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Biodiversity in montane Britain: habitat variation, vegetation diversity and some objectives for conservation

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The montane (low- to mid-alpine) zone in Great Britain (GB) lies above the potential tree-line (700–800 m, but descending to 200 m in the north). It is composed of moss and lichen heaths, snowbeds, blanket bog and dwarf-shrub (Ericaceae) health-covered solifluction/gelifluction terraces (38 communities/sub-communities). Approximately 3.0% of the land surface is covered by this – the most extensive predominantly near-natural terrestrial habitat in GB. Internationally distinctive features include oceanic and southern biotic outliers of arctic-alpine fellfield and mountain tundra, and plant communities that are either globally rare/localised or especially well represented in GB. The absence of extensive sub-alpine *Betula* spp. and *Salix* spp. scrub is striking.

The main sources of habitat diversity are climate, regional variation in topography and geology, and regional modifications due to land-use impact. Over 50 examples are given. Five important gradients in Scottish Highland vegetation are described. Only some 15% of the sampled montane vegetation is anthropogenic; the rest is semi- or near-natural. The vegetation is divided into 5 functional groups: chionophobous (avoids snow), chionophilous (prefers snow), species-rich, mires (including springs and flushes), and anthropogenic. Chionophobous and then chionophilous communities contribute most to montane vegetation diversity (calculated here as the Shannon *H* diversity index). *H* diversity increases asymptotically with montane site area but linearly with the number of communities present. A more varied topography, geology and topo-climate gives the highest *H* diversity.

Two examples of montane biodiversity reductions south of the Highlands are the loss of prostrate *Calluna vulgaris* heaths and modification of *Racomitrium lanuginosum* heaths. Five objectives for nature conservation are proposed, covering restoration of montane *R. lanuginosum* heaths, prostrate dwarf-shrub dominated heaths, sub-alpine scrub and upper treelines, and the extension of the breeding ranges of both ptarmigan (*Lagopus mutus*) and dotterel (*Charadrius morinellus*) south of the Scottish Highlands. International support for monitoring is sought.

Keywords: alpine; vegetation diversity; habitat conservation; arctic alpine vegetation; grazing impacts; snowbeds

Introduction

Mountains in Britain and Ireland (UK) have a range of ecosystems and landscapes not found elsewhere (Ratcliffe and Thompson, 1988; Thompson and Sydes, 1992). The

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climate is hyper-oceanic, land-use is mainly extractive (extensive deforestation followed by grazing range management and muirburn) and the mixture of plants (and to a lesser extent birds) drawn from high arctic through to continental regions is very diverse (Manley, 1952; Pearsall, 1950; Gimingham, 1972; Ratcliffe, 1977, 1990; Barry, 1981; Usher and Thompson, 1988; Thompson and Sydes, 1992). Across Britain, there are altitudinal life zones, arising from considerable climatic, topographical and geological variation, that parallel some of the major latitudinal belts across northern Eurasia.

In this review, we look at one component of the Great Britain (GB) uplands, the montane (low- to mid-alpine) zone, in order to assess some of the main elements of its biodiversity. Aspects of montane wildlife have been studied in considerable detail in GB (e.g. description and composition of montane vegetation – McVean and Ratcliffe, 1962; Birks and Ratcliffe, 1981; montane dwarf-shrub heaths – Watt and Jones, 1948; Summers, 1978; ptarmigan – Watson, 1965, Nethersole-Thompson & Watson, 1981; dotterel *Chardrius morinellus* –Nethersole-Thompson, 1973; Gailbraith *et al.*, 1992a,b; snow bunting – Nethersole-Thompson, 1966; and some of the invertebrates – Welch, 1981). Moreover, much has been published on the effects of downhill-ski developments in the Cairngorms (e.g. Watson, 1967, 1979, 1985; Thompson, 1986; Thompson *et al.*, 1987); human trampling on vegetation (Bayfield, 1979, 1980; Bayfield *et al.*, 1981); and on the general expansion of development and disturbance, again mainly in the Cairngorms (Watson *et al.*, 1970; Bayfield, 1980; Nethersole-Thompson and Watson, 1981; Watson, 1984, 1985; Thompson *et al.*, 1987). However, with the exception of Bayfield and Barrow's (1985) review on the impacts of recreation in mountain areas of Europe and N. America, there has been no overall assessment of the relative impacts of recreation, grazing-related pressures and acidic deposition on high mountain areas (but see Sidaway and Thompson, 1991). Ratcliffe (1977, 1990, 1991), Nethersole-Thompson and Watson (1981), Thompson *et al.* (1987) and Nature Conservancy Council (NCC), (1989) have discussed the conservation importance of montane Britain. The most recently published concerns about mountain areas have ranged from the localized impacts of rising recreation and tourism-related pressures (e.g. Countryside Commission for Scotland, 1990) to scenarios about 'global warming' (e.g. Nilsson and Pitt, 1991). This paper assesses spatial variation in both montane habitats and their vegetational diversity, gives examples of biodiversity loss because of land-use change, and finally proposes some objectives for conservation.

Montane Britain: the environment

Two upland zones

The uplands of Great Britain lie above enclosed farmland, are composed of hills, moor and mountain, and cover almost 30% of the land surface (Ratcliffe and Thompson, 1988; Thompson and Sydes, 1992). Their landscapes are dominated by dwarf-shrub heaths, grasslands and blanket-bog, and appear to lack the typical sequence of altitudinal life-zones found in continental Europe (i.e. an upward transition of coniferous forest to sub-alpine birch (*Betula pubescens* and *B. pendula*), scrub and medium shrubs to low-alpine dwarf shrubs, middle-alpine grassland, moss and lichen heaths to high-alpine stone desert, and finally to permanent ice and snow). This transition is absent in GB because the uplands have endured remarkably widespread and intensive impacts of man, marked first by deforestation and then by burning and grazing management for sheep (*Ovis aries*), cattle (*Bos taurus*), red deer (*Cervus elaphus*) and red grouse (*Lagopus lagopus scoticus*) (Ratcliffe, 1977, 1990; Birks, 1988; Ratcliffe and Thompson, 1988; Thompson and Sydes, 1992). As a consequence, there are two upland zones: *sub-montane*, with vegetation derived mainly from woodland above the limits of enclosed farmland, rising to the *montane zone* (equivalent to the Norwegian low-alpine zone with a very small extent of middle-alpine vegetation), which begins at the potential tree-line. Montane areas have moss- and lichen-dominated heaths, snowbed vegetation, blanket bog and prostrate heather-dominated solifluction/gelifluction terrain.

The montane zone is of international significance by virtue of having southern and oceanic outliers of arctic-alpine fellfield and mountain tundra, as well as some communities which are either local/absent elsewhere or particularly well represented in GB (see Ratcliffe and Thompson, 1988; Thompson and Sydes, 1992). The most striking absence is that of *Betula nana*, *B. pubescens* scrub and extensive arctic-alpine *Salix* spp. scrub above the tree-line up to late snow-lie, as found in Western Norway. Although the few remnants of montane scrub on cliff ledges inaccessible to grazing sheep and deer indicate the suppressive effects of overgrazing, it is debateable to what extent this could develop more widely over the exposed lower reaches of montane Britain.

