Contents

Land use policies are developing rapidly, especially in relation to agriculture and forestry. There is a clear emphasis on sustaining the ecological value of Britain's land. However, we need to develop and monitor policies which will deliver land rich in biodiversity, in the face of human pressures and environmental change.

Land use

Lowlands

In 1997 the European Commission published its Agenda 2000, which opens the formal discussion on the reform of the Common Agricultural Policy (CAP). The need for reform has been accepted for some time; without it, the inclusion of countries from eastern Europe would be prohibitively costly, and, in any case, changes to the CAP are likely to be required under the next round of World Trade Organisation talks. Suggested changes to the CAP with significant implications for biodiversity are the setting of a zero rate for arable set-aside (thereby eliminating it, but allowing it to be reintroduced quickly if necessary), and increased provision for agri-environment measures such as the Countryside Stewardship Scheme and aid for organic farmers. Though detailed analysis will be needed to establish fully the likely ecological implications of the new proposals, the loss of set-aside will be a major change. ITE is co-ordinating the evaluation of agronomic and environmental impacts of set-aside, and, while our results will not be reported until 1998, data already exist which suggest that set-aside has provided a resource for a range of bird and plant species to a far greater extent than anyone thought possible a decade ago.

If agriculture becomes more intensive in the wider countryside, the fates of a range of bird species in particular may become even more closely tied to formal agri-environment schemes than at present. ITE's recent research into different farming and conservation practices is likely to prove very important in ensuring that these schemes really do deliver ecological benefits. Research into wetland management, arable reversion, organic farming, game management, and the impact of structure of farmed landscapes on biodiversity all provide important insights about how policies and practices can be optimised to generate the best balance beween ecological and production interests. ITE is also heavily involved in the evaluation of existing agri-environment schemes (Tir Cymen in Wales, Environmentally Sensitive Areas (ESA) in Scotland, and Countryside Stewardship in England (CSE)), and so will have an important role in ensuring that the latest research results will be put into practice.

The effective management of lowland landscapes requires not simply an understanding of local social, environmental and economic processes, but also of the national ecological stock and how it is changing The project 'ECOlogical FACTors controlling botanical diversity in the British countryside' (ECOFACT) has been working on the interpretation of the changes in landscape and botanical diversity, as revealed by past Countryside Surveys (in 1978, 1984 and 1990) and more recent fieldwork Planning is now well advanced for the next Countryside Survey, which will take place in 1998 and will report in 2000 The results are keenly awaited, as they will provide the reference point for the changes which have taken place since 1990, against which the success or failure of particular environmental schemes and policies can be assessed

Uplands

Many of the issues in the lowlands are equally relevant in the uplands, notably the environmental impacts of land use change and the growing requirement for the development of agricultural systems and practices which favour environmental conservation and improved public access, while retaining sustainable production Because sheep grazing is the dominant land use, and there is good evidence that in many upland areas overgrazing is a key factor limiting habitat and species diversity, much attention continues to be focused on measures to reduce sheep grazing in sensitive areas

The three environmental schemes already referred to (Tir Cymen, ESA, CSE) all include incentives to farmers in the uplands to reduce stocking levels, the exact nature of which vary depending on the details of the scheme, including variations based on local requirements Evidence is beginning to emerge of success, for example with regard to the key objective in many areas of recovery of heather moorland where heavy grazing had led to the loss of heather and other dwarf shrubs and their replacement by coarse grasses ITE is playing an important part in monitoring the effects of these and other management prescriptions, some general, some more precise, and in the development of refinements which, when implemented, result in improved environmental benefits and cost-effectiveness of these schemes A particular opportunity arises in Wales with the recently announced plan for a new, single agri-environment scheme which will combine the best elements of Tir Cymen and the Welsh ESA scheme The ECOFACT project already referred to provides important data about long-term underlying change in the uplands, helping changes caused by present and future agri-environment schemes and other perturbations (eg climate change, changing air pollution levels) to be set in context

The invasion of large areas of the uplands by bracken seems set to continue, perhaps encouraged by the reduction in the number of cattle on hill farms They are believed by farmers to reduce the rate of spread by trampling the emerging fronds in spring, a control not achievable by sheep The recent outbreak of BSE has further undermined the economy of beef and milk production in the marginal uplands in the west and north of Britain, perhaps signalling a further increase of bracken While bracken can be controlled by spraying with herbicides, it has been widely suggested that a more ecologically sound solution to the problem would be to target bracken-infested land in the uplands for tree planting, as part of the planned major long-term expansion of woodland area in England and Wales Support for this approach was obtained during ITE studies for the Countryside Council for Wales and English Nature, using the ITE Land Cover Map as a key tool to characterise existing and potential woodland areas This work indicated that much of the bracken land was particularly suitable for expansion of existing woodlands or the planting of new woods However, the need for careful survey prior to the approval of particular planting applications was emphasised, to ensure that bracken areas of high conservation value are excluded The Forestry Authority in Wales launched a Bracken Challenge Fund initiative in the spring of 1997, and ITE is involved in the evaluation of planting proposals

The information gained over a long period by ITE on the impacts of conifer forests on ecology and water quality in the uplands, soon to be augmented by a new ITE study of the impacts of broadleaved woodlands, will be valuable in providing guidance in the years ahead to help minimise any adverse environmental effects of the new woods and forests The approach used in the project 'LANDscape ECOlogical NETwork as the templet for biodiversity' (LANDECONET) also has much to offer in helping to predict the detailed effects on biodiversity of major land use change in the uplands, such as that resulting from woodland expansion, and giving guidance for the selection of best options for the spatial distribution and size of new components in the landscape

L G Firbank and J E G Good

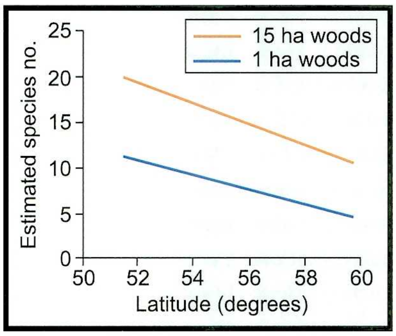


Figure 1. The relationship of woodland bird species to habitat area, based on data collected in England, The Netherlands, Denmark and Norway, augmented with published data from Sweden. The higher the latitude, the fewer the expected number of species for a given woodland size

Farm landscapes for biodiversity – the LANDECONET project

(This work was partly funded by the Third Framework Programme of the European Commission)

Biodiversity is still in decline across the farmed landscapes of northern Europe. The project 'The LANDscape ECOlogical NETwork as the templet for biodiversity' (LANDECONET) was intended to address one important issue of biodiversity loss, namely habitat fragmentation and landscape change. It was designed to encompass research and experience from many countries in producing an integrated approach for the management of agricultural landscapes for biodiversity.

The EC-funded LANDECONET consortium was developed from the CONNECT network of European Conservation Institutes. It brought ITE together with groups in Norway, Sweden, Finland, Belgium, Denmark and The Netherlands on a formal basis, and enabled close collaboration with colleagues from France and Poland. The research was structured in three sections:

- empirical field studies that related the local distributions of birds, butterflies and plants to the areas, histories and relative positions of habitat patches within farmed landscapes;
- the development of models using the data collected to help forecast the implications of landscape change on species occurrence and long-term viability;
- the production of a user guide to show how research results can be applied to help promote landscape management which addresses conservation as well as other objectives.

Species/landscape relationships

Several key findings have emerged as a result of the international collaboration. One important limitation of landscape studies is that relationships which are developed in one geographical region cannot be extrapolated to another. By using compatible procedures for field studies in a range of countries, it is possible to test the importance of this effect. For woodland birds, at least, the relationship between species number and woodland patch area differs from country to country, but in a manner which is correlated with latitude. It is now possible to use this information to estimate species/area relationships right across northern Europe (Figure 1).

Such relationships are less valuable for species which are slow to disperse across the landscape. The most important factor for many plant species remains the continuity of habitat management (Plate 1), so that, for ancient woodland species, there are strong species/area relationships in old woodlands, but not in more recent plantations (Figure 2). Landscape management therefore needs to be on the basis of adding to existing high-quality natural resources, rather than designing some form of optimum spatial configuration regardless of the history of the landscape.

