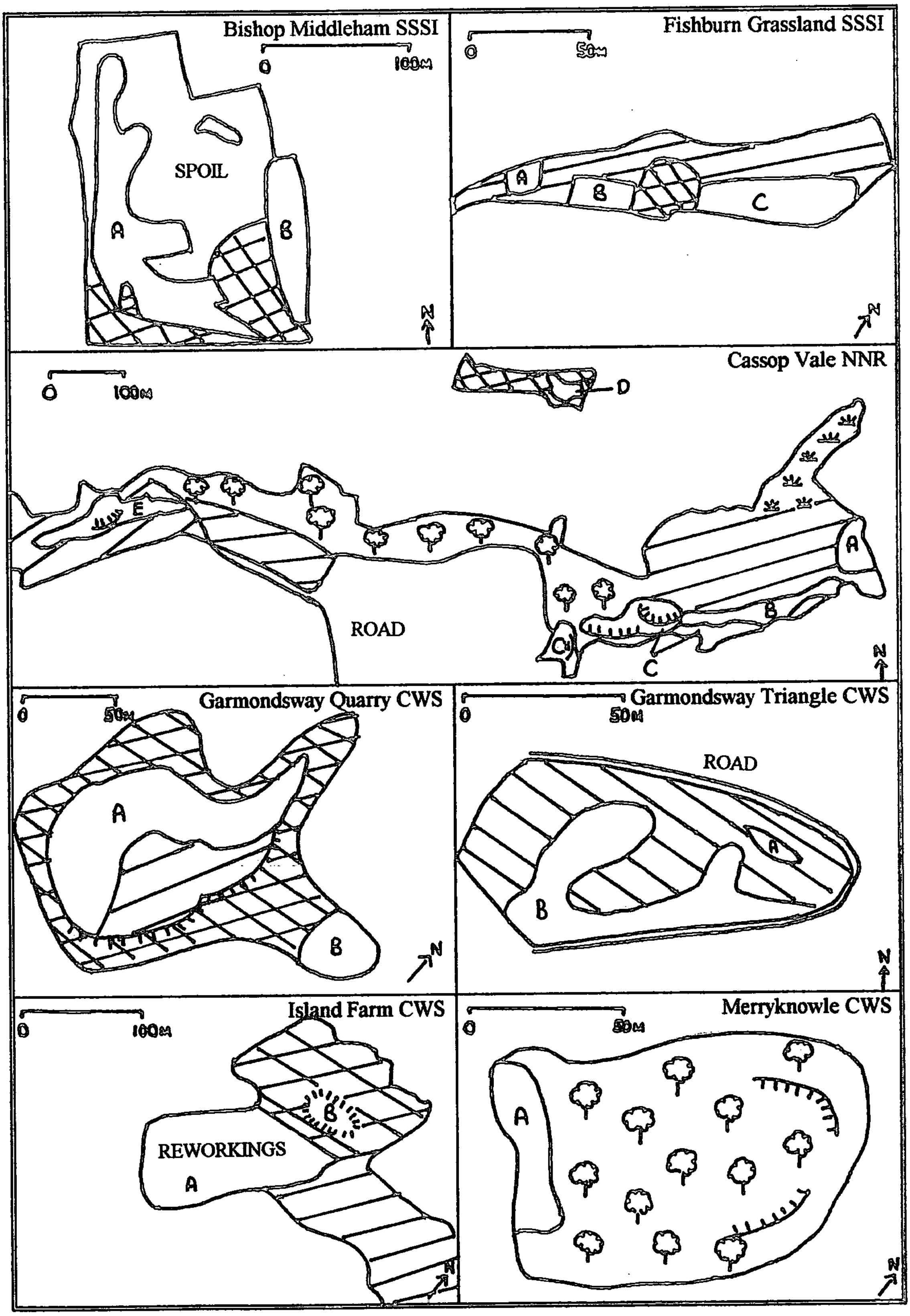
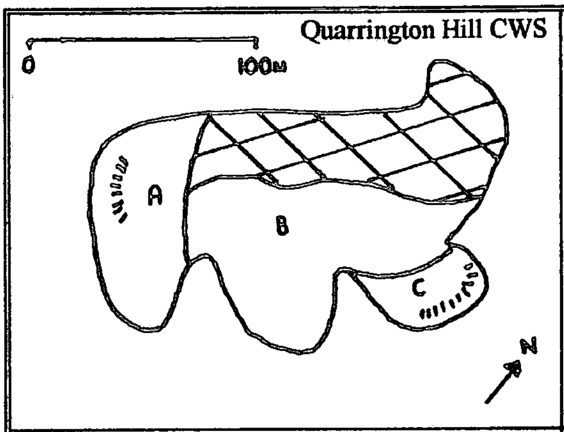
APPENDIX I : Maps of the 42 sites and the positions of the MLG fragments.

A: Western Escarpment Sites



A: Western Escarpment Sites continued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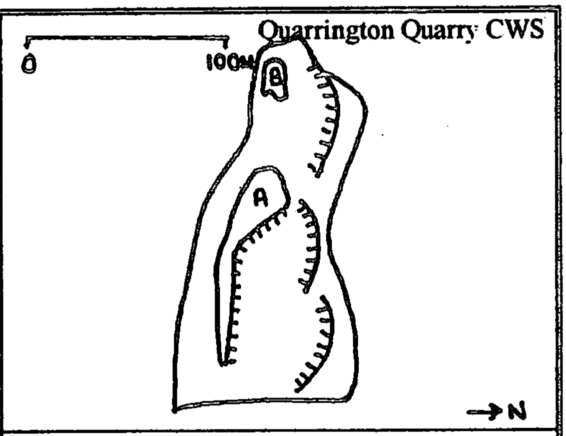
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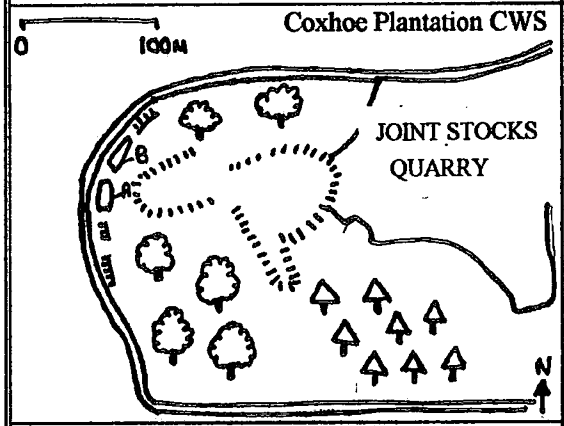
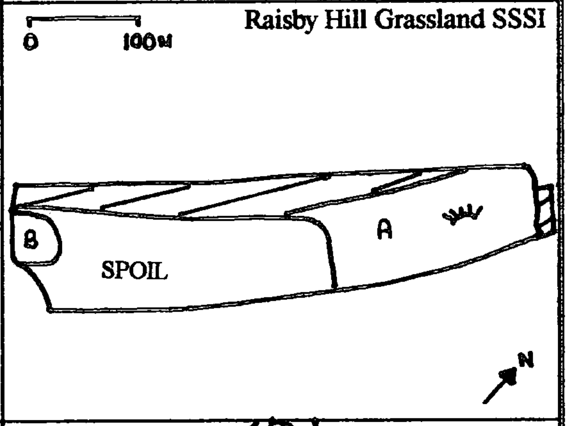
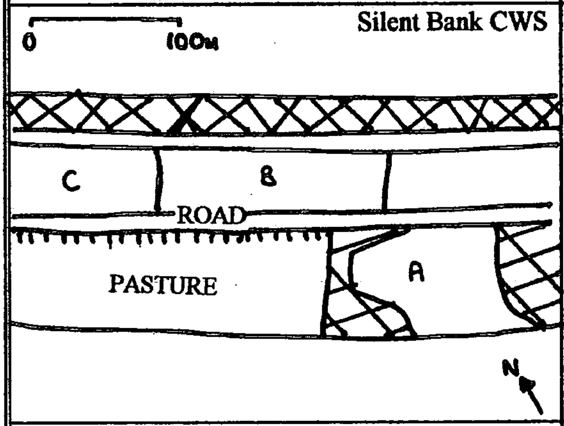
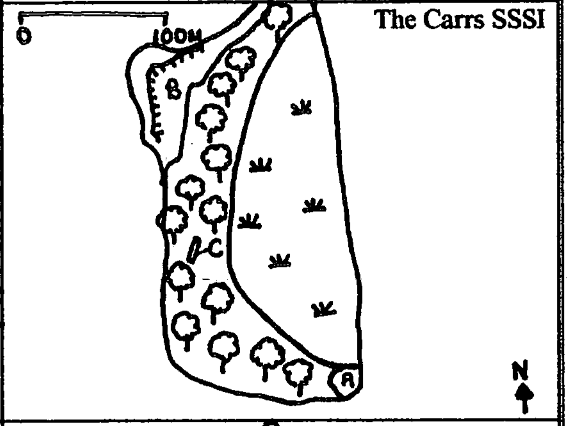
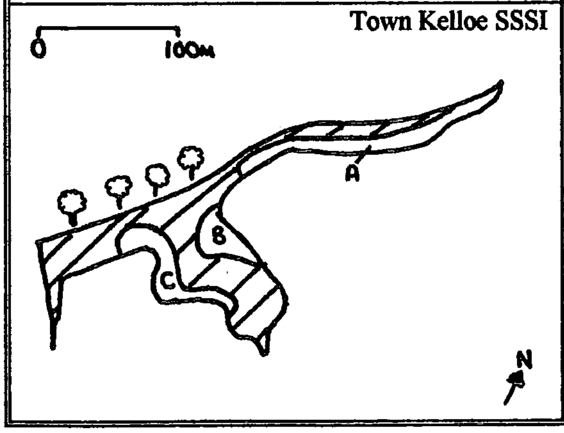
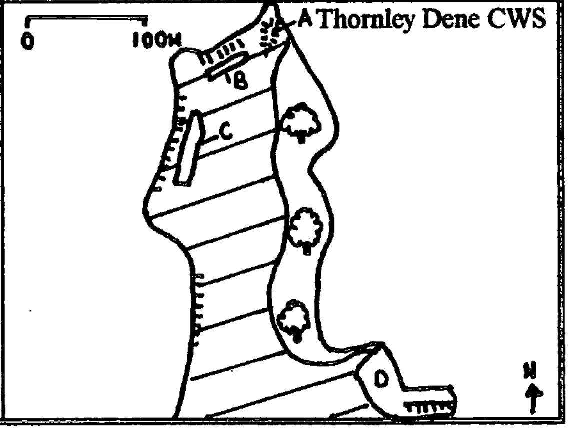