Virtually all of the montane zone is composed of short, semi-natural (and in some northern areas, near-natural) vegetation. *Semi-natural* communities would not change to another if man's influence were removed (Thompson and Horsfield, 1990) and are composed of native species with structural affinities and community processes corresponding with those of natural vegetation (Tansley, 1939). The composition and abundance of species, however, may have changed from a more natural state because of man. The same applies to *near-natural* communities, except that these have probably changed little in composition over the past 8000 years. Nevertheless, during the early Holocene (9000–8000 BP, Mesocratic phase according to Birks, 1988), when temperatures were approximately 2° C above present, the montane zone was much smaller and exceptionally local south of the Highlands. Since then, the ensuing climatic deterioration has given rise to an extended montane zone, parts of which are species-poor. In other parts, notably where there have been sheep-related grazing pressures and greater acidic deposition, stands have been modified considerably (Ratcliffe, 1977; Thompson *et al.*, 1987; Thompson and Baddeley, 1991). Compared with other terrestrial habitats in Britain (with the possible exception of some saltmarshes and sea-cliffs) the montane zone is the least modified, and is therefore highly valued (e.g. Ratcliffe, 1977; NCC, 1989). The montane zone has 121 vascular plant taxa (flowering plants and ferns), (Ratcliffe, 1991), more than 200 lower plant taxa (mosses, liverworts, lichens), 23 breeding bird species (including 3 specialists), 12 mammal species (0 specialists) and several thousand large invertebrate species (at least 100 specialists).

Extent

The montane zone, as defined here, covers approximately 3.0% of GB. Most montane habitat is in the Scottish Highlands (Fig. 1). Of all near-natural communities in Britain, the montane *Racomitrium lanuginosum*-dominated heaths appear to be the most extensive. There is still much debate about the extent of Holocene woodland in GB, and therefore about the original extent of the montane zone (e.g. Birks, 1988, 1989). One of the very few good examples of tree-line is on Creag Fhialcach in north-east Scotland, where *Pinus sylvestris* woodland reaches its maximum altitude at 640 m (Ratcliffe, 1981). This is the most continental part of Scotland and so it is not surprising that elsewhere in GB the maximum altitude of Holocene woodland is estimated to have been lower (520 m in NW Highlands, 457 m in Skye, ⩾457 m in Galloway, ⩾715 m in south Wales, ⩾635 m in north Wales, ⩾893 m in north Pennines, 760 m in Lake District (Birks, 1988)), though in the Brecon Beacons, south Wales the potential tree-line also lies at about 640 m.

Our estimates for the beginning of the montane zone are based on (i) the presence of heaths of dwarf shrubs (notably *Calluna vulgaris* and *Vaccinium myrtillus*) becoming increasingly prostrate with exposure, and (ii) increasing dominance of small herbs, mosses and lichens. This limit descends in north-westerly and northern directions, from 700–800 m in the Cairngorms and central Grampians (central Highlands), 550 m in Sutherland (north-western Highlands), 350 m in north-west Sutherland, to 200–300 m in Orkney and Shetland (two isles to the north-east of mainland Scotland, not shown on Fig. 1).

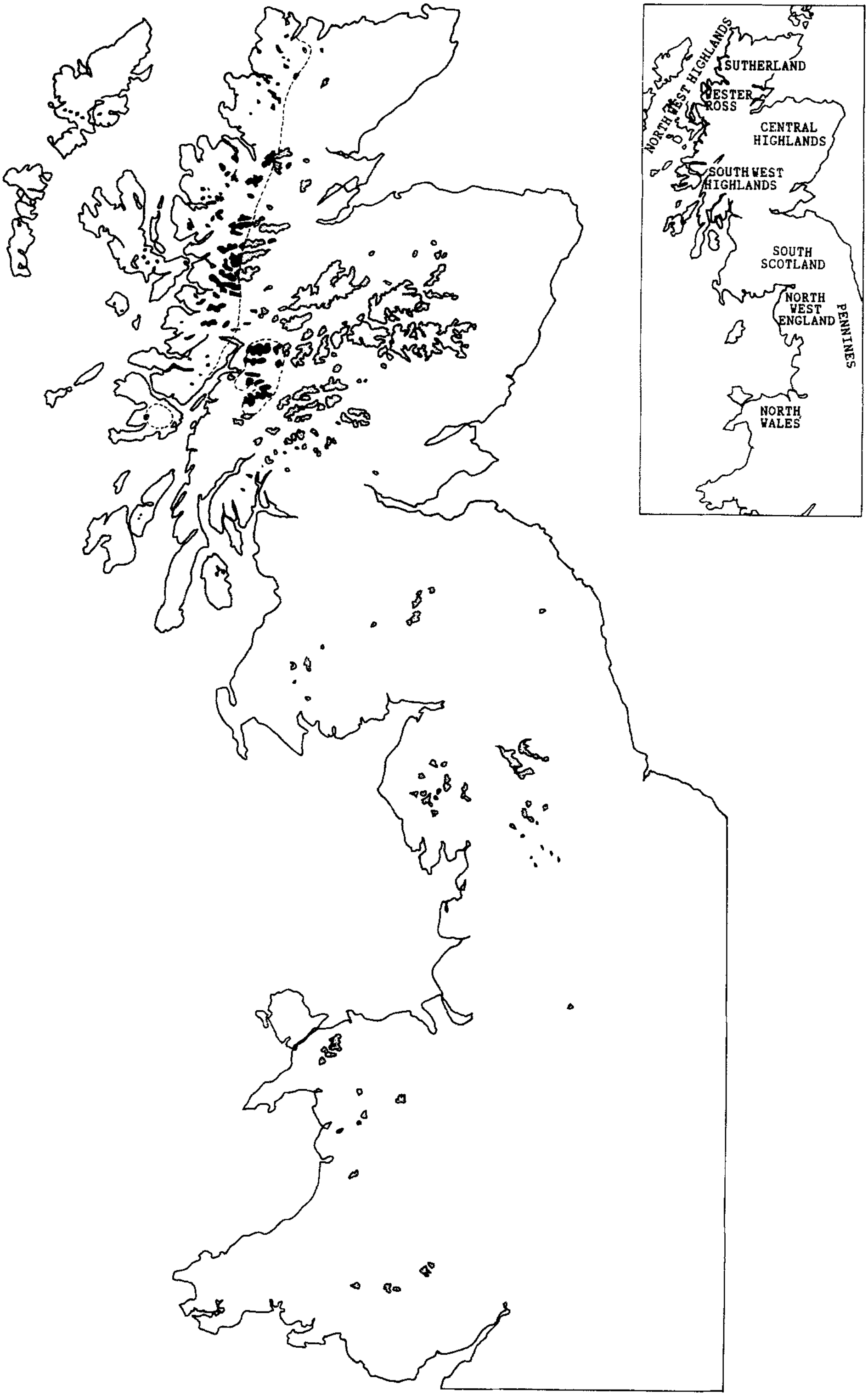
Methods

Vegetation: communities and functional groups

The vegetation has categorized according to stands (in the field) which have a fairly homogenous structure and species composition (Poore, 1957; McVean and Ratcliffe, 1962; Ratcliffe, 1977; Brown *et al.*, 1992). These stands were then classified according to vegetation types (communities) using phytosociological methods. We have used Birks and Ratcliffe's (1981) classification as it was the most sensitive to variation in montane vegetation; transpositions to Rodwell's (1991) *National Vegetation Classification* communities are given in the Appendix. Our survey methods now employ Rodwell's (1991, 1992) classification.

The 38 montane communities ($n = 27$ according to Rodwell, 1991, 1992; Thompson and Sydes, 1992) have been divided into five functional groups (Appendix): (i) chionophobous (associated with snow-free conditions and equivalent to *Rabbevegetasjon* in Norway (Fremstad and Elven, 1987)); (ii) chionophilous (found where snow accumulates and persists and including equivalents of Norwegian *Lesidevegetasjon* and *Snøleievegetasjon*); (iii) species-rich communities; (iv) mires and springs; and (v) anthropogenic commun-ities. Some communities clearly belong to one group (e.g. chionophobous lichen-rich prostrate *Calluna vulgaris* heaths, chionophilous *Nardus stricta* snowbeds) whereas others share several affinities (e.g. high altitude *Dryas octopetala* heaths are chionophilous and species-rich; *Agrostis* spp., *Festuca* spp. montane grasslands are chionophobous and anthropogenic). The distribution of some communities in relation to topography, exposure and snow-lie on acid and base-rich soils across a typical range of montane landforms is illustrated in Fig. 2.