Plate 1. A well-connected woodland landscape in Devon, suitable for the dispersal of the more mobile woodland species; grassland populations are more isolated from one another

Guidelines, landscape standards and species models

The modelling work has included approaches ranging from simple regressions based on a single season's worth of presence/absence data to complex, spatially explicit life history models. The amount of effort required to generate these models varies greatly, and it needs to be appropriate to the data and resources available and the conservation importance of the species or habitat under study (Table 1). If resources are low, then there are general guidelines based on existing knowledge. To conserve meadow butterflies, for example, there must be the required larval foodplants and nectar sources available throughout the season. Large meadows connected to others by grassland corridors are the most effective for ensuring the long-term viability of the populations.

Landscape standards have been developed for a range of species, based on more detailed modelling studies; landscapes can be tested against these standards to see whether the species are likely to be able to persist, without the need for detailed field surveys. For example, it appears that large birds such as red kites (*Milvus milvus*) need a population size of around 80 pairs in a network of habitats in order to be likely to persist for 100 years, and in Dutch landscapes an area of over 200 km^2 may be required to support this number of birds. Work to date suggests that the critical population sizes are more stable from region to region than the areas they need, which are landscape dependent. While there are few landscape standards available at the moment, it is hoped that they will become a powerful method of communicating research results in forms which landscape planners can utilise.

More complex analyses and models require survey data of the region under study, sometimes over several time periods. However, the benefits of this work can be great. For example, the false heath fritillary butterfly (*Melilaea diamina*) is becoming scarce in Finland as its meadow habitats are abandoned and become overgrown. Data from repeated surveys have enabled construction of a population dynamics model that has been used to target those grassland patches which are most important for the long-term viability of this species, and on which conservation measures can be concentrated.

The results of models can also be presented using geographical information systems, to help visualise the potential impacts of alternative land use scenarios, both in terms of the likely distribution of particular species, and also in other terms, such as the potential aesthetic impacts.

Table 1. Which analysis to use? The choice of ecological analysis depends upon the data and resources available. General guidelines about landscape management, and the standards of landscape required to support particular species can be applied with few field data, but the more detailed models for relating particular species to landscape structure require at least a single survey

	Landscape data	
Species data	*Low resolution*	*High resolution*
None	General guidelines	General guidelines
Anecdotal	Landscape standards	Landscape standards
Single survey	Correlative models	Correlative models
Repeated survey	Not cost-effective	Dynamic models

The guide to using landscape ecology in farmed landscapes

LANDECONET has brought together a range of ideas, data and tools to provide a valuable overview of how the ideas behind landscape ecology can actually be put into practice. The work has been presented in the form of a guide which explains how landscape ecology can be used by planners, farmers and conservation bodies. This guide and supporting information can be found on the World Wide Web at http://www.nmw.ac.uk/ite/econet.

L G Firbank

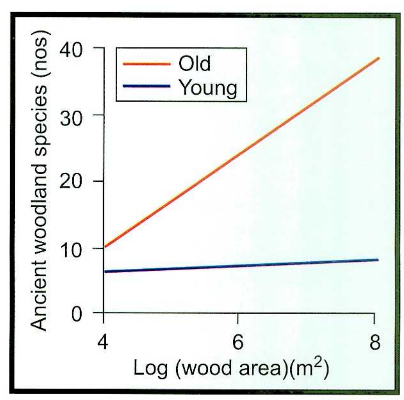


Figure 2. There is a strong relationship between the number of ancient woodland plant species and woodland area in Belgium, but only for suitable sites. This obvious point is often missed in landscape studies; both landscape structure and habitat quality are important, and they operate interactively

ECOFACT – ECOlogical FACTors controlling botanical diversity in the British countryside

(This work was co-funded by the Department of Environment, Transport and the Regions, the Ministry of Agriculture, Fisheries and Food, the Scottish Office, Agriculture, Environment and Fisheries Department, and NERC)

In 1990, a major survey of the British countryside was undertaken by ITE, which repeated and extended a baseline survey of vegetation established in 1978 Although the results of Countryside Survey 1990 (CS1990) were published by the Department of the Environment in 1993 (Barr *et al* 1993), resources did not permit a comprehensive analysis of botanical character and change The first two modules of ECOFACT were designed to complete this analysis by describing the botanical characteristics of the wider countryside in Great Britain and carrying out further analysis of the changes on sites previously recorded in 1978

A major part of the work completed to date has involved the development of a system of vegetation classification that deals consistently with the disturbed vegetation covering much of the British countryside In addition, because the new classification is based on mathematical procedures and stratified random sampling, for the first time error terms can be attached to national estimates of the extent of different types of vegetation New vegetation samples can also be assigned to the classification by a novel computer program, developed as part of this project This classification has a wide range of potential applications because it can be used by other ecologists who are not trained in botanical survey and analysis, but who need to describe the vegetation in which they are working

In CS1990, vegetation data were collected from almost 12 000 plots located in 508 one km sample squares drawn from the 32 land classes of the ITE Land Classification (Bunce *et al* 1996), over 2000 of these plots had been surveyed previously in 1978 The plots covered landscape elements (plot types) such as hedgerows and streamsides, as well as the vegetation of open fields and hillsides

The classification

The classification was derived from analysis of the vegetation data by multivariate procedures widely used in vegetation science and described by Barr *et al* (1993) The analysis was carried out on all the botanical data collected in 1978 and 1990, regardless of plot type, so that botanical diversity could be compared across the whole landscape The classification divides the British vegetation into 100 classes and, together with its associated supporting statistical analyses and descriptive interpretation, has been termed the Countryside Vegetation System (CVS)

It is difficult to give short names that are fully descriptive for such a large number of classes, but these are necessary to enable users to gain familiarity with the classification and to provide some information about the composition of the classes The names assigned to classes are simply labels based on the habitats associated with the vegetation and do not affect the structure of the classification In addition to the names provided, a one-page summary has been developed to describe the character of each class A draft of the summary page is shown in Figure 3 Users can then compare the study area with the average composition The 100 vegetation classes have also been grouped by a statistical procedure into eight aggregate classes, as shown in Table 2

Table 2 Countryside Vegetation System classification of plot and aggregate classes with area estimates (km^2)

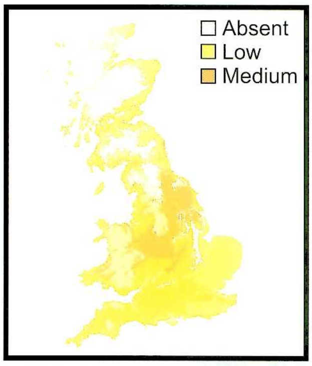
Class		Area (km^2)
I	Crop/weeds	32 400
	Crop/weeds	
	Weedy leys	
II	Tall grass/herb	4 578
	Tall grass/herb boundaries	
	Tall grass/herb streamside	
	Tall grass/herb roadside	
III	Fertile grassland	34 434
IV	Infertile grassland	28 567
	Uniform, infertile grassland	
	Calcareous grassland	
	Variable infertile grassland	
	Wetland	
V	Lowland wooded	10 425
	Hedgerows	
	Woodlands	
	Streamsides	
VI	Upland wooded	14 393
	Streamside	
	Woodland	
	Conifer plantations	
VII	Grass mosaic/moor	19 530
	Grass mosaic/moor streamside	
	Herb-rich grass mosaic	
	Moorland	
VIII	Heath/bog	39 218
	Heather moor	
	Streams	
	Mountain heath	
	Bog	
	Saturated bog	