Coxhoe Plantation CWS


Raisby Hill Grassland SSSI

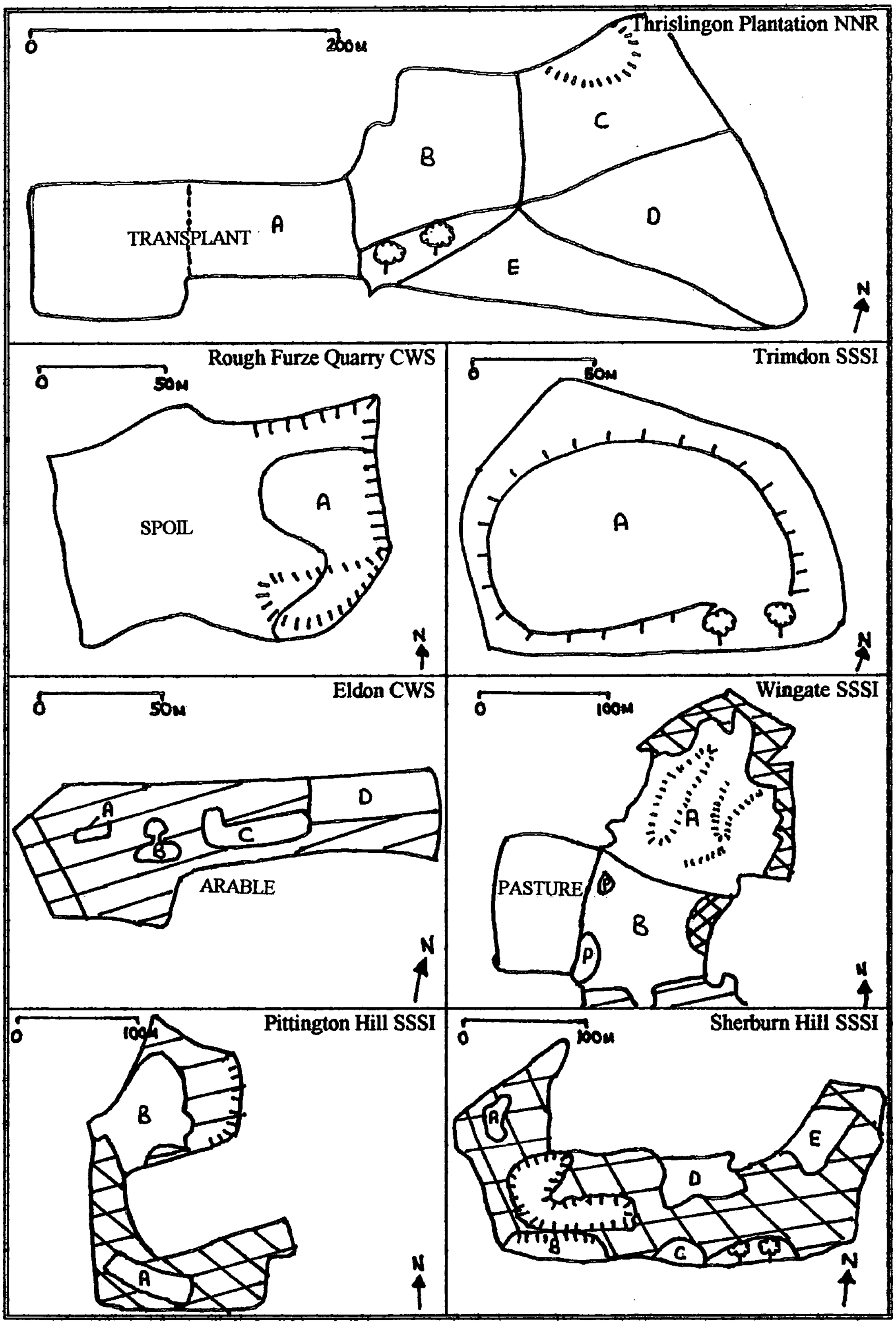

Silent Bank CWS


The Carrs SSSI

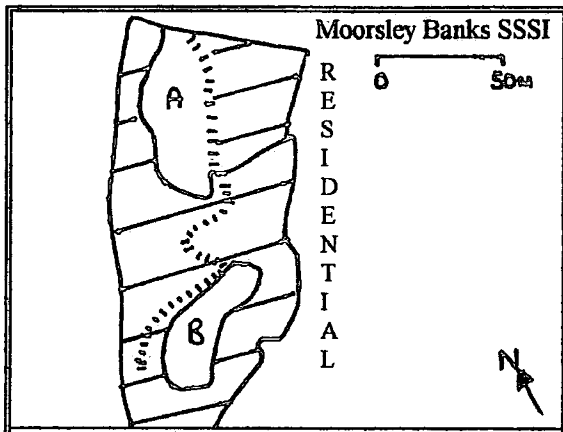

Town Kelloe SSSI

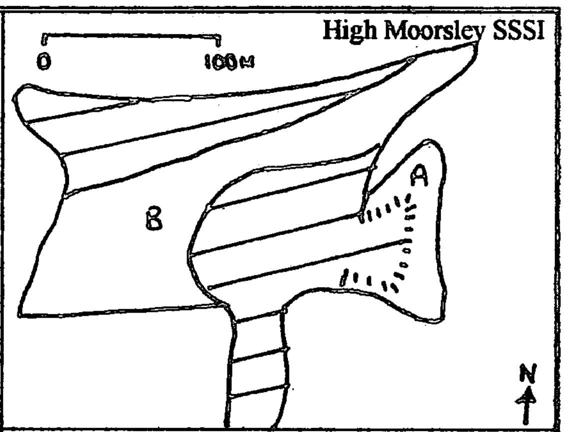

Thornley Dene CWS

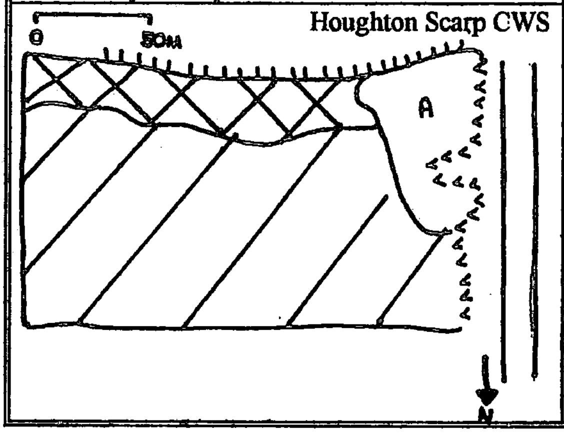
A: Western Escarpment Sites continued

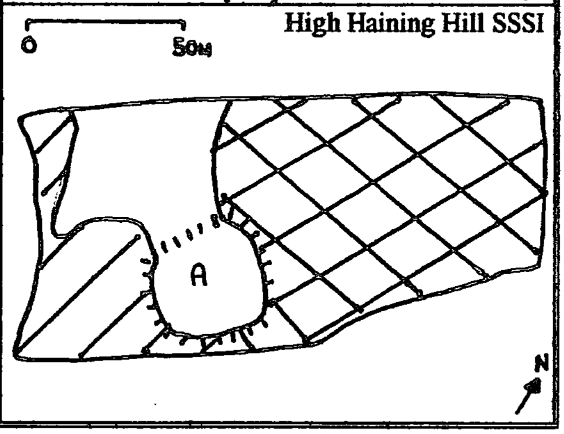


A: Western Escarpment Sites continued

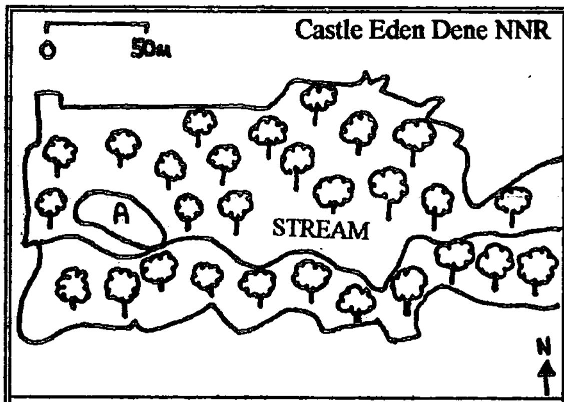

Moorsley Banks SSSI

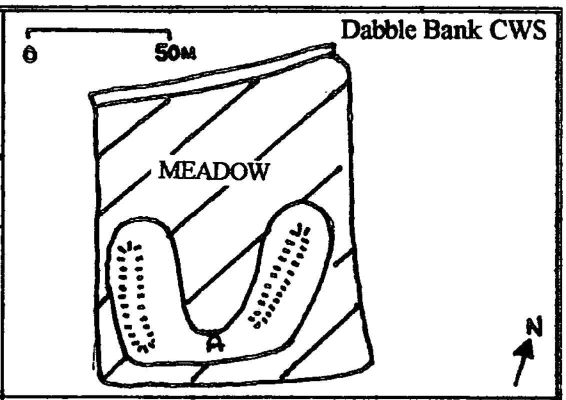

High Moorsley SSSI

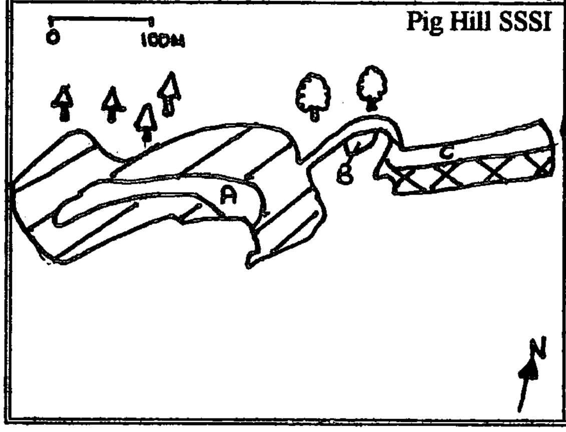

Houghton Scarp CWS

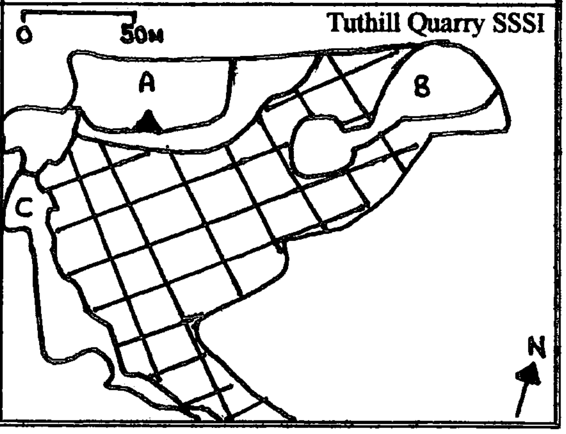

High Haining Hill SSSI

B: Reef Formation Sites

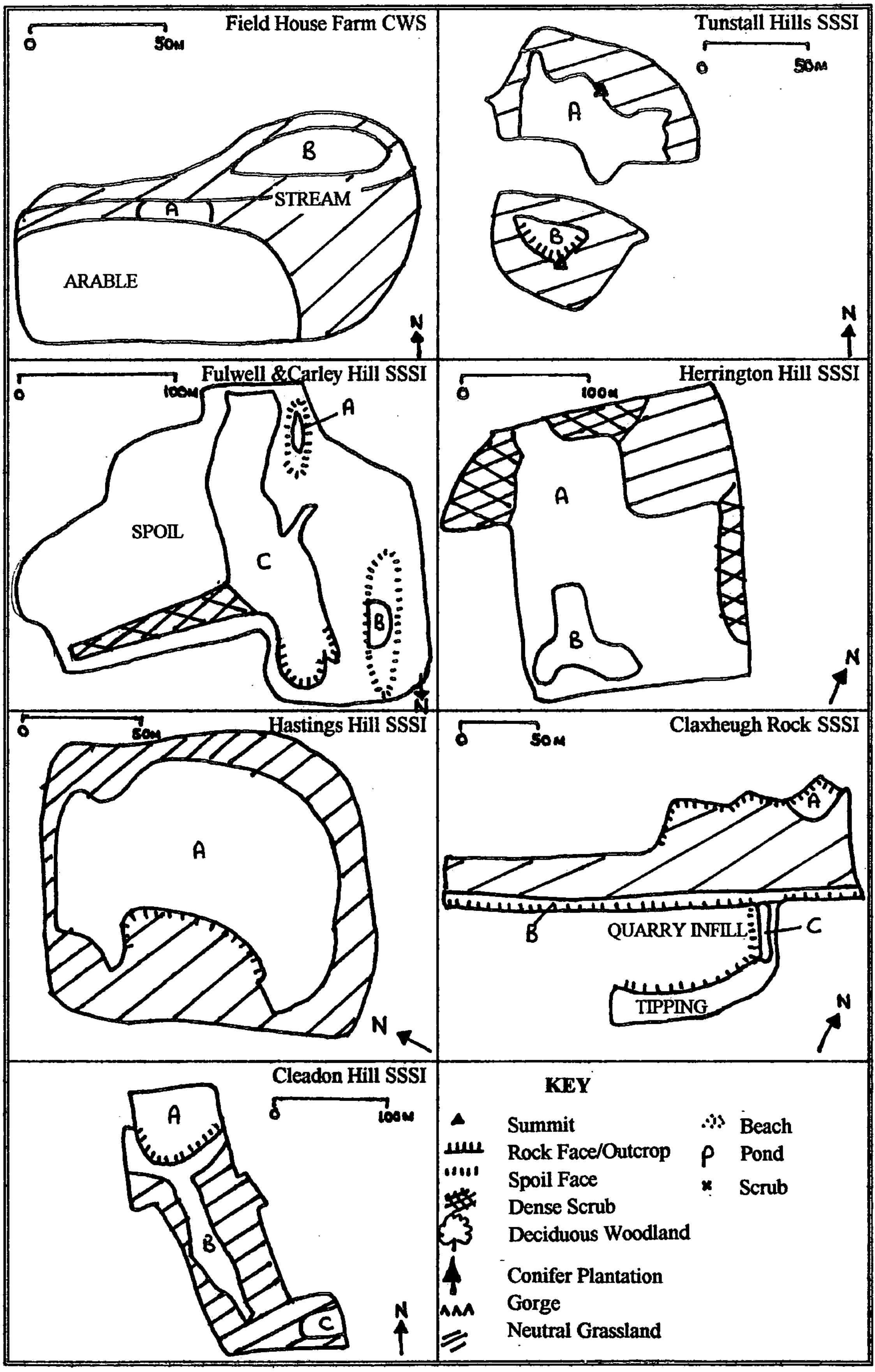

Castle Eden Dene NNR


Dabble Bank CWS

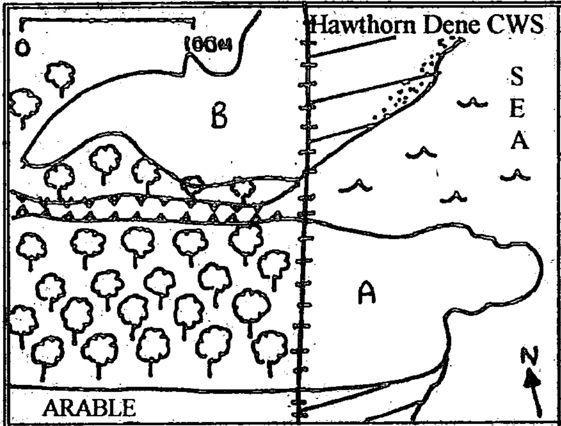

Pig Hill SSSI

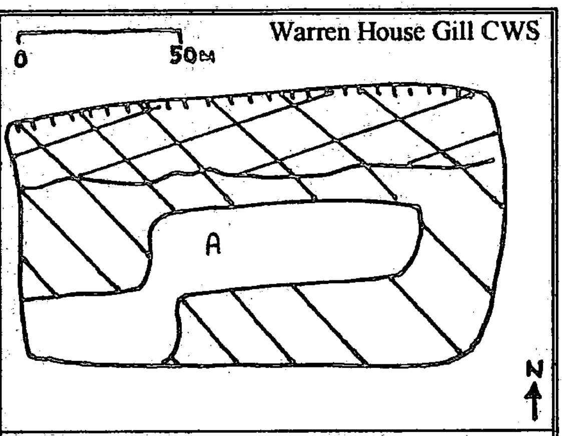

Tuthill Quarry SSSI

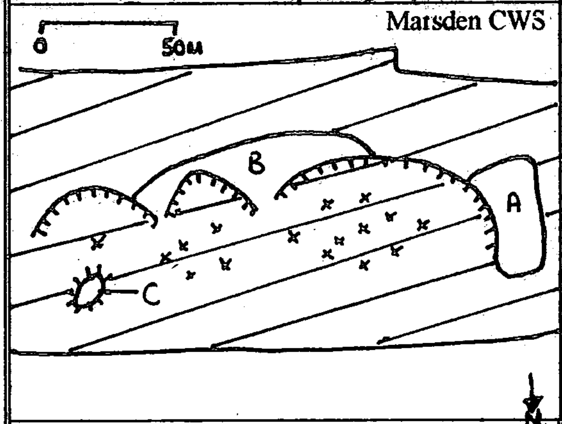
B: Reef Formation sites continued

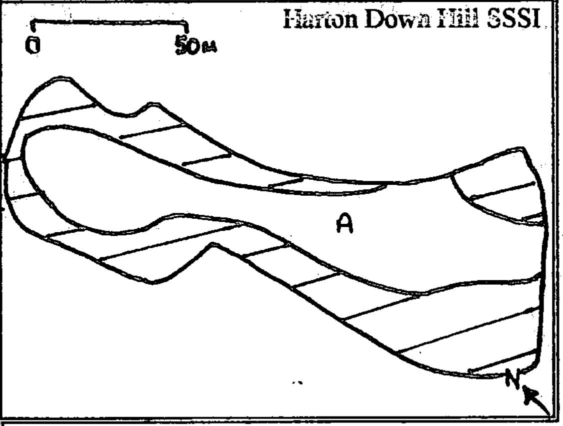


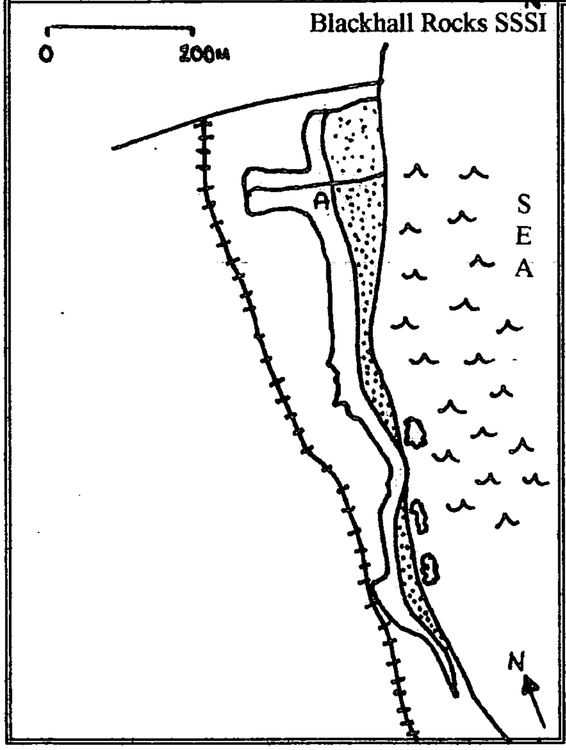
C: Coastal Sites











KEY FOR APPENDIX II

Phytogeographic Element (E)
Graham (1988)

W	Wide
WSA	Western Sub Atlantic
CN	Continental Northern
CS	Continental Southern
SSA	Southern Sub Atlantic
NM	Northern Montane
NSA	Northern Sub Atlantic
ON	Oceanic Northern
E	Endemic

Dispersal Mechanism
Grime et al (1988)

W	Wind Dispersed
A	Animal Dispersed
U	Unspecialised

Current status (CS)
Grime at al (1988)

+	abundance is increasing in response to modern methods of land use
-	abundance is decreasing in response to modern methods of land use
?	there is uncertainty

APPENDIX III: A SUMMARY OF THE PHYTOGEOGRAPHICAL ELEMENT, DISPERSAL MECHANISM AND CURRENT STATUS FOR EACH SPECIES

SPECIES	E	DM	CS	SPECIES	E	DM	CS
Achillea millefolium	W	W	?	Cirsium heterophyllum	CN	W	-
Aegopodium podagraria	W	U	+	Cirsium palustre	W	W	+
Agropyron repens	W	U	+	Cirsium vulgare	W	W	?
Agrostis capillaris	W	U	-	Cochlearia officinalis	ON		
Agrostis stolonifera	W	U	+	Coeloglossum viride	NM		
Agrimona eupatoria	W	A	-	Conopodium majus	OWE	U	-