Figure 1. The extent of the montane zone in Britain. The contour line is approximately 650 m (adapted from Bickmore and Shaw, 1963). The dark-shaded montane areas are actually more extensive than shown because of cooler summer temperatures and increased wind-exposure in this area of high oceanicity; the light-shaded areas are slightly less extensive than shown. The broken line shows the eastern limit of 220 wet days in Scotland, indicating the zone of high oceanicity.


NORTH WEST HIGHLANDS
SUTHERLAND
WESTER ROSS
CENTRAL HIGHLANDS
SOUTH WEST HIGHLANDS
SOUTH SCOTLAND
NORTH WEST ENGLAND
PENNINES
NORTH WALES

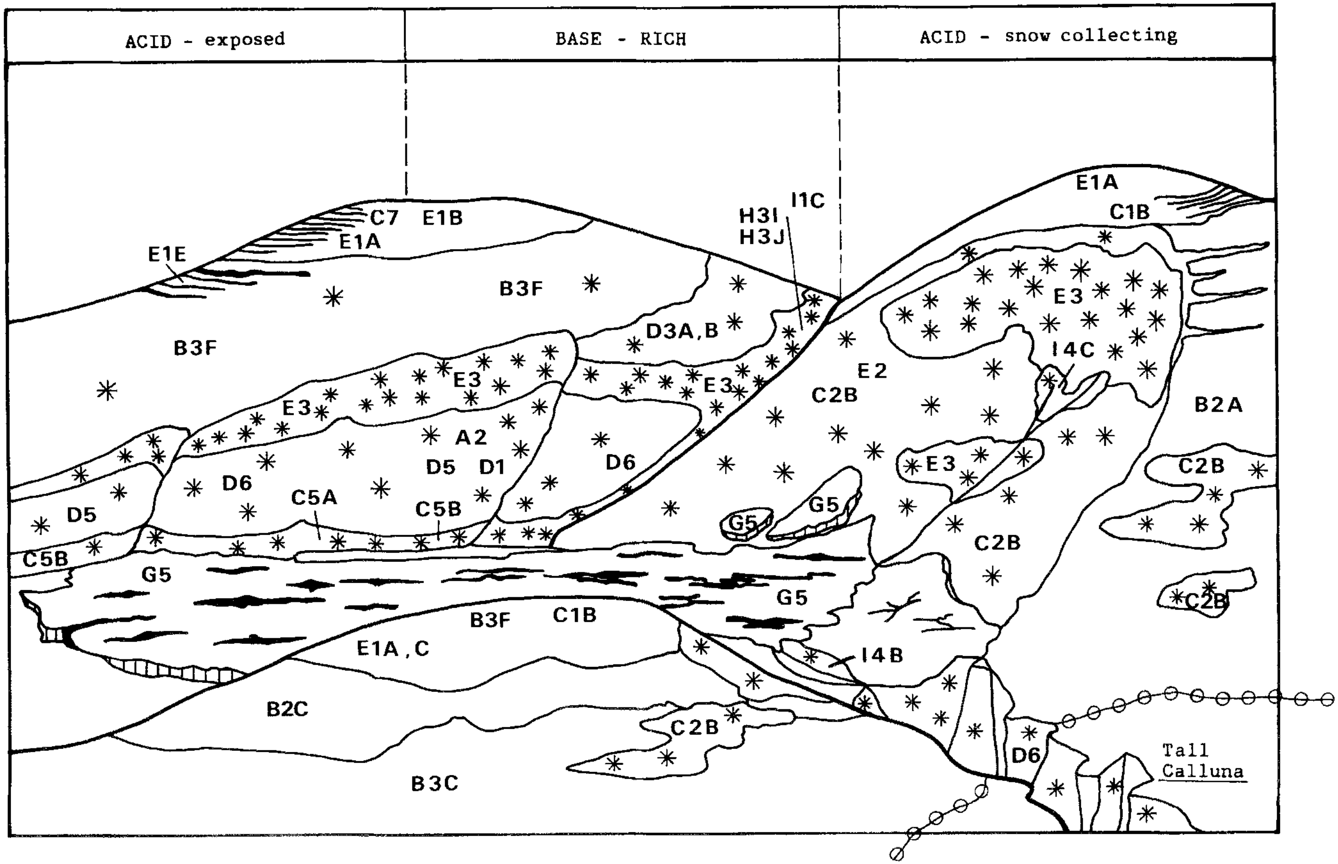


Figure 2. Composition of montane vegetation across a typical range of mountain landforms including wind-blown summits (with chionophobous vegetation), crags, corries and snow-collecting gullies (with chionophilous vegetation). The community codes (according to Birks and Ratcliffe, 1981) are given fully in the Appendix. o-o-o, tree-line; **, moderate snow-lie through to *******, late snow-lie.

Analysis and diversity indices

We analyzed data on presence/absence and extent of the 38 plant communities across 104 montane sites, mainly within Sites of Special Scientific Interest (SSSI). Brown *et al.* (1992) and Hobbs and Sydes (1988) provide details of the survey methodology. Most of the sites were topographic units with the fullest possible range of ecological variation bounded by enclosed farmland (NCC, 1989). After the vegetation was mapped on aerial photographs, the area of each community was measured and the data computerized.

Many diversity indices are available that quantify the numerical properties of communities (e.g. Hill, 1973; Pielou, 1977; Begon *et al.*, 1990). Most of them are normally applied to samples of individual animals and plants within a community. To estimate a single diversity index for vegetation within a montane site we want to combine both the number of plant communities and the evenness of the division of a given area between these communities. Essentially, this is a substitution of numbers of individuals of each species by the area of each community divided by total montane zone extent. The index should not assume any particular frequency or spatial distributions of communities, nor be influenced by montane area, and should increase with community number and with greater evenness in their share of the montane zone (see Pielou, 1977; Begon *et al.*, 1990). The index should also have additive properties so that, for example, indices of *Calluna*-dominated community diversity and of species-rich community diversity can be combined.

The Shannon diversity index (*H*) best met our requirements. The theoretically-preferred Brillouin index can only use integers so has not been used. *H* was calculated for each sampled site, taking the form:

$$H = - \sum_{i=1}^{s} Pi.\ln.Pi \qquad (1)$$

where s is community range and Pi is the proportion of all vegetation belonging to community i. In order to test the appropriateness of H in this application to vegetation diversity we took a hypothetical community mosaic and plotted H for a series of even versus uneven divisions into smaller and smaller units (see Pielou, 1977 for an algorithmic proof). H increased with a greater number of communities on a site, was not biased by total montane zone area, and was greatest where there were most communities split evenly across the site.

The H index therefore provides a useful summary of vegetation diversity on each montane site. It gives better information than merely comparing species lists or areas of communities.

Results

Sources of habitat diversity

There are three main sources of habitat diversity in montane Britain. Table 1 emphasizes the direction of the gradients as well as the communities affected, and gives 53 examples of gradients or differences. Each source of diversity is considered below briefly.

Table 1. Three major sources of biodiversity in montane Britain. The communities (codes given here) are described in the Appendix.