Vegetation class 25

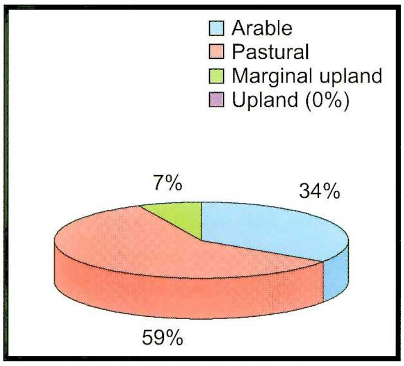
Shaded grassland/hedges

Aggregate class II
Tall grassland

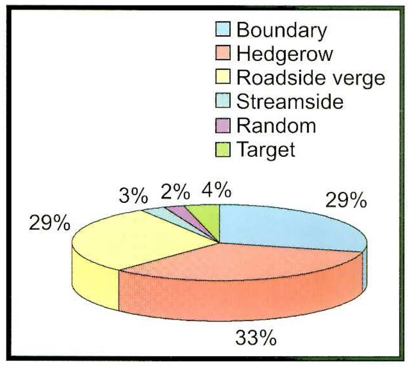
Total number of plots: 325 | Area: 607 sq km | SE: 235 sq km



Probable frequency in GB



Landscape association



Plot types

Description

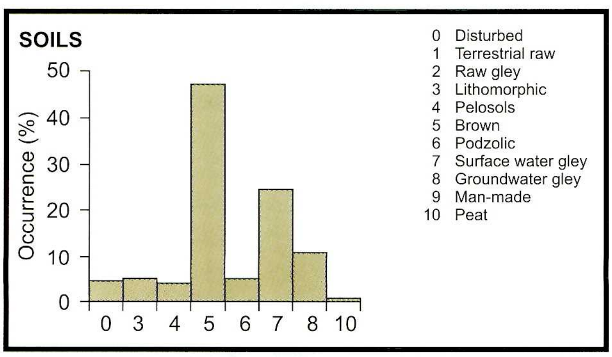
Although mainly along edges of various habitats, this class can occur in a wide variety of situations where there is some shade and some more robust woodland species are able to survive. The class is very common and hawthorn is the main hedgerow species with wild rose and blackthorn. The ground cover is mainly grasses – rye-grass, creeping bent, cock's-foot and false oat-grass. The type is quite diverse in structure and species and has characteristic plants such as bramble, ivy and hogweed. This class occurs throughout lowland Britain.

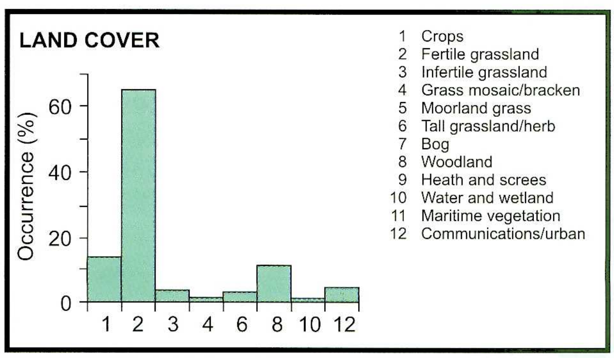
Species number: 257 (high) | No. of species groups: 9 (high) | Most frequent species group: 22

Most frequent species	%	Species with highest cover	%	Characteristic species
Dactylis glomerata	89	*Crataegus monogyna*	16	*Crataegus monogyna*
Urtica dioica	75	*Lolium perenne*	8	*Hedera helix*
Lolium perenne	72	*Agrostis stolonifera*	8	*Rosa* spp.
Holcus lanatus	67	*Dactylis glomerata*	8	*Lolium perenne*
Agrostis stolonifera	59	*Arrhenatherum elatius*	6	*Prunus spinosa*

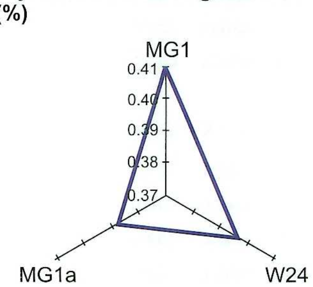
Related habitats

Biodiversity habitat: 4 | CORINE biotope: 31.8, 84 | Phase I habitat: C3, J2





Similarity with National Vegetation Classification (NVC) types (%)



Competitor-Stress tolerator-Ruderal (CSR) characterisation (%)

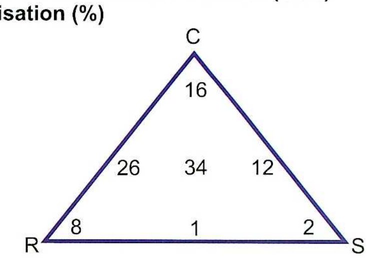


Figure 3. Example of a one-page summary describing the average composition of the 100 vegetation classes

Distribution of the vegetation classes

The frequency of the vegetation classes within the four landscape types defines the principal patterns of distribution of British vegetation. The arable landscape is dominated by crops/weeds, tall grassland/herb and fertile grassland, but it has a small element of acidic vegetation. The pastural landscape overlaps with the arable, but is dominated by fertile grassland and has a higher degree of representation of the heath/bog class. The marginal uplands still have fertile grassland as the most abundant class, but, because they are inherently variable in character, they have almost a complete range of classes. The upland landscape is characterised by moorland heath and bog.

A novel procedure for estimating the area of vegetation classes and associated standard errors has been developed for this project, to replace the plot frequencies presented by Barr *et al.* (1993). The area covered by any given vegetation class depends upon its frequency of occurrence and the area of vegetation in the sample squares covered by the class. The areas at the higher level of the hierarchy, given in Table 2, correspond to the similar categories of land cover estimated by Barr *et al.* (1993).

Using statistical procedures, the results reveal that there is still a wide range of botanical diversity within the British countryside. Figure 4 shows that, even in the intensively managed arable landscapes of the lowlands of Britain, there is a surprisingly similar degree of variation to the pastural lowlands, as represented by the number of vegetation classes. This is because small fragments of vegetation still remain in these landscapes and the fields are more variable than they appear. However, the major division is between the lowlands/marginal uplands and the uplands, which have fewer plot classes present but more semi-natural vegetation. The variation is therefore surprisingly evenly dispersed between the plot types, which means that, as Bunce and Hallam (1993) reported, most variation is in the linear features.

More detailed analysis has shown that the reduction in species numbers in woodlands is largely in the arable and pastural landscapes.

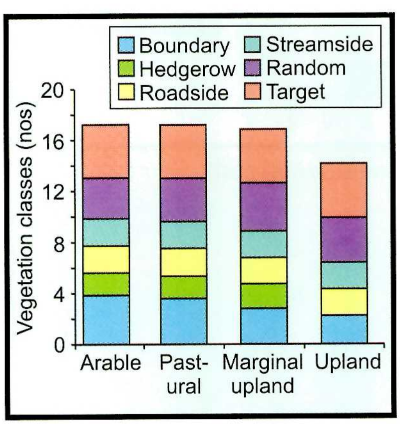


Figure 4. Average occurrence of the vegetation classes within the four landscape types described by Barr *et al.* (1993)

Vegetation change 1978–90

Whilst all the 100 vegetation classes are required to express the variation within the data, many of the classes do not have sufficient plots to determine change between 1978 and 1990. As in CS1990, the major analyses of change have therefore been carried out using the aggregate vegetation classes combined with the four landscape types determined by grouping the ITE land classes. The results confirm the changes reported in CS1990, but add further detail. Thus, there are reductions in the diversity in arable fields, semi-improved grasslands and woodlands, but an increase in species number in the moorland of marginal and upland landscapes. However, the more detailed analysis has shown that species numbers in woodlands are only reduced in the upland wooded aggregate class. The species diversity of landscape features also showed changes, with a reduction in diversity of the ground flora of hedgerows in the pastural landscape, whereas characteristic meadow species declined in roadside verges across all landscapes. Characteristic wet meadow species were lost from streambanks in the lowlands.

The CVS allows comparisons of change to be carried out for all landscape components together. Separate analyses have also been carried out for the plot types from the different landscape components, to compare trends that may be taking place within them and to ensure that the quadrat size has not affected the results.

The vegetation classes are arbitrary points along vegetation gradients. The principal vegetation gradient has been shown by statistical analysis to be highly correlated with fertility, the secondary gradient being shade and the third soil moisture. Shifts between individual plots from 1978 to 1990 can therefore be interpreted in terms of environmental changes.