Ajuga reptans	WSA	A	-	Crepis capillaris	WSA	W	+
Alchemilla vulgaris	CN	A	-	Cynosaurus cristatus	W	U	-
Anacamptis pyramidalis	SSA	W	-	Dactylis glomerata	W	U	?
Anemone nemorosa	W	A	-	Dactylorhiza fuchsii	CN	W	?
Angelica sylvestris	W			Dactylorhiza purpella	WSA		
Antennaria dioica	NM			Danthonia decumbens	W	A	-
Anthoxanthum odaratum	W	A	-	Daucus carota	W	A	-
Anthriscus sylvatica	W	U	?	Deschampia cespitosa	W	A	?
Anthyllis vulneraria	WSA	W	-	Epilobium angustifolium	W	W	+
Aquilegia vulgaris	W			Epilobium montanum	W	W	?
Arabis hirsuta	CS	U	-	Epipactis atrorubens	CN		
Armeria maritima	OWE			Epipactis palustris	W		
Arrhenatherum elatius	W	A	+	Equisetum arvense	W		
Astragalus danicus	CN			Erigeron acer	W	W	?
Avenula pratensis	WSA	A	-	Eupatorium cannabium	W	W	?
Avenula pubescens	CN	A	-	Euphrasia officinalis	CN	W	-
Barberea vulgaris	W	W	?	Festuca arundincea	W	A	?
Bellis perennis	WSA	U	+	Festuca ovina	CN	A	-
Blackstonia perfoliata	CS			Festuca pratensis	W	A	-
Brachypodium pinnatum	W	U	?	Festuca rubra	W	A	-
Brachypodium sylaticum	W	A	-	Festuca tenuifolia	C	A	-
Briza media	C	U	-	Filipendula ulmaria	CN		
Bromus erectus	SSA	A	?	Fragaria vesca	W	A	-
Bromus mollis	W			Galium aparine	W	A	+
Campanula glomerata	C			Galium cruciata	CS	U	-
Campanula rotundifolia	W	W	-	Galium verum	W	U	-
Carduus acanthoides	C	W	?	Gentianella amarella	CN	W	?
Carduus nutans	CS	W	-	Geranium molle	W	A	?
Carex caryophyllea	W	U	-	Geranium pratense	W		
Carex flacca	WSA	U	-	Geranium robertianum	W	A	+
Carex panicea	W			Geranium sanguineum	W	A	-
Carex pulicaris	WSA	U	-	Geranium sylvaticum	CN		
Carlina vulgaris	CS	W	-	Geum rivale	W	A	-
Centaurea nigra	WSA	U	+	Gymnadenia conopsea	W	W	?
Centaurea scabiosa	W	U	-	Helianthemum nummul.	W	A	-
Centaurium erythraea	WSA	W	+	Heracleum sphondylium	WSA	W	+
Cerastium fontanum	W	U	+	Hieracium spp.	W	W	+
Cirsium arvense	W	W	?	Hieracium pilosella	W	W	-

SPECIES	E	DM	CS	SPECIES	E	DM	CS
Holcus lanatus	W	U	+	Ranunculus acris	W	A	-
Hypericum hirsutum	W	W	-	Ranunculus bulbosus	W	A	-
Hypericum montanum	C			Ranunculus ficaria	W	A	?
Hypericum perforatum	W	W	+	Ranunculus repens	W	A	+