Sources and postulated mechanisms	Direction of gradient	Communities involved (favoured) by factor increasing (unless otherwise indicated)	References
A. Upland climate			
1. Low temperatures			a,b,c,
— reduced physiological activity — reduced growing season — increased likelihood of frost and snow — reduced CO_2	Temperature decrease as: altitude increase lapse rate = 7° C km^{-1}	All types (within range of low alpine)	
2. High winds			a,d,e,f
— causes physical damage by buffeting — may carry abrasive grits and ice particles — turbulent mixing of free air with surface air to steepen near-ground gradients of temperature and moisture — redistribute snowfall to snowbeds — high winds and low temperatures combine in 'exposure'	Wind increases as: altitude increases, distance to coast decreases (features of oceanic air masses are not always found in other mountains)	B2(H13,H14) E1E(U9,U10C) C7(U9)	
3. High precipitation and cloud cover			a,g,h
— wet soils: podsols, gleysols, histosols (blanket peat) — cold soils in early summer — leaching to give acid soils — local flushing (at lower levels)	Precipitation increases as: altitude increases distance W increases, (strong orographic	All snowbeds, springs and flushes G5 (M19C)	

— high snowfall to snowbeds — soil moisture important in active solifluction — cloud cover reduces insolation and ground temperature — light levels decrease with elevation	component of precipitation; prevailing wet westerly winds)		
B. Regional variation in topography and synoptic climate			
4. Latitudinal temperature lapse rate and decreasing solar elevation — colder in northern summers (see 1.) — increasing influence of aspect on temperature	Temperature decreases as: distance N increases (roughly 2° C mean temperature between SE England and N Scotland)	All types	a,e,c,i,h
5. Western peak-eastern plateaux eastern plateaux have: — large summit areas — summits more continuous and joined by montane habitat — large snow-collecting grounds (for snowbeds) — large sheltered high gullies (for snowbeds) — sluggish drainage and peat-formation western ridges have: — small rocky summits and ridges — very isolated summits or long ridges — well-drained high slopes — steep N-facing slopes (for snowbeds)	Summit area increases as: distance N increases distance E increases (larger areas of high ground are in Scottish Highlands; declining lower limit of montane ground to NW – see 6.)	E3 (U11,U12), 14C(M33) G5 (M19C)	d,j,k,l

Table 1. *Continued*

Sources and postulated mechanisms	Direction of gradient	Communities involved (favoured) by factor increasing (unless otherwise indicated)	References
6. East to west increase in precipitation and oceanicity — increasing rainfall (see 3.) — increasing number of rainy days — increasingly cold summers and mild winters (see 1.) — declining lower montane limit with exposure (see 2.) — calcicole less preferential in strongly oceanic climates	Oceanicity increases as: distance to sea decreases distance to W coast decreases (there are few major summits near to the east coast; the prevailing westerly winds blow the oceanic influence further inland from the west)	Moss-dominated types increase B2B(H14), E1A,B,E(U10), E2 (U13B); lichen-dominated types decrease: B2C(H13), B3F(H19), E1B(U10C)	d,l,m d
7. Regional occurrence of calcareous rocks — presence of scarce nutrients (in heavy leaching conditions) — most (rare) upland vascular plants are calcicole — most base-rich rocks also have locally base-poor soils — increases plant productivity of widespread species (e.g. *Calluna*) — may attract heavy/preferential sheep and deer- — grazing		Favours calciphile types e.g. B4B(CG14), C5B(U17C), D3(CG12). Heavy grazing/dunging may replace: B2A(H13), E1A(U10) by anthropogenic types: B3C(H18B), E1C(U10A), C1B(U4E).	
8. Regional plant refugia — refugia on high, northern summits — refugia on high-lying calcareous rocks — key relict species in some communities		B4B(CG14)	d

C. Regional and local modification (secondary sources of diversity)			
9. Sheep/deer grazing — removes primary production and woody vegetation — local nutrient enhancement from urine and dunging — trampling may maintain diversity of sp.-rich types — peat-erosion increased by deer — locally associated with large-patch burning extending from upper fringes of sub-montane *Calluna* heaths — may be accompanied by local large-patch burning of woody species	Sheep grazing impacts greatest south of Highlands (notably Wales and NW England). Deer impacts appear greatest in central Highlands	B2A(H13), E1A(U10), B3C(H18B), E1C(U10A), C1B(U4E) (see 7.)	d,l,n,o
10. Trampling/vehicles — loss of fragile species (e.g. *Cladonia*/lichens) — local peat erosion and loss of topsoil/vegetation		B2C(H13), B3F(H19B)	l
11. Botanical collecting — 19th Century collection of arctic-alpines, pteridophytes — locally reduces species richness, but rarely loss of community			l
12. Acidic deposition — direct deposition from clouds very important (see 3.) — most montane soils are acid with low buffering potential	Greatest in NW England, Wales and SW Scotland	Possibly all types with lower plants dominant (U8,U9,U10, U11,U12,H14,H15,H19,H20, M7,M12,M31,M33). Changes not well known.	n,p

NOTES

1. Communities given according to Birks and Ratcliffe (1981) and transposed to Rodwell (1991, 1992) in brackets. See Appendix 1 for full descriptions.
2. References: a (Barry, 1981), b (Harrison and Harrison, 1988), c (Tivy, 1973), d (McVean and Ratcliffe, 1962), e (Geiger, 1965), f (Dahl, 1986), g (Ballantyne, 1983), h (Manley, 1971), i (Chandler and Gregory, 1976), j (Haynes, 1973), k (Poore and McVean, 1957), l (Ratcliffe and Thompson, 1988), m (Ratcliffe, 1968), n (Thompson and Baddeley, 1991), o (Rodwell, 1991), p (Baddeley, 1991).

Climate. The greater extent of montane habitat in the north arises not just from greater average summit heights and area, but also from steep lapse-rates northwards in summer temperature, north-eastwards in winter temperature and snowfall, and north-westwards in rainfall and oceanicity (little seasonal variation in precipitation and temperature, high atmospheric humidity, low insolation and high winds). The Atlantic air mass has a major influence on the whole of upland Britain, but south of the Scottish Highlands this is ameliorated by the westward bulk of Ireland (see maps in Page, 1982; analysis of atlantic bryophyte distribution in Ratcliffe, 1968; and discussion on world ombrotrophic bog distribution in Lindsay *et al.*, 1988).

Regional variation in topography and geology. Much of the regional pattern in mountain landforms is a result of differential quaternary glaciation. In eastern Britain there are high, deeply dissected plateaux and large virtually continuous summits and ridges. The central Highlands have the most massive mountains. Towards the west the mountains have sharper, rockier ridges and steep, isolated peaks, especially in the region of the Loch Lomond glacial re-advance (Haynes, 1974). Further south, the gently contoured tops of the Pennines contrast with the rugged peaks in Lakeland and Snowdonia. Most of the British uplands are made up of acid rocks with only locally important calcareous exposures (many of which are masked by drift). The Dalradian limestones and calcareous schists in Perthshire, Argyll and Angus, and the Durness dolomitic limestone in the north-western Highlands, for example, give rise to heightened biotic diversity and productivity.

Secondary sources of habitat diversity. The secondary influences of land-use practice provide an additional source of variation. In montane Britain, the highest densities of grazing sheep occur south of the central Highlands (particularly in north Wales and Lakeland) and highest densities of grazing red deer are in the central Highlands. Pollution also varies across the country, with acidic deposition (notably of nitrates) highest in north Wales, Lakeland and south-western Scotland (Baddeley, 1991; Thompson and Baddeley, 1991).