Implications for faunal diversity

Much of the vegetation in the British countryside has been overlooked because it consists of highly disturbed assemblages of common, widespread species. However, these assemblages and species often form important food resources for birds, butterflies and bees (Plate 2). Changes in the distribution and abundance of these assemblages and plant species can, therefore, have consequential impacts on faunal populations. Analyses carried out under the ECOFACT project have explored correlations between the status of a number of butterfly and bird species and their foodplants. The results suggest that the reduction in the food resource, as shown by the 1978 and 1990 vegetation data, may be an important factor in the recorded decline of some bird and butterfly species.

Broader applications

The CVS has been compared with other classifications such as the National Vegetation Classification, to enable wider use of the results, for example in Biodiversity Action Plans. The computer program for assigning new vegetation data to the classification has been incorporated into the Countryside Information System, which enables regional estimates to be obtained. The

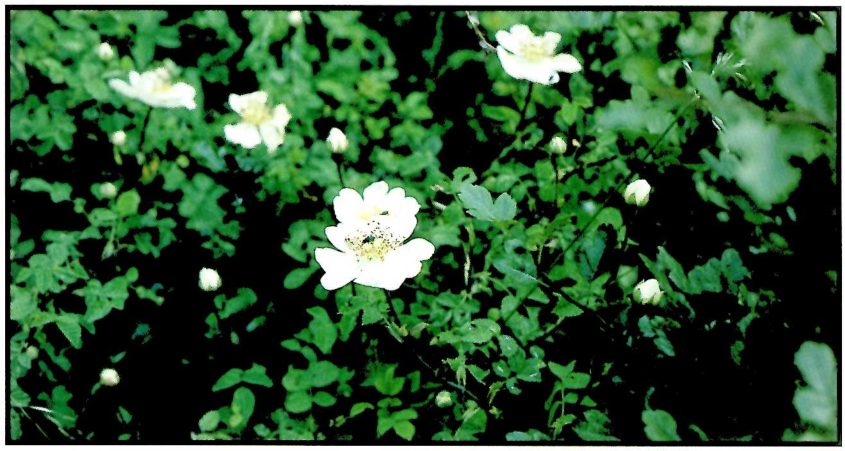


Plate 2. Wild rose (*Rosa* spp.) is a traditional feature of British hedgerows and is not found elsewhere in the landscape. It also supports a wide range of insect species

development of a Modular Analysis of Vegetation and Interpretation System (MAVIS) to enable comparisons between all the main systems of vegetation classification in use in GB is also under way.

Further work

A full description of the CVS is in preparation and a detailed report on Modules 1 and 2 of the ECOFACT project will be published by DETR. Further work on the causes of change in botanical diversity in the wider countryside is continuing with funding from DTER, MAFF and SOAEFD.

R G H Bunce, J W Watkins, S M Smart and H M Van de Poll

The reduction in food resources may be an important factor in the recorded decline of some bird and butterfly species.

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Coastal zone management

(This work has been partly funded by NERC and the University of East Anglia through a Research Fellowship in Coastal Environmental Science and Management)

The UK has a long and varied coastline, much of which is sensitive to change and under increasing pressure. Almost a third of the coastline of England and Wales is developed and 40% of UK manufacturing industry is situated on or near the coast. A significant proportion of the coast is known to be at risk from erosion or flooding, a problem compounded by natural factors such as rising relative sea level and increased storm activity, and by human exploitation of coastal resources and piecemeal coastal defence initiatives. The development of policies for the sustainable management of coastal biotopes and resources requires both comprehensive resource assessment and a more integrated approach (Turner 1997).

Changes in sediment level have been measured at different elevations in the different biotic communities on salt marshes and mudflats.

Such an approach must be interdisciplinary, assessing the role of natural, physical and biological processes as well as changing social demands. A 'pressure–state–response' framework is a useful way of formulating the problem (Figure 5). Once pressures on the coastal resource have been clearly identified, future trends can be modelled and policy responses developed.

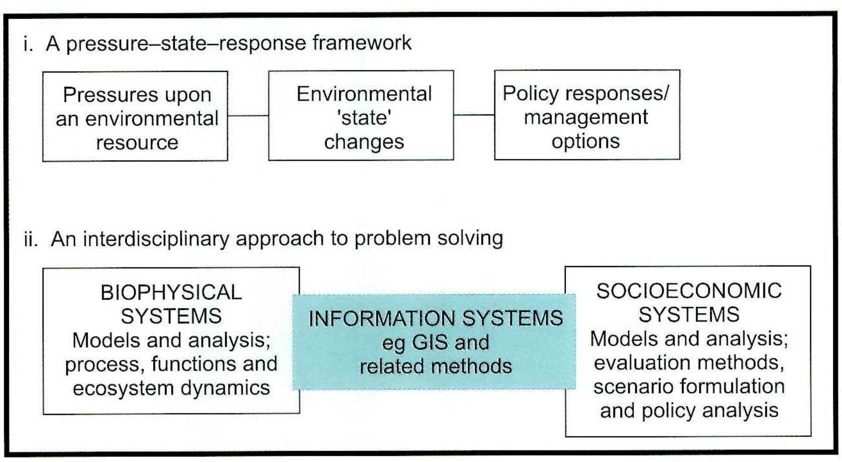

Figure 5. A framework for integrated coastal zone science and management

An opportunity to develop novel methodologies, incorporating scientific, social and economic knowledge, has been provided through the Research Fellowship. The scientific research work underpinning this study is mainly the NERC Land–Ocean Interaction Study (LOIS), and particularly the ITE project 'Biological Influence On InterTidal Areas' (BIOTA). This project aims to quantify, and model, sediment fluxes on east coast mudflats and salt marshes between Norfolk and the Tweed.

Although sedimentation patterns are determined to a large extent by the duration of tidal cover, concentration and density of suspended sediment and other physical factors, they are also influenced by biological factors. For example, sediment may be mobilised or stabilised by various biotic components on mudflats, and net deposition on marshes may be influenced by vegetation type and cover. In turn, vegetation communities track sediment accretion as different species colonise with rising elevation. Changes in sediment level have been measured at different elevations in the different biotic communities which exhibit zonation on salt marshes and mudflats. The lower elevational limits of many saltmarsh plant species are mainly controlled by factors related to inundation and some index of exposure to wave energy, so that simple models can be derived to relate species to elevation.

Models of sediment and vegetation changes will be linked to remotely sensed data on vegetation and mudflat types, such as the imagery produced from aircraft fitted with a Compact Airborne Spectrograph Imager (CASI), an important element of the LOIS programme.

CASI enables the large-scale mapping of land surface type, biotic components, and material fluxes over time. ITE is active in producing reliable imagery through geocorrection and validation of surface features and vegetation components from *in situ* observations (ground-truthing). The extensive datasets produced with this technology will provide the basis for developing tools for the strategic management of coastal cells.

A CASI image of an area of Welwick salt marsh on the Humber estuary is shown in Figure 6. Surface level measurements over 22 months along two transects at Welwick show that the greatest net accretion occurred in the middle marsh and pioneer zone in continuous mixed vegetation dominated by the common saltmarsh-grass (*Puccinellia maritima*) (Figure 7). The upper marsh experiences fewer tidal inundations and is relatively starved of sediment supply. At the marsh front there is a slower, but generally steady,