Hypericum pulchrum	WSA	W	-	Reseda lutea	SSA		
Hypochoeris radicata	W	W	-	Rhinanthus minor	W	W	-
Juncus articulatus	W	A	-	Rumex acetosella	CN	W	?
Knautia arvensis	W	A	-	Rumex obtusifolius	WSA	A	+
Koeleria macrantha	CS	U	-	Sanguisorba minor	CS	U	-
Lathyrus pratensis	W	U	-	Sanicula europea	WSA	A	-
Leontodon autumnalis	W	W	+	Scabiosa columbaria	CS	A	-
Leontodon hispidus	W	W	?	Sedum acre	W	W	-
Leucanthemum vulgare	W	U	-	Senecio erucifolius	CS	W	-
Linum catharticum	W	U	?	Senecio jacobea	W	W	-
Linum perenne ang	E			Serratula tinctoria	C	W	-
Listera ovata	W	W	-	Sesleria albicans	NSA	A	-
Lolium perenne	W	U	+	Silaum silaus	C		
Lotus corniculatus	W	U	-	Silene alba	W	W	+
Luzula campestris	W	A	?	Silene dioica	W	W	-
Medicago lupulina	W	U	?	Silene vulgare	W	W	+
Molinia caerula	W	U	-	Sonchus asper	W	W	+
Mysostis arvensis	W	A	?	Sonchus oleraceus	W	W	+
Onobrychis viciifolia	C			Stachys officinalis	W	U	-
Ononis repens	WSA	U	-	Stachys sylvatica	W		
Ononis spinosa	WSA			Stellaria graminea	W	U	-
Ophrys apifera	SSA	W	-	Succisa pratensis	W	A	-
Orchis mascula	W	W	-	Taraxacum spp.	W	W	+
Origanum vulgare	W	U	-	Teucrium scorodonia	SSA	U	-
Parnassia palustris	CN			Thalictrum minus	WSA		
Pimpinella saxifraga	W	W	-	Thymus praecox .	OWE	U	-
Pinguicula vulgaris	CN			Torilis japonica	C	A	+
Plantago lanceolata	W	A	+	Tragopogon pratense	W	W	?
Plantago major	W	A	+	Trifolium medium	C	A	-
Plantago maritima	WSA	A	?	Trifolim pratense	W	A	?
Plantago media	W	A	?	Trifolium repens	W	A	+
Poa annua	W	U	+	Trisetum flavescens	CS	A	-
Poa pratensis	W	U	-	Trollius europaeus	NM		
Poa trivalis	W	U	+	Tussilago farfara	W	W	+
Polygala vulgaris	WSA	A	-	Valeriana dioica	C		
Potentilla anserina	W	U	?	Valeriana officinalis	W	W	-
Potentilla erecta	W	U	-	Veronica chamaedrys	W	U	-
Potentilla reptans	W	U	+	Veronica officinalis	W	U	-
Potentilla sterilis	WSA	U	-	Vicia cracca	W	U	-
Primula farinosa	NM			Vicia sativa	W	U	?
Primula veris	CS	W	-	Vicia sepium	W	U	-
Primula vulgaris	WSA	A	-	Viola hirta	W	A	-
Prunella vulgaris	W	A	+	Viola odorata	W	A	-
Pyrola rotundifolia	CN			Viola reichenbachiana	SSA		
				Viola riviniana	W	A	-