Broad regional trends in habitat diversity

There are three major montane regions: Scottish Highlands, South Scotland and the rest of GB. In the Scottish Highlands the evidence of vegetation distribution suggests that there are five important gradients: (i) the greater extent of eastern plateaux broadens the range and extent of boreal montane bog and late snowbeds; (ii) there is an east-west switch from lichen-dominated to moss-dominated heaths; (iii) wind exposure increases westwards with an increase in prostrate heather moor and open, wind-ablated *Racomitrium lanuginosum* heaths; (iv) species tolerance of infertile soils increases in the west (McVean and Ratcliffe, 1962); and (v) in parts of the Breadalbanes and towards the north and west there is an increase in strongholds of rare plants and refugia for relict species (see Ratcliffe, 1991). Southern Scotland, northern England and Wales are strongly influenced by anthropogenic change, and by far the most widespread recognisable near-natural montane communities are *Racomitrium lanuginosum-Carex bigelowii* communities and their more continental equivalent *Vaccinium myrtillus-Cladonia arbuscula* heaths. Brown *et al.* (1992) describes more fully regional variations in Scottish upland vegetation. Local diversity in these regions is enhanced by the presence of strongly calcareous rocks (see above) and by the topographic juxtaposition of groups of functionally-related communities (e.g. late snow-bed communities irrigating associated wet grasslands and mire communities). The best example of both types of enhancement is in the complex of *Polytrichum norvegicum-Kiaeria starkei* snow-bed (E3), *Carex saxatilis* mire (CH3J) and species-rich *Deschampsia cespitosa* grassland (C5b) (see Fig. 2).

Extent of anthropogenic vegetation

Fifteen percent of sampled montane habitat is composed of anthropogenic communities as opposed to near-natural/semi-natural communities (Fig. 3). Clearly, much greater areas would be anthropogenic if the *Racomitrium lanuginosum* heaths and *Nardus stricta* snowbeds were modified by man. Changes and losses in montane blanket bog and *Vaccinium myrtillus* heaths, however, would not have the similar impacts on the extensive quality of montane habitat.

Diversity of vegetation across Britain

The greatest montane vegetation diversity (highest *H*) occurs in the central Highlands and Wester Ross (Fig. 4a). The five montane sites with the highest *H* diversity indices are, in descending order, Ben Lawers (central Highlands), Monar forest (western Ross), Cairngorm (central Highlands), Ben Lui (west-central Highlands) and Meall na Samhna (central Highlands). Sites in north-western Scotland have high *H* diversity chionophobous communities but have few chionophilous communities; south of the Highlands,

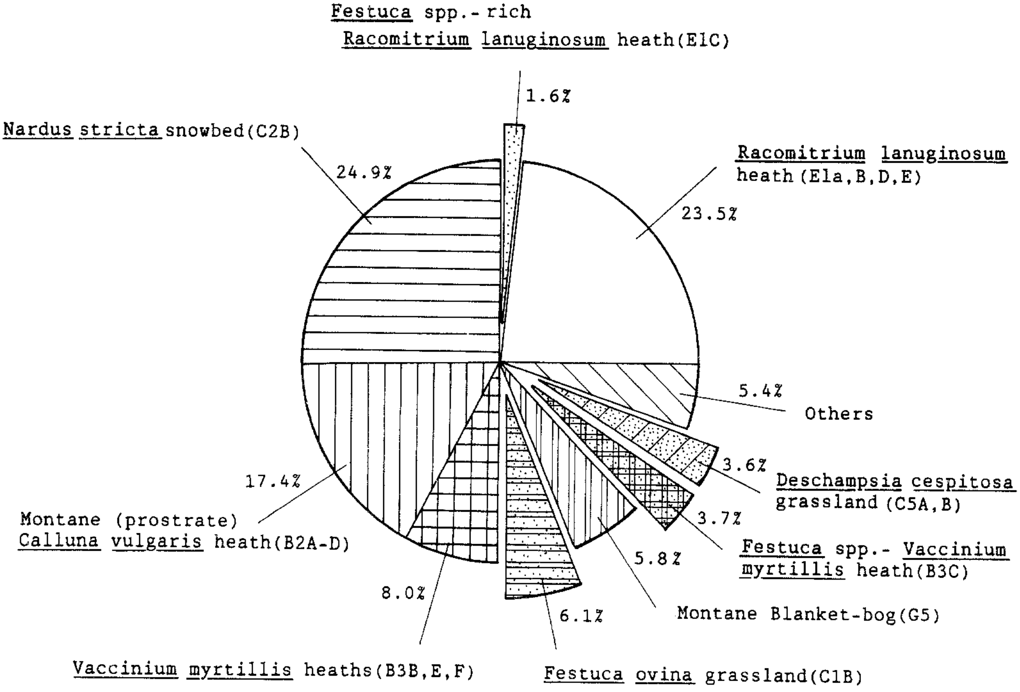
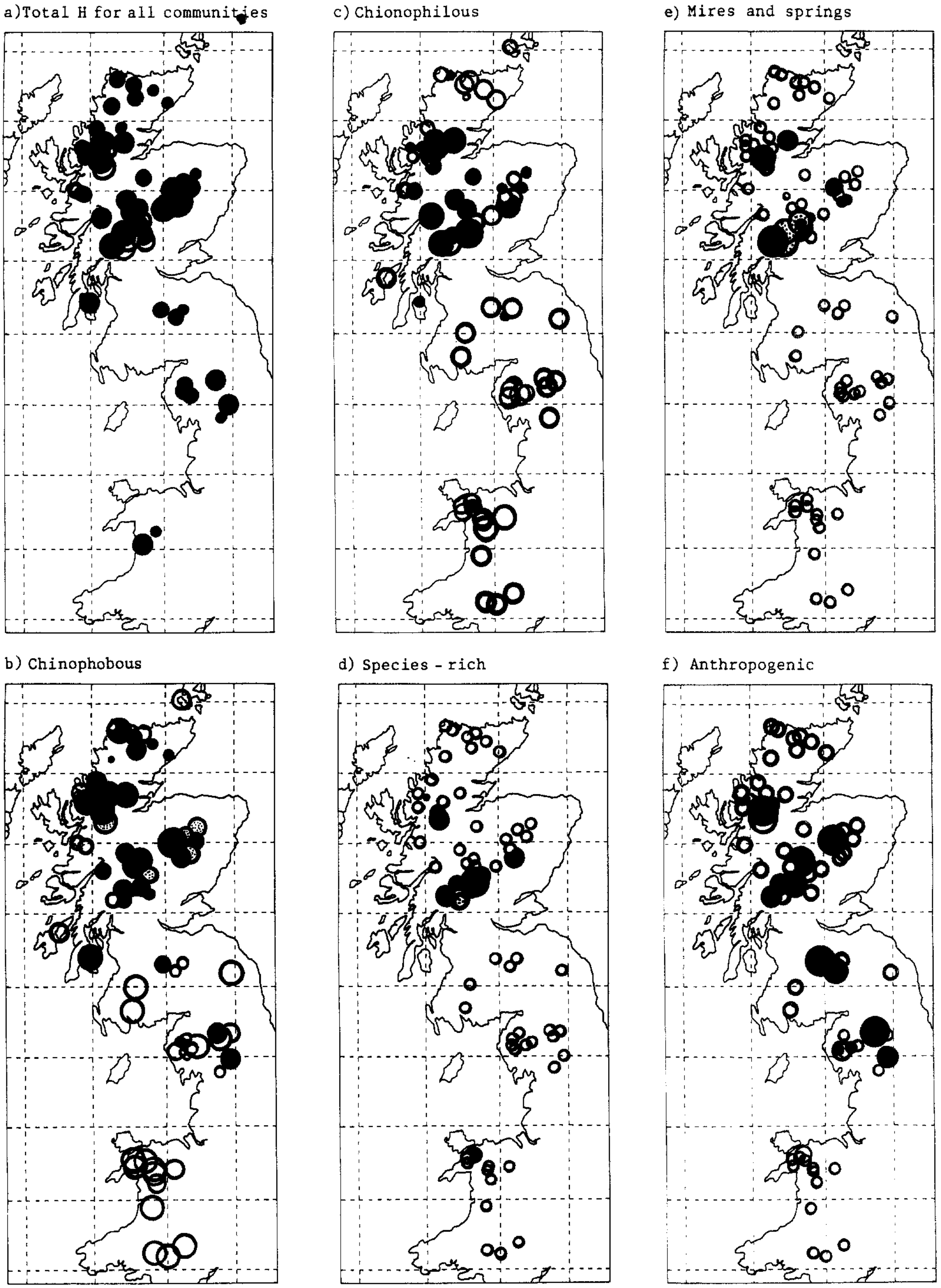