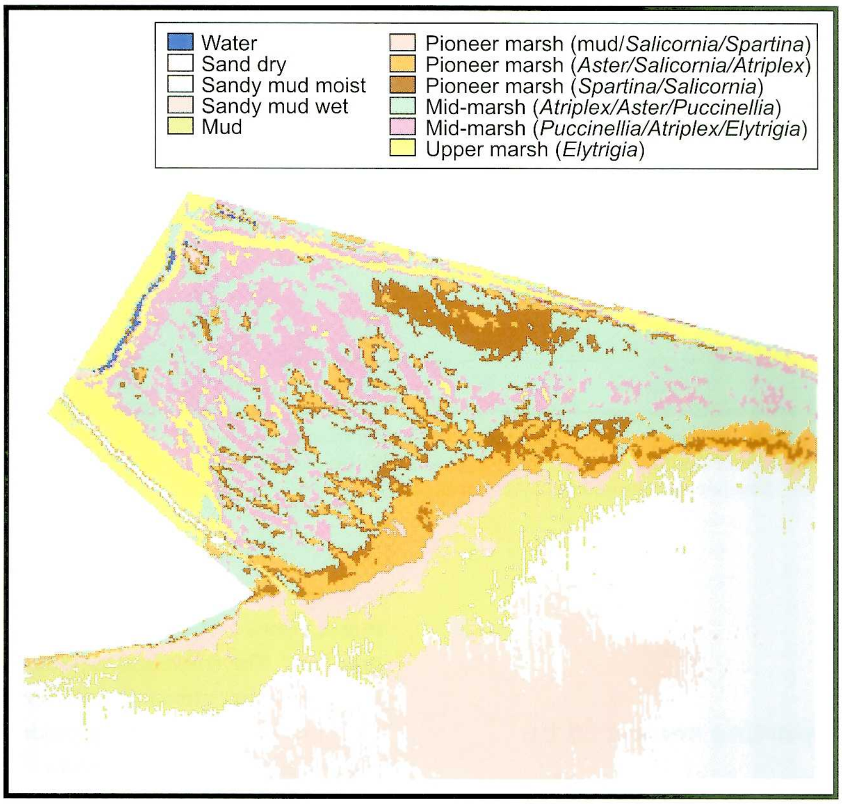

Figure 6. CASI image of Welwick salt marsh

increase in elevation. This lowest limit of salt marsh is colonised by the common cord-grass (*Spartina anglica*), which has expanded rapidly in many of our salt marshes after widespread planting earlier this century. ITE is interested in the

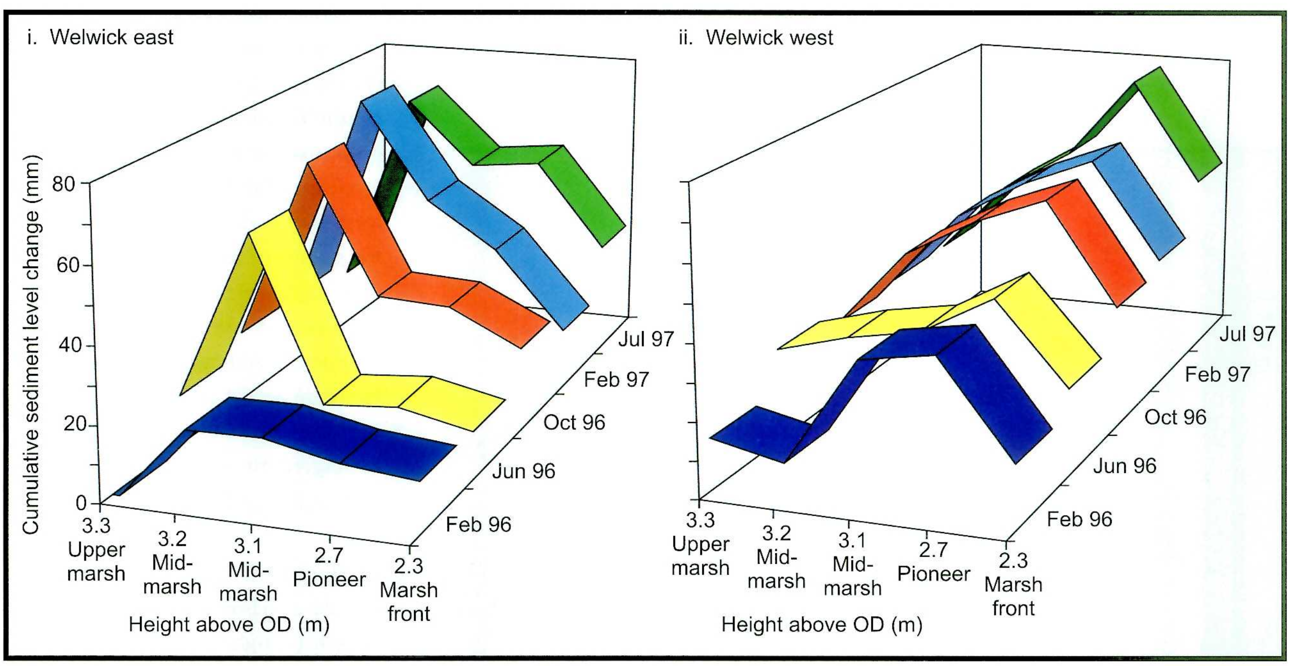

Figure 7. Cumulative sediment level changes on two saltmarsh transects at Welwick, Humber estuary (OD=Ordnance Datum). Baseline measurements taken in September 1995

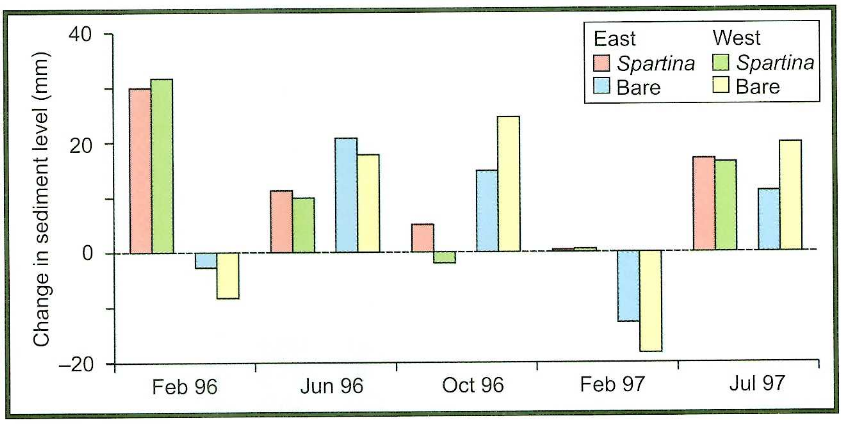

Figure 8. Sediment level changes (between measurement intervals) in *Spartina anglica* and on adjacent bare mud at two marsh front sites, Welwick east and Welwick west. Baseline measurements taken in September 1995

Spartina seems to be important as a sediment stabiliser during cycles of erosion and deposition.

impact of this species on the flux of sediments between the lower marsh zones and adjacent mudflats. The conventional view is that *Spartina* enhances sediment trapping, but the role of vegetation may be site specific, affected by local topography, wave climate, sediment supply, and vegetation patch size. In the Humber, there is no consistent evidence of enhanced deposition within the *Spartina*, and sedimentation is often greater on adjacent mudflats. However, *Spartina* seems to be important as a sediment stabiliser (through binding by plant root systems and reduced resuspension of sediment) during cycles of erosion and deposition, so that net accretion may be apparent over the long term. Figure 8 shows that differences in sediment level between measurement periods are greater and more variable on the adjacent unvegetated surfaces than within the vegetated front edge (Plate 3).

Plate 3. Colonisation of intertidal sediments by *Puccinellia* and *Spartina*

Periodic cycles of erosion during storm events, and accretion in response to such perturbations, mean that longer-term measurements are needed to establish trends (Pethick 1996). Studies within BIOTA will continue on selected transects to establish how representative are current observations. Data on accretion rates generated from the BIOTA programme and from other sources collected over a variety of spatial and temporal scales can be linked with models relating vegetation types to elevation and CASI imagery, to produce models of marsh development and plant successional changes. The BIOTA data centre at ITE has developed a spatial decision support system (DSS) (Brown *et al.* 1997) based on a hybrid distributed database and a geographical information system. Databases and models can be integrated to create interactive simulation models under different conditions, for example to produce predictive models of saltmarsh response to changing environmental factors such as sea level rise, sediment supply, frequency of storms, and to anthropogenic influences. Systems such as DSS will be valuable tools for coastal management as they facilitate access to the diverse sets of information needed to evaluate management options and develop sustainable policies.