APPENDIX III: Raw data values for each variable at a fragment scale

	FSR	Area	Perim	SRNN	MD NN	Dist58	No5km	No2.5km	SR2.5km	QSR	WSR	ASR	USR	AVH
Eldon A	23	198.35	60.55	22	10.56	7927.78	3	3	24.00	8	10	7	6	19
Eldon B	22	215.01	60.31	23	10.56	7896.80	3	3	24.33	8	7	9	6	21
Eldon C	18	54.62	34.52	32	14.32	7866.76	3	3	25.67	7	6	4	8	22
Eldon D	32	1208.71	148.02	18	14.32	7824.51	3	3	21.00	8	10	10	12	18
TK A	45	4191.47	496.75	64	83.64	83.64	34	17	55.29	10	14	16	14	17
TK B	64	1245.70	157.62	62	30.93	30.93	34	17	54.18	14	22	25	16	8
TK C	62	2142.96	225.81	64	30.93	30.93	34	17	54.29	14	20	25	16	8
Fish A	58	228.63	59.53	71	16.00	16.00	25	7	51.86	15	20	21	16	13
Fish B	71	481.93	97.65	58	16.00	16.00	25	7	50.00	13	20	26	24	12
Fish C	72	1503.22	217.09	71	50.26	50.26	26	8	52.25	14	22	28	21	17
Harton A	57	3600.75	373.82	36	1140.51	21843.42	6	6	38.17	14	17	21	17	11
F&C Quar A	27	116.05	60.99	47	24.25	16060.82	10	2	39.50	7	9	6	10	12
F&C Quar B	32	346.18	85.71	47	34.11	16179.14	11	2	37.00	8	13	5	14	20
F&C Quar C	47	5944.47	396.03	27	24.45	16113.05	11	2	29.50	12	16	13	17	14
Cleadon A	56	3780.19	352.82	35	0.00	19545.66	9	6	38.33	14	18	20	18	9
Cleadon B	35	8092.73	579.83	56	0.00	19392.50	9	6	41.83	9	11	13	11	17
Cleadon C	24	619.67	98.36	35	149.80	19498.67	9	6	43.67	8	9	7	8	21
Marsden A	36	235.66	67.85	44	175.60	20916.94	9	6	41.67	9	14	12	10	10
Marsden B	44	2053.94	285.80	34	91.51	20995.73	9	6	40.33	11	13	16	15	12
Marsden C	34	70.72	35.19	44	91.51	21174.82	8	6	42.00	9	13	9	11	15
Clax A	41	815.08	106.22	43	100.00	13429.12	10	2	33.00	10	13	11	17	17
Clax B	43	2172.66	620.15	23	23.94	13109.10	10	2	32.00	10	15	12	15	22
Clax C	23	447.73	100.19	43	23.94	13277.39	10	2	42.00	8	8	4	10	16
Tunstall A	49	6398.84	373.62	36	132.02	11769.59	9	1	36.00	9	12	16	17	20
Tunstall B	36	1263.03	138.91	49	132.02	11671.48	9	1	49.00	11	12	11	12	13
Hastings	44	4430.76	368.27	49	1558.08	10131.51	9	2	43.50	13	16	15	13	10
Raisby A	67	5070.47	379.21	50	392.62	2084.77	48	13	46.08	9	20	28	19	20
Raisby B	52	2586.05	202.03	67	392.62	392.62	48	12	49.75	11	17	18	14	9
Wingate A	69	73404.98	1559.70	44	3.46	498.01	33	9	50.67	13	25	22	19	16
Wingate B	44	34507.75	917.51	69	3.46	3.46	32	9	53.44	11.5	17	15	12	20
Trimdon A	69	5118.56	267.15	62	1721.98	1721.98	42	10	54.00	10.6	26	21	20	13
Silent A	44	2674.57	456.44	47	915.62	1179.57	35	20	49.20	10	13	14	16	24
Silent B	35	1268.65	364.05	47	81.59	1220.46	35	20	49.65	11	12	8	15	17
Silent C	47	1103.36	260.19	35	81.59	1310.30	36	21	48.14	9	13	19	14	9
BM A	85	16859.71	482.15	61	81.30	81.30	29	15	51.93	12	35	25	22	13
BM B	61	2513.06	258.65	85	81.30	81.30	28	14	53.79	10	21	18	20	14

	ScrubDen	AvBG/BR	Prim %	Aspect	SlopAng	Wide %	Scrubrem	Wood	Flushing	Neut Gld	Acid Gld	Arable	Grazing	No.Habit
Eldon A	23	0	100	315	7	83	0	1	1	1	0	1	0	3
Eldon B	20	0	100	315	7	82	0	1	1	1	0	1	0	3
Eldon C	15	0	100	315	7	78	0	1	1	1	0	1	0	3
Eldon D	13	1	100	315	7	81	0	1	1	1	0	1	0	3
TK A	1	0	100	0	35	73	0	0	1	1	0	0	1	2
TK B	0	0	100	225	40	69	1	1	1	1	0	0	1	3
TK C	1	0	100	40	40	69	1	1	1	1	0	0	1	3
Fish A	4	5	100	315	15	67	0	1	1	1	0	0	0	3
Fish B	5	35	100	315	15	70	1	1	1	1	0	0	0	3
Fish C	2	10	100	315	18	71	1	1	1	1	0	0	0	3
Harton A	0	10	100	45	45	63	0	0	0	1	0	0	0	1
F&C Quar A	5	10	0	0	0	62	0	0	0	1	0	0	0	1
F&C Quar B	3	30	0	90	50	81	0	0	0	1	1	0	0	2
F&C Quar C	9	25	0	225	55	60	0	0	0	1	1	0	0	2
Cleadon A	0	0	100	330	5	64	0	0	1	1	0	0	0	2
Cleadon B	3	0	100	200	5	69	0	0	0	1	1	0	0	2
Cleadon C	0	0	0	0	0	83	0	0	0	1	1	0	0	2
Marsden A	0	20	100	10	5	69	0	0	0	1	0	0	0	1
Marsden B	4	5	100	0	0	57	0	0	0	1	0	0	0	1
Marsden C	0	25	0	70	40	65	0	0	0	1	1	0	0	2
Clax A	3	10	100	45	15	63	1	0	1	1	0	0	1	2
Clax B	5	35	0	55	20	56	0	0	1	1	1	0	0	3
Clax C	0	40	0	270	25	78	0	0	1	1	1	0	0	3
Tunstall A	1	0	100	100	10	63	0	0	1	1	0	0	0	2
Tunstall B	5	10	100	5	50	67	0	0	1	1	0	0	0	2
Hastings	0	3	90	270	35	55	0	0	1	1	0	1	1	2
Raisby A	5	2	100	10	25	73	1	1	1	1	0	0	1	3
Raisby B	1	25	0	0	0	60	0	1	0	1	0	0	0	2
Wingate A	5	7	25	0	25	65	0	1	1	1	0	0	0	3
Wingate B	2	2	100	230	15	68	0	1	1	1	1	0	0	4
Trimdon A	1	20	0	0	0	64	1	1	0	1	0	0	0	2
Silent A	5	0	100	225	35	73	0	0	1	1	1	1	0	3
Silent B	6	10	0	0	0	63	0	0	0	1	0	0	0	1
Silent C	1	30	100	180	45	62	0	0	0	0	0	0	0	0
BM A	4	15	25	90	30	65	0	1	1	1	0	0	0	3
BM B	7	8	100	0	0	61	0	1	0	1	0	0	0	2