Figure 3. Proportion of near natural and anthropogenic vegetation (shown as detached slices) in the montane zone. Data for 104 (approximately 78 000 ha) upland Sites of Special Scientific Interest (SSSI). The codes are according to Birks and Ratcliffe (1981).



a)Total H for all communities

c) Chionophilous

e) Mires and springs

b) Chinophobous

d) Species - rich

f) Anthropogenic

Figure 4. Relative values of montane vegetation diversity (H, see Equation 1) for all communities, and for the five functional groups. In (a) circle size is proportional to H; in (b-f) circle size shows the deviation from mean H, with filled circles showing site $H >$ mean, empty circles diversity showing site $H <$ mean.

Table 2. Shannon diversity indices (*H*) for the five functional groups of montane vegetation.

Community functional groups	No.	Mean (SD) no. per site	Mean (SD) area (ha) per site	Mean (SD) *H* per site	Correlation between *H* for functional group and overall *H*
Chionophobous heaths	13	3.9 (2.8)	465.7 (829.2)	67.7 (54.2)	High
Chionophilous heaths	19	3.3 (3.7)	213.8 (519.3)	43.0 (47.2)	Low
Species-rich communities	10	1.0 (1.5)	13.7 (47.6)	13.7 (33.0)	High
Mires and springs	7	0.7 (1.4)	27.6 (122.8)	10.7 (24.4)	High for some sites, low for others
Anthropogenic communities	4	1.0 (0.9)	86.2 (167.3)	10.2 (20.9)	Very low

Data for 84 montane sites.

sites score particularly lowly for these two groups. The *H* diversity for anthropogenic communities, however, is greatest towards the south (Fig. 4f).

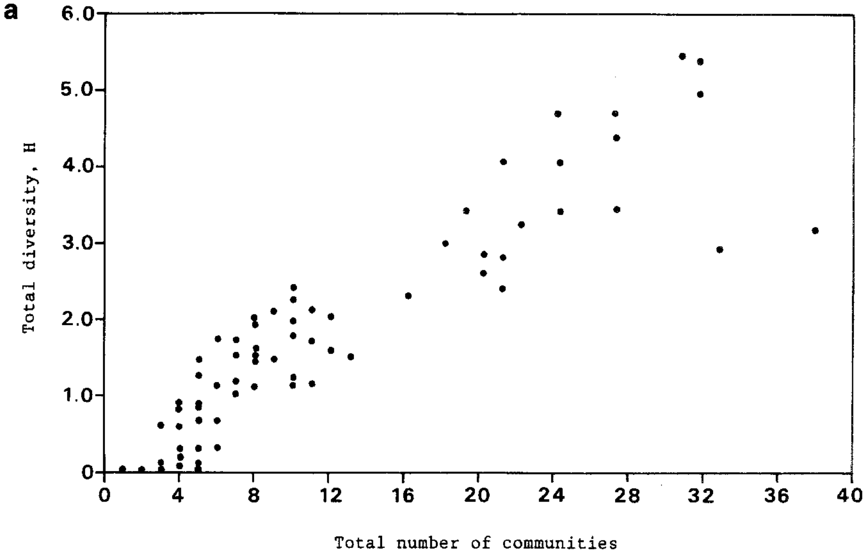
Of the five functional groups of vegetation, the chionophobous heaths are the most diverse (dominated by *Carex bigelowii-Racomitrium lanuginosum* heaths, *Vaccinium myrtillus-Cladonia arbuscula* heaths, mixed *Calluna/Arctostaphylos* heaths, and *Festuca ovina-Agrostis capillaris* grassland) followed by chionophilous heaths (notably *Nardus stricta-Carex bigelowii* snowbed) (Table 2). There is relatively greater variance in chionophilous heaths than in chionophobous communities reflecting greater local variation in montane summit composition. Interestingly, the strongest correlations between overall *H* diversity on each site and the *H* diversity values for each functional group are with chionophobous and species-rich communities (Table 2). High *H* diversity in anthropogenic communities and chionophilous communities contributes relatively little to the total *H* diversity score (summarised in Table 2, right hand column).

For given montane sites, *H* diversity increases linearly with the number of communities present (Fig. 5a), but asymptotically with montane site area (Fig. 5b). It does not follow, therefore, that the largest montane areas contain the greatest diversity of plant communities. Instead, a more varied topography, geology and topo-climate (*sensu* Barry, 1981) affords the highest diversity in montane vegetation. This bears out the point made previously about calcareous rocks and topographically juxta-posed functional groups (and illustrated by example in Fig. 2).

Conservation and the loss of diversity

There is remarkably little information on historical changes in montane vegetation. In part, this is because of considerable problems involved in carrying out pollen or macrofossil studies (Birks, 1988), but also because virtually no long-term monitoring has been undertaken. We have studied photographs, field notes made by naturalists and the contemporary composition of some plant communities across montane Britain in order to infer changes and causes of these. Two examples of change are given here.

Montane Racomitrium lanuginosum *heaths*. These are most prevalent in the north and west (Fig. 6a) where they occur as a pure moss heath carpet with much *Carex bigelowii*



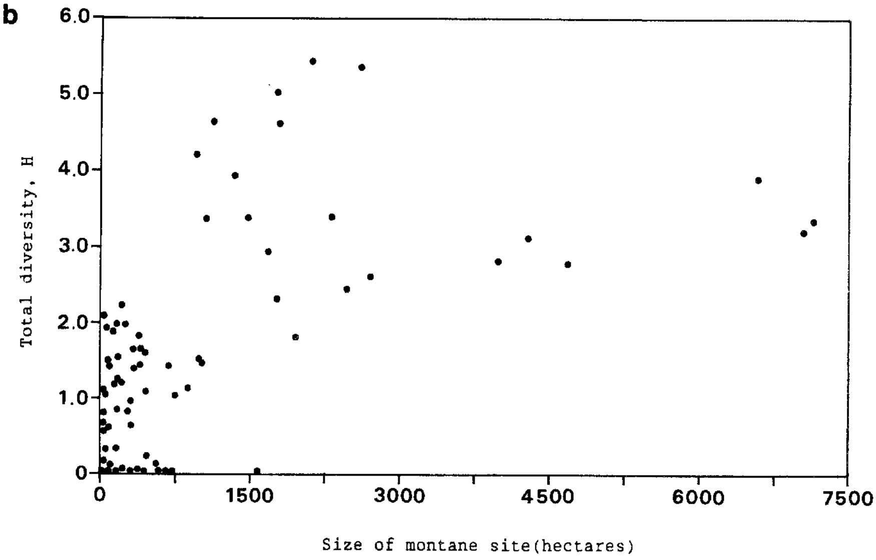


Figure 5. Relationships between montane site *H* and (a) number of montane communities ($r = +.921, p < 0.001$), and (b) size (hectares) of montane site ($r = +.548$, $p < 0.01$). Data for 83 sites. Some points correspond to more than one site.

and *Vaccinium myrtillus*. South of the Highlands the heath is much less continuous and consists of more grasses and bedstraw (*Festuca ovina*, *F. vivipara*, *Galium saxatile*) and less *R. lanuginosum* (Fig. 6b). Thompson *et al.* (1987) and Thompson and Baddeley (1991) have suggested that the more sustained pressures from grazing sheep in the south, combined with slightly less oceanic conditions, account for these grassier heaths. Work by D.A. Ratcliffe and D.B.A. Thompson in northern Wales in 1989 (unpublished), repeating earlier surveys by DAR in 1952 (e.g. Ratcliffe, 1959), found declines in the percentage cover of *R. lanuginosum* on three summits from 34% to 9%, 36% to 8%, and 20% to 1%. In the Lake District *R. lanuginosum* heaths are now absent or fragmentary on summits where they were formerly described as prevalent (Pearsall and Pennington, 1973). It seems most likely that trampling, defecation and urination by sheep causes the *R. lanuginosum* heath to disintegrate whilst enhancing growing conditions for the grasses which gradually overwhelm the moss. In one part of the southern uplands of Scotland, where some sheep have been removed, the montane heath has shown signs of recovery with particularly long shoots of *C. bigelowii* evident.