Feeding such information on the natural dynamics of the coastal zone into higher-level, multidisciplinary models will allow a range of management options to be explored, from a 'business-as-usual' position to a range of possible new approaches These options can be assessed using techniques such as multi-criteria decision analysis (MCDA), which is a way of assessing management options by their relative impact on a range of criteria (such as conservation value, financial costs, value for tourism) Mathematical models based on optimisation can be used to derive the best management options, with the critical problem of weighting individual criteria being subjected to sensitivity analysis The policy implications of the various options will be investigated in co-operation with researchers at the Centre for Social and Economic Research on the Global Environment at the University of East Anglia

S L Brown, S McNally and A J Gray

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The conventional view is that *Spartina* enhances sediment trapping, but the role of vegetation may be site specific, affected by local topography, wave climate sediment supply, and vegetation patch size.

Biodiversity, the variety of life, can be investigated at different organisational levels from genes to ecological systems (landscapes), and at different spatial scales from a few square metres to continents.

Biodiversity

In practice, much of the research on biological diversity deals with species' patterns and attempts to identify associations with environmental factors that vary in both space and time. While the characterisation of biodiversity, spatial pattern and temporal change in biodiversity comprise one of four elements of the CEH research programme on biodiversity, a larger proportion of the effort is focused on the fundamental population processes upon which biological diversity depends. In particular, our research in ITE investigates model systems of the reciprocal interactions between species, and between populations and their environment. An understanding of the mechanisms underlying population demography and natural selection is crucial to our understanding of the evolution and maintenance of biodiversity.

Biodiversity characterisation, pattern and monitoring

This research is concerned with describing species and identifying patterns in both space and time. At a continental scale, the number of species in a unit area tends to increase from higher latitudes (polar regions) to lower latitudes (the tropics). Climate, in particular temperature, is probably the major factor associated with this trend in biological diversity. Patterns of species' distribution at a more regional scale also reflect climatic gradients. For example, in Great Britain, proximity to the sea, altitude and latitude are the main factors determining the distribution of animals and plants. The article by Carey and Hill describes the data and methodology that lead to a bioclimatic zonation for the whole of Great Britain. Ten bioclimatic zones are distinguished. Information on the presence/absence of species recorded in each 10 km grid square is used to identify a suite of species that are most characteristic of a particular zone yet different from other zones.

Population processes underlying biodiversity

These processes can be divided into two groups:

- those dealing with interactions between individuals within a population, and
- those dealing with interactions between species.

In practice they may not be mutually exclusive. In both cases, one is concerned with mechanisms that lead to changes in abundance.

However, it is becoming increasingly clear that our ability to predict changes in numbers depends to a large extent on the spatial substructure of a population, which may lead to different local dynamics and selection within subsets of the population In the first instance, a major difficulty arises with identifying an appropriate spatial scale at which to explore contrasting dynamics An approach to this problem is described in studies of red deer and Soay sheep by Albon and colleagues In both species, local population density influences juvenile survival, despite the fact that they have contrasting temporal dynamics, with red deer showing reasonably stable dynamics compared to Soay sheep, which tend to fluctuate markedly In red deer, but not Soay sheep, local population density interacts with both phenotype and genotype to influence sex ratio and maintain genetic diversity

For much of this century ecologists have sought to understand the pronounced population cycles shown by species of voles and some game birds, notably red grouse and ptarmigan One of several potential mechanisms that may explain these cycles is predation In Scandinavia, vole populations are thought to cycle because of reciprocal changes in predators like weasels, though avian predators, including owls, may also be important The report by Redpath and colleagues investigates the controversial issue of whether hen harriers and peregrines have a significant impact on red grouse on heather moors in northern Britain The evidence to date is that increasing numbers of these raptors prevented the recovery of the population of red grouse after they had declined to low numbers for some other reason As a result, there were too few grouse to shoot, and, as a major source of revenue for landowners was lost, this may pose a longer-term threat to the maintenance of heather moors in parts of upland Britain

The CEH research programme on biodiversity has been reviewed by an independent panel ('programme review group') The panel felt that the structure of the programme, covering the following four themes, was apt

- biodiversity characterisation, pattern and monitoring,
- ecosystem function and biodiversity,
- population processes underlying biodiversity,
- conservation and restoration of biodiversity

Now that this structure has been endorsed by the panel, it will form the basis for an annual review process

An understanding of the mechanisms underlying population demography and natural selection is crucial to our understanding of the evolution and maintenance of biodiversity.

S D Albon

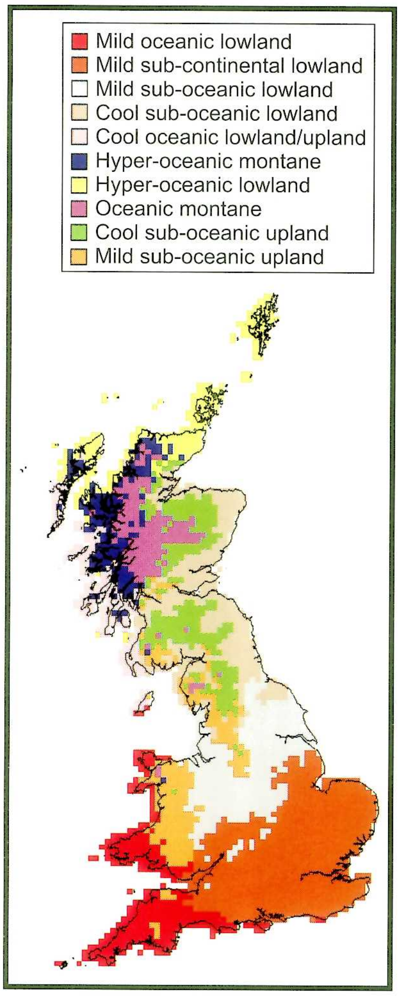

Figure 9. The bioclimatic zones of Great Britain

Bioclimatic zones in Great Britain

ITE's Land Classification (Bunce *et al.* 1996) groups the 240 000 one km squares of Great Britain into 32 land classes. It has been widely used as a means of dividing the country into ecologically and geographically homogeneous units. The land classification is a general-purpose classification and does not explicitly take account of species' distributions. It is based on a suite of attributes for each square, specifying climate, geology, human geography and topography.

At the scale of Great Britain, the broad patterns of species' distribution are determined mainly by climate and proximity to the sea. Other influences, resulting from differing geology, slope, aspect, soil type and land use, may also have a marked effect, but mainly at a more local scale. Whilst local influences are themselves of great interest, they are likely to stand out most clearly if they are separated from large-scale ones. As a step towards this separation, we produced a relatively coarse zonation of Scotland, designed to reflect species' distributions (Carey *et al.* 1995). We describe here a comparable but purely bioclimatic zonation for the whole of Great Britain, obtained using the same methodology.

Data

Data on species' presence in 10 km squares were obtained from ITE's Biological Records Centre for diurnal insects, moths, terrestrial molluscs, flowering plants, ferns, mosses and liverworts. Data on the occurrence of breeding birds were supplied by the British Trust for Ornithology. The environment of each 10 km square was specified by six climatic variables (mean January and July temperature, annual precipitation and relative humidity, annual number of rain days and sunshine hours) and six topographic variables (minimum and maximum altitude, percentage of and presence of sea in the square itself, percentage of and presence of sea in a 30 km square centred on the 10 km square). Climatic attributes for each 10 km square were interpolated from 30-year normals for British meteorological stations by the Climatic Research Unit of the University of East Anglia. Topographic variables were taken, or calculated, from ITE's own datasets.

Table 3. Characteristic species of two bioclimatic zones

Zone	Species	Preference index
Oceanic montane	Sibbaldia (*Sibbaldia procumbens*)	9.176
	Dwarf cudweed (*Gnaphalium supinum*)	7.934
	Ptarmigan (*Lagopus mutus*)	7.691
	Downy willow (*Salix lapponum*)	7.386
	Dwarf cornel (*Cornus suecica*)	7.269
Mild sub-oceanic lowland	Ruddy duck (*Oxyura jamaicensis*)	0.677
	Brown hawker (*Aeshna grandis*)	0.606
	Yellow wagtail (*Motacilla flava*)	0.541
	Great burnet (*Sanguisorba officinalis*)	0.488
	Little ringed plover (*Charadrius dubius*)	0.452

Clustering the 10 km squares

The climate and topography of each 10 km square were specified by its position in an environmental space. The original environmental axes were transformed by a method of multivariate analysis, detrended canonical correspondence analysis (DCCA), to four axes that reflect species' differences. The 10 km squares were grouped into ten clusters (Figure 9) by a minimum-variance clustering algorithm. The resulting bioclimatic zones can be interpreted in terms of a north-west/south-east gradient of summer warmth and sunshine and an east/west gradient of winter temperature and moisture. Superimposed on these gradients are the effects of hills and mountains, which show up clearly in the zones.