	FSR	Area	Perim	SRNN	MD NN	Dist58	No5km	No2.5km	SR2.5km	QSR	WSR	ASR	USR	AVH
Garm Tri A	18	57.41	31.25	40	10.84	549.28	45	15	60.53	7	5	7	6	23
Garm Tri B	40	1647.73	243.64	18	10.84	520.10	45	16	59.06	9	9	15	16	25
Garm Qu A	61	31117.32	706.13	49	32.22	840.90	38	19	56.37	12	22	24	15	15
Garm Qu B	49	1104.29	135.50	61	32.22	32.22	38	19	57.00	11	18	17	14	22
Cassop A	65	2349.59	191.54	81	127.61	127.61	36	20	50.45	14	18	27	20	15
Cassop B	81	8353.17	427.62	73	54.25	54.25	36	20	49.65	16	30	28	20	14
Cassop C	73	4202.51	259.92	81	54.25	54.25	36	22	48.73	11	28	21	21	17
Cassop Cii	45	656.13	114.72	73	104.90	104.90	36	20	50.60	12	14	17	13	10
Cassop D	48	3257.56	223.20	73	398.76	398.76	34	19	50.89	11	18	17	12	15
Cassop E	52	4238.07	307.10	35	703.65	855.75	34	15	50.00	12	16	21	14	14
Sherburn A	30	4186.76	256.08	31	149.80	473.72	31	5	46.26	9	3	14	13	17
Sherburn B	31	1430.63	163.59	30	149.80	302.43	31	7	44.14	8	12	9	10	10
Sherburn C	44	1222.95	156.64	62	106.66	106.66	32	7	42.29	9	16	13	13	15
Sherburn D	62	6858.47	322.56	44	106.66	2623.46	32	7	39.71	13	16	24	19	16
Sherburn E	47	1369.55	166.21	62	163.17	163.17	32	7	41.86	11	12	16	19	18
Herring A	49	15316.73	584.37	38	0.00	8431.24	9	4	46.25	12	14	19	15	15
Herring B	38	2827.33	217.00	49	0.00	8416.94	9	4	49.00	10	16	10	11	11
CED A	52	313.25	89.92	44	3989.09	4131.64	6	0	0.00	9	14	21	17	10
Hawth A	52	3049.95	261.06	46	95.42	11050.69	2	1	46.00	11	14	14	22	18
Hawth B	46	7251.82	410.80	52	95.42	10852.15	2	1	52.00	14	15	16	15	20
Warren A	53	662.56	120.16	68	3336.67	5694.97	4	0	0.00	12	18	18	16	21
Tuthill A	37	2004.61	200.05	59	62.06	62.06	7	4	57.75	12	13	9	15	17
Tuthill B	65	5396.50	299.34	37	63.70	165.70	7	3	53.67	10	24	19	20	12
Tuthill C	59	3374.17	403.81	37	62.06	165.70	7	4	52.25	12	22	18	19	14
FHF A	43	54.72	31.53	36	8.92	9384.00	4	1	36.00	7	15	16	12	13
FHF B	36	170.72	54.01	43	8.92	9404.13	4	1	43.00	8	11	13	12	24
High Moor A	54	942.37	228.70	54	61.34	637.39	15	5	54.80	9	19	15	20	8
High Moor B	51	7375.77	421.64	51	61.34	587.17	14	5	55.40	10	16	18	17	14
Moor Bk A	47	3855.84	286.83	51	90.93	1429.02	16	5	56.20	11	16	12	18	18
Moor Bk B	51	5592.76	345.14	47	90.93	1211.21	15	5	55.40	14	17	16	17	12
Thris A	77	39727.45	1067.12	59	0.00	0.00	24	13	55.69	18	23	28	25	13
Thris B	59	21644.47	668.83	77	0.00	0.00	24	15	54.73	10	15	28	15	9
Thris C	63	35498.34	792.33	59	0.00	0.00	29	16	52.19	16	18	26	17	9
Thris D	55	37528.02	866.40	63	0.00	0.00	25	16	52.69	12	15	25	14	8
Thris E	55	29350.44	991.75	77	0.00	0.00	25	16	52.69	13	15	25	14	10
R Furze A	51	2458.21	272.26	55	58.07	231.73	24	14	56.36	8	19	14	16	13

	ScrubDen	AvBG/BR	Prim %	Aspect	SlopAng	Wide %	Scrubrem	Wood	Flushing	Neut Gld	Acid Gld	Arable	Grazing	No.Habit
Garm Tri A	0	0	0	0	0	67	0	0	1	1	0	1	0	2
Garm Tri B	0	0	0	0	0	75	0	0	1	1	1	1	0	3
Garm Qu A	13	2	100	270	35	64	0	1	1	1	0	0	0	3
Garm Qu B	1	5	100	350	10	65	0	1	0	1	0	1	0	2
Cassop A	3	5	100	320	15	71	0	0	1	1	0	0	0	2
Cassop B	5	3	100	345	30	68	1	1	1	1	0	0	1	3
Cassop C	3	10	0	0	0	70	1	1	1	1	0	0	0	3
Cassop Cii	0	35	100	75	50	58	0	0	0	0	0	0	0	0
Cassop D	15	5	100	175	30	67	1	0	1	1	1	0	1	3
Cassop E	7	2	20	305	30	65	0	0	1	1	1	0	1	3
Sherburn A	12	0	100	225	25	53	0	1	1	1	0	0	0	3
Sherburn B	3	50	0	170	30	65	0	0	0	1	0	0	0	1
Sherburn C	1	40	100	190	15	68	1	1	1	1	1	0	0	4
Sherburn D	1	0	100	175	5	76	1	1	1	1	1	0	0	4
Sherburn E	2	0	100	130	10	70	0	0	1	1	1	0	0	3
Herring A	2	2	100	10	30	63	0	1	1	1	0	0	1	3
Herring B	3	25	0	220	5	71	0	0	0	1	0	0	1	1
CED A	0	0	100	0	0	64	0	1	1	1	0	0	0	3
Hawth A	1	5	100	0	0	62	0	1	1	1	0	0	0	3
Hawth B	1	1	100	320	5	70	0	1	1	1	0	0	1	3
Warren A	3	0	100	135	5	70	0	0	1	1	1	1	1	3
Tuthill A	3	2	0	350	40	73	0	1	1	1	0	0	1	3
Tuthill B	6	7	100	310	30	63	0	1	1	1	0	0	1	3
Tuthill C	9	5	0	0	0	61	0	0	1	1	0	0	1	2
FHF A	10	5	100	10	35	72	0	0	1	1	0	1	0	2
FHF B	6	0	100	170	20	75	0	0	1	1	1	1	0	3
High Moor A	7	10	80	250	40	61	0	0	1	1	0	0	0	2
High Moor B	1	0	100	260	10	61	0	0	1	1	0	0	0	2
Moor Bk A	3	1	100	355	20	68	0	0	1	1	0	0	0	2
Moor Bk B	1	5	100	280	40	69	0	0	1	1	0	0	0	2
Thris A	2	3	100	0	0	66	1	1	1	1	0	0	1	3
Thris B	3	5	100	170	10	64	0	1	1	1	0	0	1	3
Thris C	6	4	100	195	5	62	0	1	1	1	0	0	1	3
Thris D	6	1	100	5	10	60	0	1	1	1	0	0	1	3
Thris E	4	1	100	355	15	62	0	1	1	1	0	0	1	3
R Furze A	6	50	0	0	0	69	0	1	1	1	0	0	0	3

	FSR	Area	Perim	SRNN	MD NN	Dist58	No5km	No2.5km	SR2.5km	QSR	WSR	ASR	USR	AVH
Merryknowle A	52	440.48	100.54	39	900.46	1273.57	25	11	54.82	10	13	19	19	25
Island Farm A	49	924.74	115.18	49	108.79	1356.97	23	12	58.92	9	22	11	15	22
Island Farm B	39	324.86	80.56	39	108.79	1270.97	25	11	58.18	11	11	13	15	8
Houghton A	48	1896.12	234.32	55	1110.00	6101.04	7	3	47.33	9	16	15	17	20
High Haining A	55	2446.49	205.45	48	1110.00	6691.79	7	3	45.00	13	20	19	14	11
Pittington A	67	3420.07	268.25	58	128.71	128.71	17	5	52.20	15	18	24	24	15
Pittington B	58	15592.20	476.58	67	128.71	128.71	15	5	54.00	12	21	19	17	7
QQ A	58	5607.39	410.10	35	340.66	625.59	38	17	50.65	11	19	20	17	12
QQ B	35	934.06	116.69	58	340.66	340.66	37	16	52.13	9	7	12	16	20
Coxhoe A	31	231.96	63.49	40	17.17	1449.19	43	11	51.64	8	9	10	12	22
Coxhoe B	40	795.93	130.12	31	17.17	1465.74	44	11	50.82	9	15	11	13	22
Quarr Hill A	47	2248.52	210.05	55	52.00	619.55	38	24	50.63	12	15	17 -	13	8
Quarr Hill B	55	8442.04	388.41	47	52.00	624.57	39	24	50.29	10	24	13	16	15
Quarr Hill C	46	546.74	93.58	55	72.37	560.32	39	24	50.67	11	15	15	12	8
The Carrs A	47	337.26	68.35	35	232.61	912.13	21	8	56.13	10	17	18	11	9
The Carrs B	54	3962.49	279.18	35	205.96	1111.62	21	8	55.25	14	18	19	17	15
The Carrs C	35	84.55	44.87	54	205.96	1026.11	21	8	57.50	11	8	16	10	13
Pig Hill A	56	6190.12	567.53	19	247.35	870.67	20	3	42.00	12	16	19	19	10
Pig Hill B	19	165.08	54.63	42	46.67	1063.95	17	3	54.33	7	3	9	7	20
Pig Hill C	42	1317.29	224.24	19	46.67	1062.57	17	5	47.20	11	12	15	15	20
Dabble Bk A	65	5783.25	437.49	56	870.67	2136.39	21	6	46.33	12	20	19	24	20
Thornley A	29	451.80	90.26	40	104.54	555.75	35	18	52.11	12	7	10	12	8
Thornley B	40	1928.84	231.84	44	58.03	472.18	34	19	52.74	12	15	14	10	7
Thornley C	44	815.10	122.20	40	58.03	378.92	34	19	52.53	11	13	20	10	12
Thornley D	59	2532.18	285.63	44	378.92	498.01	35	15	55.53	13	21	22	15	10
Blackhall A	68	33564.63	2414.96	53	3336.67	8374.16	1	0	0.00	11	18	21	22	20
Mean	48.418367	6065.2916	314.10143	48.693878	288.8252	4342.7486	22.306122	9.4489796	46.689388	10.89898	15.693878	16.530612	15.193878	14.928571
Variance	204.01904	127438033	110225.37	231.69914	448892.57	39547794	179.84347	47.157164	136.31548	5.1279371	30.441405	35.715548	17.044498	23.448454
Median	48	2210.59	233.08	47	81.3	969.12	24	7	50.525	11	15.5	16	15	15