The geographical division between the moss- and grass-dominated heaths is not total, for as Fig. 6b shows the latter is found on Skye. However, this outlier is on the basalt plateau of the Trotternish ridge where base-rich geology favours the grasses and attracts high sheep grazing pressure (Ratcliffe, 1977).

Montane Calluna vulgaris *heaths*. The mats of prostrate *Calluna vulgaris* are virtually unique to Britain (Thompson and Sydes, 1992; Thompson *et al.*, 1992). Fig. 6c indicates a marked Scottish Highland stronghold, with strong representation in the east Highlands and West Ross. Comparison with the extent of sub-montane *C. vulgaris* moorland shows a much wider distribution across upland Britain, though again the Scottish Highlands have the main expanses (Fig. 6d). What is striking, however, is the low density and near absence of montane *C. vulgaris* southwards from the south-western Highlands, despite the presence of suitable exposed ridges (see Fig. 2). This suggests a marked deleterious impact of grazing sheep on this community, so that it gives way to more grass-dominated heaths. This inference is reinforced by the corresponding reduction in the area of submontane *C. vulgaris* heath (Fig. 6d). Our work (see also Stevenson and Thompson, 1992) in southern Scotland and north-western England suggests that prostrate *C. vulgaris* was formerly far more extensive in montane Britain prior to significant increases in grazing pressure.

The ptarmigan (*Lagopus mutus*) depends on montane dwarf shrubs for food, and its disappearance from mountains south of the Scottish Highlands has been linked to losses of the heaths under heavy sheep grazing pressures (Galbraith *et al.*, 1988; Ratcliffe, 1990). Ptarmigan were present in the Lake District until the late 1700s and in the Southern Uplands until the early 1800s; attempted re-introductions have failed, presumably because the grassier hills offer unsuitable feeding habitat.

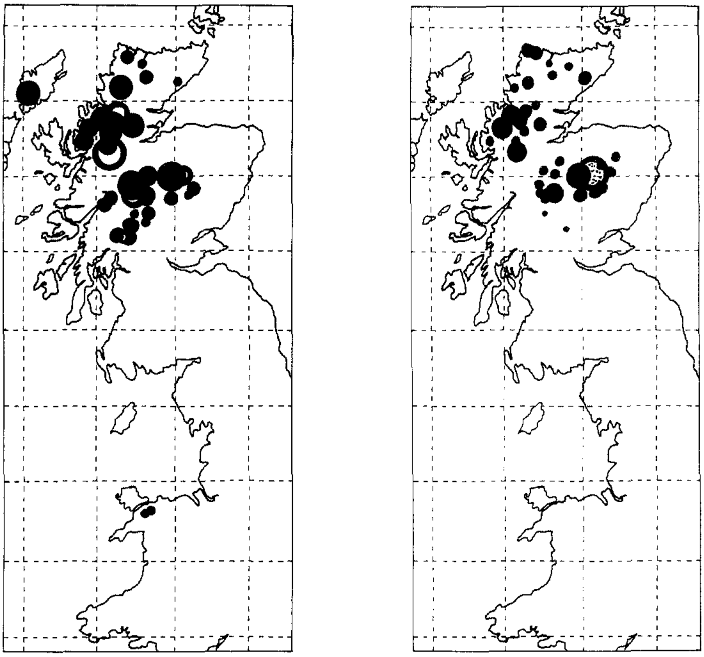
Discussion

Value of vegetation diversity indices in assessing the biodiversity of montane Britain

The Shannon *H* diversity index has enabled us to rank montane sites and to interpret differences according to the functional types of communities found. What has emerged is

a) Racomitrium heaths

c) Montane Calluna heaths



b) Agrostis spp - Festuca ovina grasslands

d) Sub-montane Calluna moorland

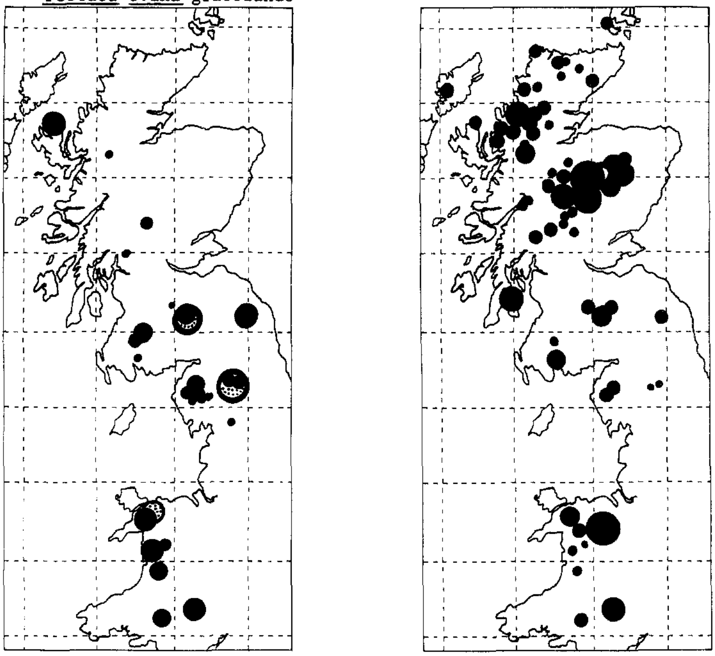


Figure 6. Distribution of 4 montane communities across the study sites. (a) Montane *Racomitrium lanuginosum* heath (E1A); (b) montane *Agrostis-Festuca* grassland (C1B); (c) montane prostrate *Calluna* heath (B2A-D); (d) sub-montane *Calluna* moorland. Size of shaded circle is proportional to the contribution of each site's community towards the total British extent.

the clearly dominant contribution of chionophobous communities to total diversity, giving a picture of montane Britain having extensive cold, exposed summit heaths which tend to be cleared of snow by prevailing strong winds. This emphasizes the climatic influence of extreme oceanicity with its high winds and steep temperature lapse rate, rather than particularly cold winters (mean January temperatures at sea-level in Britain are above 0° C, contrasting with −5° C or lower just inland from the Norwegian coast at the same latitude). Other groups of vegetation, such as the chionophilous heaths, mires and springs, add to the greater extent and richness of the community composition of the most diverse sites. However, this contribution is limited by their virtual restriction to the Scottish Highlands and the requirements of some communities for a calcareous substrate which is very localized in the British uplands (the mostly calciphile species-rich group has a very limited distribution). The anthropogenic group adds little to total diversity, partly because the few composite communities do not always occur together on a given site, but also because they tend to replace an otherwise more natural community from one of the other groups.