Characteristics of zones

The species characteristic of each zone were ranked in order of a 'preference index' (Table 3). The more extreme zones, such as the oceanic montane zone, which includes Britain's highest mountains, are indicated by a suite of highly characteristic species, four plants and a bird, the ptarmigan (*Lagopus mutus*). They are frequent in the zone and virtually absent outside it. The intermediate zones such as the mild sub-oceanic lowland zone have less characteristic species. These include three birds, of which the ruddy duck (*Oxyura jamaicensis*) and little ringed plover (*Charadrius dubius*) are recent colonists, a dragonfly and a flowering plant. All of these species are frequent in the English Midlands, but occur widely elsewhere in England or Wales, although they are scarce or absent in Scotland.

The bioclimatic zones illustrated in Figure 9 have recently been made available in electronic form compatible with the Countryside Information System (as advertised in Version 3 of the Environmental Catalogue, available to download from the World Wide Web at http://mwnta.nmw.ac.uk/ceh/cis/ciscat.htm). Correspondence between the bioclimatic zones, the Countryside Commission/English Nature Character Map and the ITE Land Classification is being assessed using the Countryside Information System as part of an exercise to evaluate reporting options for Countryside Survey 2000.

P D Carey and M O Hill

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Population substructure and the dynamics of large herbivores

(This work was funded by a research grant from NERC. The long-term projects on Rum and St Kilda have also been funded by the Biotechnology and Biological Sciences Research Council, the Royal Society and the Wellcome Trust)

Animal populations are rarely homogeneous. Individuals vary in phenotype and genotype and commonly have access to food resources that differ in quality and quantity. Increasingly, ecologists are becoming aware of the importance of substructure in populations and beginning to appreciate how heterogeneity may influence the ability to predict future trends in abundance. Although the demographic consequences of population substructure have been explored theoretically, there are currently few empirical examples describing the extent and nature of variation in life history and demography in substructured populations. The paucity of effort in this area may reflect the fact that there are still few species where accurate measures of reproduction and survival can be associated with genetic identities at the individual level, and at the same time quantify the response to environmental heterogeneity. However, the studies of natural selection in the food-

There are currently few empirical examples describing the extent and nature of variation in life history and demography in substructured populations.

Plate 4. Red deer stag at bay (photo T H Clutton-Brock)

limited populations of red deer (*Cervus elaphus*) on Rum (Plate 4) and Soay sheep on St Kilda (Scotland), conducted in association with the Institute of Zoology and the Universities of Cambridge and Edinburgh, provide model systems for investigating these questions.

Identifying spatial scales of local dynamics

In juveniles of both red deer and Soay sheep spatial heterogeneity in group size contributed to the probability of survival over the first winter.

Because environmental heterogeneity tends to lead to spatial aggregation of individuals, and therefore the substructuring of populations, it is likely that there is variation in local dynamics within populations, which in turn will influence the dynamics of the whole population. However, the choice of spatial scales at which to explore these dynamics is often not apparent in populations of mobile individuals. Previously for deer we have used four discrete subdivisions based on the fact that female relatives (matrilines) were aggregated in clans around the better grazings (Guinness, Clutton-Brock & Albon 1978). Although there were differences in life histories and resulting changes in local density, Albon *et al.* (1992) showed that spacing behaviour was density dependent and matrilineal associations were breaking down, indicating that a more dynamic approach to the problem was required. With Dr T Coulson at the Institute of Zoology, we developed a hierarchical cluster analysis as a novel approach to explore population substructure over about 20 scales of fusion, ranging from many groups of two individuals to one group, the entire population (Coulson *et al.* 1997). These scales defined clusters or groups of different sizes that effectively represented local population density. We identified the appropriate scale of fusion as that at which variation in local population density best explained calf winter survival, the key factor contributing to individual variation in reproductive success and population abundance. In deer, the scale of clustering identified by the above methods was far more efficient in explaining fitness variation than the previous four subdivisions or matriline identity. In general, there were 10–12 clusters identified each year but membership of these groups was fluid between years and only loosely fixed in space. In sheep, local density was also important but, in contrast to deer, the hierarchical clustering analysis consistently grouped individuals into three hefts.

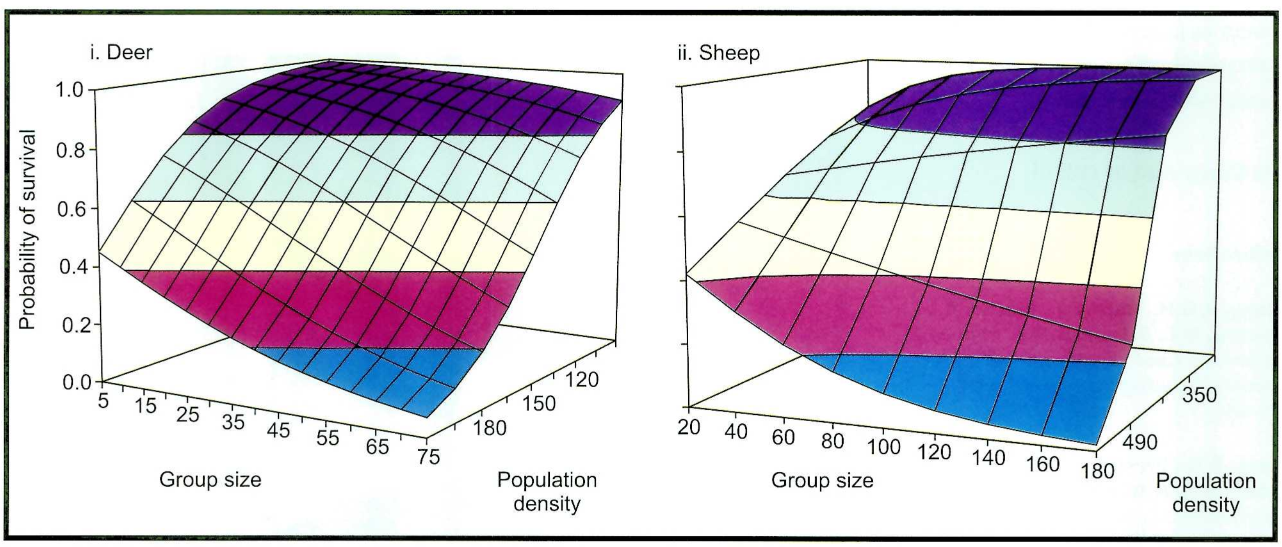

Figure 10. A 3-D surface showing the probability of first-winter survival declining in relation to both spatial variation in local density (group size) and temporal variation in total population density in (i) deer and (ii) sheep

Spatial variation in density dependence

In juveniles of both red deer and Soay sheep, spatial heterogeneity in group size (local population density) contributed to the probability of survival over the first winter (Coulson *et al.* 1997). Within years, first-winter survival was lower at high local density (group size axis in Figure 10).

Phenotype by local population density interactions

In red deer, but not Soay sheep, the relationship between survival over the first winter and local population density differed between the sexes. In small groups, male and female calves had similar probabilities of survival (10 adults, P_s=0.92 & 0.90, respectively) but in large groups males had a significantly lower probability of survival than females (60 adults, P_s=0.46 & 0.66, respectively). Thus, if environmental heterogeneity leads to a few large clusters or groups, the differential survival of the two sexes could lead to a skew in the recruitment sex ratio, biased against males, compared to a population of similar total size but subdivided into many small clusters or groups.