	ScrubDen	AvBG/BR	Prim %	Aspect	SlopAng	Wide %	Scrubrem	Wood	Flushing	Neut Gld	Acid Gld	Arable	Grazing	No.Habit
Merryknowle	8	0	100	0	0	62	0	1	1	1	0	0	0	3
Isl Farm A	5	40	0	5	5	74	0	0	0	1	1	1	0	2
Isl Farm B	2	20	80	40	35	67	0	1	1	1	1	0	0	4
Houghton A	3	7	100	235	55	69	0	1	1	1	1	1	0	4
High Haining	6	1	100	160	20	69	0	0	1	1	1	0	1	3
Pittington A	11	3	100	220	30	67	0	1	1	1	0	0	1	3
Pittington B	3	5	0	325	15	66	0	0	1	1	0	0	1	2
QQ A	4	12	0	10	15	71	0	0	0	1	0	0	0	1
QQ B	3	1	100	0	0	63	0	1	1	1	0	0	0	3
Coxhoe A	7	10	100	260	20	68	0	1	1	1	0	0	0	3
Coxhoe B	11	15	100	300	35	68	0	1	1	1	0	0	0	3
Quarr Hill A	3	8	60	345	15	72	0	0	1	1	0	0	0	2
Quarr Hill B	2	25	0	330	10	71	0	0	0	1	0	0	0	1
Quarr Hill C	2	15	100	195	25	61	0	0	1	1	0	0	0	2
The Carrs A	9	40	100	40	40	72	0	1	1	1	0	0	0	3
The Carrs B	4	5	0	0	0	67	0	1	1	1	0	0	0	3
The Carrs C	7	2	100	95	35	71	0	1	1	1	0	0	0	3
Pig Hill A	1	15	100	350	40	64	1	1	1	1	1	1	1	4
Pig Hill B	2	0	100	5	40	74	0	1	1	1	0	1	0	3
Pig Hill C	6	0	100	30	25	74	0	1	1	1	0	0	0	3
Dabble Bk A	0	1	100	175	30	68	0	0	1	1	1	1	0	3
Thornley A	1	15	100	115	35	83	0	0	1	1	0	0	1	2
Thornley B	3	50	100	120	55	75	0	0	1	1	0	0	1	2
Thornley C	3	7	100	140	40	73	0	0	1	1	0	0	1	2
Thornley D	5	7	100	230	30	68	0	1	1	1	0	0	1	3
Blackhall A	0	15	100	95	55	59	0	0	1	1	0	1	0	2
Mean	4.2346939	4.3287671	10.214286	73.265306	151.68367	20.77551								0.2959184
Variance	18.428887	21.918189	171.44845	1856.7536	16485.538	276.50579								0.2104986
Median	3	3	5	100	165	19								0

APPENDIX IV: Raw data values for each variable at a site scale

	SSR	AREA	PERIM	SRNN	MD NN	DIST 78	NO 5KM	NO2.5KM	SR 2.5KM	AVH	SCR DEN	% BG/BR	PRIM %	SLOP ANG	WIDE %	No HABIT
Eldon	42	1676.69	303.40	83	6994.97	6994.97	0	0	0.0	20	18	0	100	7	80.9	3
TK	87	7580.13	880.18	66	425.51	1689.80	12	5	79.8	14	1	1	100	38	70.5	3
Fishburn	95	2213.78	374.27	52	1759.65	2765.58	11	4	57.3	13	7	17	100	16	69.5	3
Harton	57	3600.75	373.82	54	1140.51	21843.42	2	2	60.0	11	0	10	100	45	63.2	1
F&C Quar	59	6406.70	542.73	60	2853.21	16060.82	3	0	0.0	15	6	22	0	37	67.6	2
Cleadon	66	12492.59	1031.01	54	1232.78	19392.50	3	2	55.5	16	1	0	90	3	72.1	2
Marsden	54	2360.32	388.84	57	1140.51	20916.94	3	2	61.5	12	1	17	85	15	63.6	2
Clax	60	3435.47	826.56	59	2853.21	13109.10	4	0	0.0	18	3	28	20	20	65.8	3
Tunstall	60	7661.87	512.53	44	3789.34	11671.48	4	0	0.0	16	3	5	100	30	65	2
Hastings	44	4430.76	368.27	61	1558.08	10131.51	5	1	61.0	10	0	3	90	35	54.5	3
Raisby	84	7656.52	581.24	44	1273.39	1926.58	18	7	66.3	15	3	13	50	12	66.4	3
Wingate	74	107,912.73	2477.21	66	498.01	812.08	12	3	74.0	18	3	5	25	20	66.7	3
Trimdon	69	5118.56	267.15	87	1721.98	1721.98	16	6	74.3	13	1	20	0	0	63.8	2
Silent	72	5046.58	1080.68	110	1034.88	1069.76	13	5	82.6	17	4	13	80	26	65.8	2
BM	89	19372.77	740.80	68	840.90	1088.03	13	7	65.3	13	6	12	50	15	62.7	3
Garm Tri	40	1705.14	274.89	68	516.33	1394.15	17	7	77.6	24	0	0	0	0	70.9	3
Garm Qu	68	32221.61	841.63	40	516.33	840.90	16	8	72.6	18	7	3	100	22	64.6	3
Cassop	110	23057.03	1524.10	80	619.55	619.55	12	6	71.3	14	7	5	70	30	66.4	3
Sherburn	78	15068.36	1065.08	72	2117.04	2565.89	10	1	72.0	15	4	18	95	17	66.4	4
Herring	61	18144.06	801.37	44	1558.08	8416.94	5	3	49.0	13	3	13	75	17	67.2	3
CED	52	313.25	89.92	74	3989.09	4684.67	3	0	0.0	10	0	0	100	0	63.5	3
Hawth	72	10301.77	671.86	53	3548.71	10582.15	1	0	0.0	19	1	3	100	3	65.5	3
Warren	53	662.56	120.16	68	3336.67	5694.97	3	0	0.0	21	3	0	100	5	69.8	3
Tuthill	82	10775.28	903.20	65	2136.39	5259.46	3	2	70.5	14	6	5	70	23	65.4	3
FHF	57	225.44	85.54	60	4229.05	9384.00	2	0	0.0	18	8	2	100	28	73.6	3
High Moor	69	8318.14	650.34	64	428.27	587.17	6	2	73.5	11	4	5	90	25	60.9	2
Moor Bk	64	9448.60	631.97	69	428.27	1211.21	7	2	76.0	15	2	3	100	35	68.4	2
Thris	94	163,748.72	4386.43	51	58.07	912.13	13	6	66.5	10	4	4	100	8	62.8	3
R Furze	51	2458.21	272.26	94	58.07	58.07	10	5	78.8	13	6	50	0	0	68.6	3
Merryknowle	52	440.48	100.54	68	900.46	1273.57	11	5	72.0	25	4	0	100	0	61.5	3
Island Farm	68	1249.60	195.74	52	900.46	1270.97	11	5	70.8	15	4	30	20	20	70.1	4
Houghton	48	1896.12	234.32	55	1110.00	6101.04	5	1	58.0	20	3	7	100	55	68.8	4
High Haining	55	2446.29	205.45	48	1110.00	6691.79	5	1	54.5	11	6	1	100	20	69.1	3
Pittington	83	19012.27	744.83	69	587.17	2565.89	6	2	66.5	11	7	4	40	22	66.4	3
QQ	79	6541.45	526.79	110	487.74	487.74	14	5	78.0	16	4	7	20	7	66.8	3
Coxhoe	44	1027.89	193.61	84	1273.39	1273.39	17	4	88.3	22	9	12	100	27	67.6	3
Quarr Hill	80	11237.30	692.04	79	560.32	560.32	14	7	77.4	10	2	16	45	17	68	2
The Carrs	83	4384.29	392.40	94	912.13	912.13	9	2	72.5	12	7	15	40	25	70.1	3
Pig Hill	76	7672.49	846.40	82	2424.85	2424.85	7	2	73.5	17	3	5	100	35	70.6	4
Dabble Bk	65	5783.25	437.49	76	870.67	2172.98	8	2	79.0	20	0	1	100	30	67.7	3

Thornley	66	5727.92	729.93	87	425.51	425.51	13	6	82.0	9	3	20	100	40	74.5	3
Blackhall	68	33564.63	2414.96	53	3336.67	8374.16	1	0	0.0	20	0	15	100	55	58.9	2
Mean	67.380952	14152.34	732.90	67.238095	1608.48	5189.05	8.2857143	3.047619	55.2	15.33333	3.9047619	9.7619048	72.738095	21.07142857	66.957143	2.80952381
Variance	251.02207	859352090	601890.32	287.16144	2024965.081	35085814	26.940767	6.29036	916.6600987	16.22764	11.210221	104.67364	1273.4175	211.5313589	19.513728	0.401858304
Median	67	6094.98	561.99	66	1125.26	2298.92	7.5	2	68.5	15	3	5	92.5	20	66.75	3

REFERENCES

Allchin, E. (1993) *A comparison between primary grasslands and abandoned quarries of the Magnesian Limestone in County Durham with special reference to scrub invasion.* MSc Thesis, University of Durham.

Arrhenius, O. (1921) Distribution of the species over the area. Meddelanden från K Vetenskapsakademiens. *Nobelinstitut* 4:1-6.

Bartley, D.D., Chambers, C. & Hart-Jones, B. (1976) The vegetational history of parts of South and East Durham. *New Phytologist* 77:437-468.

Beerling, D.J., Huntley, B. & Bailey, J.P. (1995) Climate and the distribution of *Fallopia japonica*: use of an introduced species to test the predictive capacity of response surfaces. *Journal of Vegetation Science* **6**: 269-282

Belsley, D.A., Kuhn, E., Welsch, R.E. (1980) *Regression diagnostics: Identifying influential data and sources of co-linearity.* John Wiley & Sons, New York.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**: 445-449.

Cook, R.R. (1995) The relationship between nested subsets, habitat subdivision and species diversity. *Oecologia* **101**:204-210.

Cutler, A. (1991) Nested faunas and extinction in fragmented habitats. *Conservation Biology* **5**: 496-505

Dalby, G. (1991) *Magnesian Limestone - The scientific interest and national importance.* Internal North East England Nature Conservancy Council Report.

Doody, J.P. (1977) The conservation of the semi-natural vegetation of the Magnesian Limestone. *Vasculum* **62**: 17-32

Doody, J.P. (1980) Grassland. In *The Magnesian Limestone of County Durham* (ed. Dunn, T.C.), pp.44-50. Durham County Conservation Trust.

Elmes, G.W. & Free, A. (ed) (1994) *Climate change and rare species in Britain.* Institute of Terrestrial Ecology Research Publication No. 8

Graham, G.G. (ed) (1988) *The flora and vegetation of County Durham.* The Durham Flora Committee and the Durham County Conservation Trust, Durham.

Grime, J.P., Hodgsen, J.G. & Hunt, R. (1988) *Comparative Plant Ecology - A functional approach to common British species.* Cambridge University Press, Cambridge.

Hamilton, T.H., Rubinoff, I., Barth, R.H. & Bush, G.L. (1963) Species abundance: natural regulation of insular variation. *Science* **142**: 1575-1577.

Hanski, I. (1982) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* **38**:210-221

Heslop-Harrison, J.W. & Richardson, J.A. (1953) The Magnesian Limestone area of Durham and its vegetation. *Transactions of the Northern Naturalist Union* **2**: 1-28

Houghton, J.T., Callander, B.A. & Varney, S.K. (eds) (1992) *Climate Change 1992. The supplementary report to the IPCC Scientific Assessment.* Cambridge University Press, Cambridge

Houghton, J.T., Jenkins, G.J. & Ephraums, J.J. (eds.) (1990) *Climate Change: The IPCC Scientific Assessment.* Cambridge University Press, Cambridge.

Hubbard, C.E. (1984) *Grasses.* Penguin, London.

Huntley, B. (1991) How plants respond to climate change: migration rates, individualism and the consequences for plant communities. *Annals of Botany* **67**: 15-22.

Huntley, B., Berry, P.M., McDonald, A.P. & Cramer, W. In Press. Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography.*

James, F.C. & McCulloch, C.E. (1990) Multivariate analysis in ecology and systematics: panacea or pandora's box. *Annual Review of Ecology and Systematics* **21**: 129-166.

Janzen, D.H. (1983) No park is an island: increase in interference as park size decreases. *Oikos* **41**: 402-410.

Johnson, M.P. & Simberloff, D.S. (1974) Environmental determinants of island species numbers in the British Isles. *Journal of Biogeography* **1**:149-154.

Kadmon, R. (1995) Nested species subsets and geographical isolation - a case study. *Ecology* **76**:458-465

Kadmon, R. & Pulliam, H.R. (1993) Island Biogeography - the effect of geographical isolation on species composition. *Ecology* **74**: 977-981.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography.* Monographs in Population Biology. Princeton University Press, New Jersey.

Magurran, A. (1988) *Ecological diversity and its measurement.* Croom Helm, London.

McCoy, E.D. & Connor E.F. (1976) Environmental determinants of island species number in the British Isles: a reconsideration. *Journal of Biogeography* **3**: 381-382.

McGuinness, K. (1984) Equations and explanations in the study of species-area curves. *Biological Review* **59**:423-440.

Merraim, G. & Wegner, J. (1992) Local extinctions, habitat fragmentation and ecotones. In *Landscape Boundaries - consequences for biotic diversity and ecological flows* (ed. Hansen, A.J. & Di-Castri, F.), pp.150-169. Springer-Verlag, New York.

Meusel, H., Jäger, E. & Weinert, E. (1965) *Vergleichende Chorologie der Zentraleuropäischen Flora. Vol.1 (Karten).* Gustav Fischer Verlag, Jena.

Mitchell, J.F.B.(1983) The seasonal response of general circulation models to changes in CO_2 and sea temperature. *Quarterly Journal of the Royal Meteorological Society* **109**: 113-152.

Monserud, R.A. (1990) *Methods for comparing global vegetation maps.* WP-90-40, IIASA, Laxenburg.

Norusis, M.J. (1993) *SPSS for Windows Base System User's Guide Release 6.0.* SPSS Inc, Illinois.

Ouborg, N.J. (1993) Isolation, populations size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dutch Rhine-system. *Oikos* **66**:298-308.

Parry, M.L., Hossell, J.E., Jones, P.J., Rehman, T., Tranter, R.B., Marsh, J.S., Rosenzweig, C., Fischer, G. & Carson, I.G. In Press. Integrating global and regional analyses of the effects of climate change: A case study of land use in England and Wales. *Climatic Change*

Patterson, B.D. (1990) On the temporal development of nested subset patterns of species composition. *Oikos* **59**:330-342.

Peters, R.L. (1992) Conservation of biological diversity in the face of climate change. In: *Global Warming and Biological Diversity* (ed. by Peters, R.L. & Lovejoy, T.E.), pp. 15-30. Yale University Press, New Haven, CT.

Pettigrew, T.H. (1980) Geology. In: *The Magnesian Limestone of Durham County* (ed. by Dunn, T.C.), pp.7-26. Durham County Conservation Trust.

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography* **19**:117-134.

Preston, F.W. (1962) The canonical distribution of commonness and rarity I. *Ecology* **43**:185-215.

Pritchard, A. (1989) *A strategy for Magnesian Limestone grassland.* Internal Nature Conservancy Council Report. Nature Conservancy Council, Newcastle.

Quinn, J.F. & Harrison, S.P. (1988) Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. *Oecologia* **75**: 132-140.

Quinn, R.M., Lawton, J.H., Eversham, B.C. & Wood, S.N. (1994) The biogeography of scarce vascular plants in Britain with respect to habitat preference, dispersal ability and reproductive biology. *Biological Conservation* **70**: 149-157.

Reed, T. (1981) The number of breeding landbird species on British Islands. *Journal of Animal Ecology* **50**: 613-624

Richardson, J.A., Davis, B.N.K. & Evans, M.E. (1980) Disused Quarries. In *The Magnesian Limestone of Durham County* (ed. Dunn, T.C.) pp.61-68, Durham County Conservation Trust.

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science* **235**: 167-171.

Rodwell, J.S. (1992) *British Plant Communities, Volume 2 Grasslands and montane communities.* Cambridge University Press, Cambridge.

Rose, F. (1981) *The Wild Flower Key.* Penguin Books, London.

Schlesinger, M.E. & Zhao, Z.-C. (1989) Seasonal climatic changes induced by doubled CO_2 as simulated by the OSU atmospheric GCM/mixed-layer ocean model. *Journal of Climatology* **2**: 459-495. CHECK

Shimwell, D.W. (1968) *The phytosociology of calcareous grasslands in the British Isles.* PhD Thesis, University of Durham.

Simberloff, D.S. (1976) Experimental zoogeography of islands: effects of island size. *Ecology* **57**:629-648.

Simberloff, D.S. & Abele, L.G. (1982) Refuge design and island biogeographic theory: effects of fragmentation. *American Naturalist* **120**:41-50.

Soulé, M.E. & Simberloff, D.S. (1986) What do genetics and ecology tell is about the design of nature reserves? *Biological Conservation* **35**: 19-40.

Sykes, M.T., Prentice, C. & Cramer, W. In press. A bioclimatic model of potential distribution of North European tree species under present and future climates. *Journal of Biogeography.*

Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991) What to protect? Systematics and the agony of choice. *Biological Conservation* **55**: 235-254.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon* **21**: 213-251.

Williams, C.B. (1943) Area and the number of species. *Nature* **152**:264-267.

Woodward, F.I. (1992) A review of the effects of climate on vegetation: ranges, competition and composition. In *Global Warming and Biological Diversity* (ed. by Peters, R.L. & Lovejoy, T.E.), pp. 105-123. Yale University Press, New Haven, CT.

Woodward, F.I. & Smith, T.M. (1994) Global photosynthesis and stomatal conductance: modelling controls by soil and climate. *Advanced Botanical Research*. **20**: 1-41.

Wright, D.H. & Reeves, J.H. (1992) On the meaning of nestedness of species assemblages. *Oecologia* **92**:416-428.