Genotype by local population density interactions

In both red deer and Soay sheep the association between fitness and genotype commonly involved interactions with environmental variables. In deer, for example, our work with Dr J Pemberton of the University of Edinburgh identified associations between winter survival of calves and genotypes at two out of three polymorphic protein loci and five out of ten microsatellite loci investigated in the deer. Of these seven associations, five involved interactions with environmental variables, and four showed density-dependent selection. Here, we show that first-winter survival of calves with different allozymes at the di-allelic isocitrate dehydrogenase (Idh-2) locus, a protein involved in fat metabolism, varied with spatial variation in local population density (group size) (Figure 11). FF homozygous individuals survived better than S-bearing individuals (FS, SS) in small clusters or groups, but *vice versa* in large clusters or groups.

In summary, this work has identified that environmental heterogeneity which leads to substructuring of populations may influence major fitness components, illustrated here in terms of survival over the first winter, through local density dependence or group size effects. Indeed, the number of observed phenotype–environment and genotype–environment interactions suggests that these interactions may be a common source of fitness variation in natural populations. Furthermore, because phenotypes and genotypes show differential selection in relation to local density dependence, this will contribute to the maintenance of phenotypic and genotypic variation in natural populations.

S D Albon

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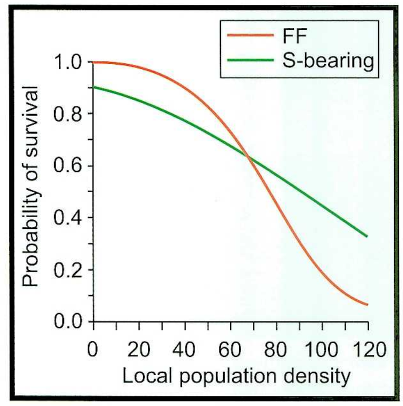

Figure 11. The interaction of over-winter survival in deer calves and allozymes of the protein isocitrate dehydrogenase (Idh-2) with local population density. Initially FF homozygotes are favoured at low local densities; as local density increases, however, the survival of homozygotes is lower than S-bearing individuals (SS homozygotes and FS heterozygotes)

This work has identified that environmental heterogeneity which leads to substructuring of populations may influence major fitness components.

Plate 5. Langholm moor. This photograph shows a mosaic of heather patches caused by burning and a large area of grass-dominated moorland to the north

The impact of raptors on red grouse populations

(This work was partly funded by The Buccleuch Estates, Peter Buckley of Westerhall Estates, Game Conservancy Trust, Game Conservancy Scottish Research Trust, Joint Nature Conservation Committee, Royal Society for the Protection of Birds and Scottish Natural Heritage)

The management of upland heather moors for red grouse (*Lagopus lagopus scoticus*) maintains landscapes that are important, not only for their unique character, but also for the wildlife they sustain. The overall aim of grouse management is to maximise the number of birds available for shooting in autumn, and to this end one of the main jobs of gamekeepers is to control predators. Because hen harriers (*Circus cyaneus*) and peregrines (*Falco peregrinus*) eat grouse, many keepers continue to control them despite the fact that these raptors have long been protected by law. Until recently there was little clear, scientific evidence on whether raptors have any effect on grouse populations, so in 1992 a five-year collaborative project between ITE and the Game Conservancy Trust (funded by a consortium of other interest groups) was set up to examine this issue. The study was based at Langholm in south-west Scotland (Plate 5), but was also extended to five other study moors elsewhere in Scotland. As raptor removal experiments were not possible, we estimated on each moor the abundance of grouse, songbirds and small mammals, and monitored the breeding numbers, breeding success and diet of hen harriers and peregrines. At Langholm, we also studied grouse mortality and raptor hunting behaviour, in addition to measuring a number of habitat features. On all moors, numbers of foxes (*Vulpes vulpes*) and crows (*Corvus corone*) were controlled by gamekeepers.

By use of archival photographs, we estimated that 48% of heather-dominant vegetation was lost from Langholm moor between 1948 and 1988, mostly at lower altitudes. This loss of heather (*Calluna vulgaris*), and consequent increase in grass, was attributed to heavy grazing from sheep. The numbers of grouse shot on the same moor showed a general downward trend since 1913, and a tendency to fluctuate over a six-year period, with the last peak in 1990. Given that raptor breeding densities were very low before 1990, it is unlikely that raptors were responsible for either the long-term decline or the regular fluctuations in grouse numbers.

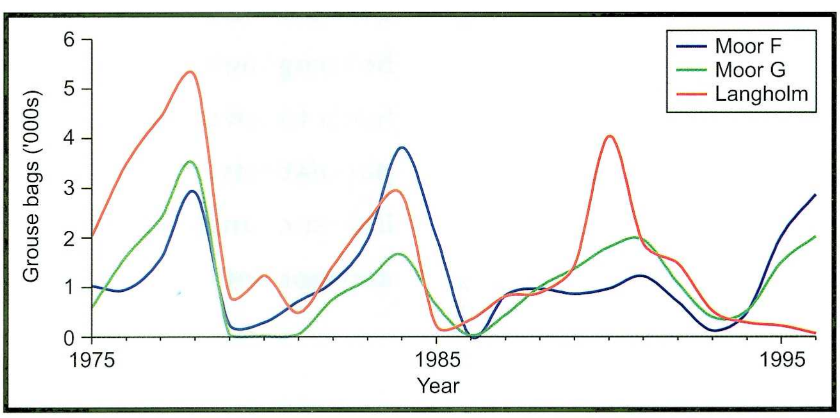

Figure 12. Grouse bags on Langholm moor, where harriers and peregrines bred at high density from 1993, and bags on two other nearby moors where raptors occurred at low density

On various study moors, the average density of breeding harriers increased for up to five years following protection from suspected illegal killing and other interference. During 1992–96, harrier numbers at Langholm increased from two to 14 breeding females. Peregrine numbers on all the moors were generally more constant over time, although at Langholm numbers increased from three to five or six pairs.

Through systematic searches for grouse carcases and radiotracking techniques, we estimated that raptor predation in spring removed approximately 30% of the potential breeding stock of grouse from Langholm moor. In the summers of 1995 and 1996, we also estimated, through watches at harrier nests (Plate 6) and counts of grouse broods, that harrier predation removed on average 37% of grouse chicks. Most of these adult and chick losses were probably additive to other forms of mortality, and together they reduced the post-breeding numbers of grouse by an estimated 50% within a single breeding season. Raptors also killed approximately 30% of the grouse from October to March, but it was not possible to determine what proportion of these grouse would have survived in the absence of raptor predation. A simple, mathematical model of the grouse population at Langholm, combining the estimated reduction in breeding production with observed density dependence in winter loss, predicted that over two years grouse breeding numbers would have increased 1.3 times and post-breeding numbers would have increased 2.5 times had there been no breeding harriers or peregrines on the moor.

During 1992–96, grouse numbers on Langholm moor were at a relatively low level; they did not change significantly from year to year and throughout were insufficient to support driven shooting. Grouse bags did not peak in 1996 as expected from past records. In contrast, grouse bags on two other nearby moors, which had previously fluctuated in synchrony with Langholm, increased to high levels in 1996 (Figure 12). These moors held only low densities of raptors. Predation by much larger numbers of raptors was considered the most likely explanation for the continued low grouse density and low grouse bags on Langholm moor during the study period.

Plate 6. A female harrier tending her young at the nest (photo T Pickford)

Comparing different moors, breeding densities of harriers and peregrines were not primarily related to grouse densities. The highest densities of breeding harriers occurred on moors where meadow pipits (*Anthus pratensis*) and small mammals were most abundant, and these prey appeared to prefer moors with a high ratio of grass/heather, such as those subject to heavy grazing. Peregrine breeding densities were lower in the Highlands than the north of England, probably because of differences in the abundance of pigeons (*Columba palumbus*), their main prey. Extrapolating from data on harrier and peregrine diet, we judge that the impact of raptor predation will be greatest on moors with grouse densities below approximately 12 pairs per km^2. We thus predict that the impact of raptors is likely to be greater on southern, grassy moors when grouse are at low densities.

The conclusions outlined above are based largely on circumstantial evidence and should be regarded as tentative until they can be tested by experiment.

S M Redpath, S J Thirgood[1] and I Newton

[1]The Game Conservancy Trust

We predict that, in the absence of persecution, the impact of raptors is likely to be greater on southern, grassy moors when grouse are at low densities.