The *H* diversity index offers a useful quantitative index for assessing ecological diversity. However, our functional division of vegetation points to the *H* index being more valuable for site evaluation and comparisons within rather than between regions. Since Ratcliffe's (1977) work appeared, biological diversity (but naturalness, foremost) has been equated with conservation value (Usher, 1986). Yet there are remarkably few conservation-related assessments of vegetational diversity, and the implicit assumption that vegetational and faunistic diversity are correlated is rarely tested. Whilst we know that in upland Britain there is not a significant positive correlation between bird species richness and the diversity of plant communities (on a grid of 50 km square, A. Brown and D.B.A. Thompson, unpublished observations; bird species richness simply increases northwards (Ratcliffe, 1990)) we should not in any case expect one. The distribution and composition of a given bird assemblage may be affected as much by structural complexity and management of habitat as by predation pressure, ensuing competition, weather conditions in spring and proximity to wintering grounds (e.g. Haworth and Thompson, 1990; Ratcliffe, 1990). The same sorts of arguments can be applied to plant-invertebrate species richness and/or diversity correlations where we see the roles of habitat structure (horizontal and vertical) and management being important influences on invertebrate distribution (e.g. Usher, 1992).

On-going work on habitat use and diet in dotterel (*Charadrius morinellus*) (Galbraith *et al.*, in press a; Whitfield *et al.*, 1991; D.B.A. Thompson, S. Holt and D.P. Whitfield, unpublished observations) suggests that montane areas with high habitat diversity support highest numbers of these birds for three reasons: (i) adults and chicks take different arrays of prey associated with different communities; (ii) where these communities are juxtaposed broods they should be close knit and less likely to be predated; and (iii) areas with high vegetation *H*, and therefore greater evenness in preferred communities, are most economically exploited by broods. However, there are major differences between montane sites in the availability and use of communities by dotterel which complicate these findings. Table 3 indicates one element of this by contrasting the relative abundance of invertebrate prey and foraging dotterel habitat preferences across six montane communities on two sites. The tipulids and beetles *Otiorrhynchus* spp., followed by *Byrrhus* spp., are the favoured prey of adults. Chicks feed mainly on *Symphyta* adults. *Juncus trifidus* and *R. lanuginosum* heaths are preferred on one site,

Table 3. The rank order of invertebrate abundance across six plant communities in two montane study sites. The underlined values refer to communities preferred by foraging dotterel in each site. 1 is highest, 5 is lowest, 0 is virtually absent, P is present, – means that the community is absent from site.

	Invertebrates			
Plant community[d]	*Byrrhus* spp.[a]	*Otiorrhynchus*[a] spp.	Symphyta[b]	*Tipula montana*[c]
Racomitrium lanuginosum heaths (E1A)	2/2	3/1	0/0	2/1
Montane bog (G5)	–/5	–/5	–/1	–/5
Juncus trifidus heaths (C7)	1/–	1/–	0/–	1/–
Empetrum nigrum-Vaccinium myrtillus heaths (B3)	3/3	3/3.5	P/0	3/2
Prostrate *Calluna vulgaris* heaths (B2)	5/4	5/3.5	P/P	4/3
Nardus stricta snow-beds (C2B)	5/1	3/2	P/P	5/4

[a] sampled by pitfall traps
[b] according to D. Horsfield (unpublished)
[c] sampled by transect counts
[d] codes in brackets refer to community codes given in Appendix.

whereas *R. lanuginosum* heaths are strongly preferred on the second site (also Galbraith *et al.*, 1992b).

Work on dotterel suggests that, when breeding distribution and habitat use are measured at the right scale, clear-cut correlations should emerge between both of these and vegetation diversity. We expect similar correlations for other birds breeding in montane environments (notably ptarmigan, snow bunting *Plectrophenax nivalis*, golden plover *Pluvialis apricaria*, dunlin *Calidris alpina* and possibly even wheatear *Oenanthe oenanthe*). These relationships could then be used to estimate populations in unsurveyed or remote areas, for which aerial photographic/satellite-determined vegetation maps are available, to predict population changes in response to habitat loss or modification.

Some objectives for conservation in montane Britain

There are at least three adverse consequences of the deterioration in montane vegetation described above: (i) extensive mosaics of near-natural vegetation are deteriorating into more uniform stretches of less diverse habitats; (ii) the potential value of these near-natural communities for wide-scale monitoring of the ecological consequences of climate change and acidic deposition becomes more limited; and (iii) birds and invertebrates dependent on the near-natural montane communities will be at risk of decline and range fragmentation.

Taking the last point, there is good evidence for the local extinction of ptarmigan. The dotterel, protected under the European Community Directive on the Conservation of Wild Birds, 79/409/EEC (Stroud *et al.*, 1990), has virtually disappeared from south of the Highlands, possibly because its main breeding habitat, montane *R. lanuginosum* heaths, has deteriorated and fragmented under sheep-grazing pressure (Thompson *et al.*, 1987; Thompson and Baddeley, 1991; Thompson and Whitfield, 1992). The GB government is currently being urged to designate at least three montane Special Protection Areas under the EC Birds Directive, and further areas will be proposed in order to protect at least 80% of the EC dotterel population (Galbraith *et al.*, 1992a).

On the basis of information presented here we propose two regionally founded target objectives to improve the conservation of montane Britain:

(i) Enhance moss cover in montane *R. lanuginosum* heaths where these are fragmenting, and restore them where these have been lost. This would require a reduction (not elimination) in numbers of grazing sheep. To be a top priority in northern Wales, north-western England (and north Pennines), southern Scotland, northern Ireland, and on base-rich tops in the Scottish Highlands.
(ii) As above, enhance/restore prostrate dwarf-shrub heaths by reducing grazing pressures: top priority in north-western England and southern Scotland.

In addition, three further demonstration projects would be appropriate to further the conservation of the montane environments in Britain. These should be experimental in order to determine the level of reduction in sheep grazing pressures required to facilitate recovery. First, sub-alpine scrub and upper treelines should be restored by reducing grazing pressures: a top priority in Scottish Highlands, north-western England and northern England (Cheviot, north Pennines and Craven). Second, dwarf-shrubs and bryophytes in sub-alpine dwarf-shrub heaths and grasslands should be enhanced: a top priority for north-western England and northern Wales; less of a priority for southern Scotland, south-western Highlands and north-western Highlands. Third, the range of breeding ptarmigan should be extended by a re-introduction programme to southern Scotland following the restoration of dwarf-shrub heaths, and the breeding range of dotterel should be improved following restoration and enhancement of *R. lanuginosum* heaths in southern Scotland, northern England and northern Wales. It is unfortunate that there is not extensive experimental field evidence on which to base stronger proposals. Nevertheless, there are copious anecdotal examples of habitat and faunal losses, and the recovery of both following a release from severe grazing pressures should be assured so long as there are sufficient sources of input.

The Commission of European Communities (1990) *Habitats Directive* proposes the conservation of examples of snowbed and summit heaths. This ought to be clarified to cater for the plant communities contributing most to montane diversity and of greatest international importance. Along the Atlantic seaboard of Europe (notably in Ireland, western Norway, Faeroes, Iceland and GB) international cooperation is needed to identify montane oceanic areas (i) at risk of damage/loss, (ii) with indicator groups for trans-country monitoring, and (iii) with particularly good examples of natural tree-lines, dwarf-shrub heaths and oceanic moss- and liverwort-dominated heaths.

Outside Europe, the more oceanic mountain areas should be examined in relation to vegetation diversity and ecological change. Candidate regions include: Newfoundland and Nova Scotia, and the near-coast Pacific mountains in Alaska and Canada; the southern mountains of Chile and Tierra del Fuego; the Southern Ocean islands of Tasmania, Southland in South Island, New Zealand and Stewart Island just south of there; and the Kamchatka, Hokkaido and N. Japan mountains in east Asia. All of these areas have high year-round rainfall, high relative humidity and a cool climate with minor seasonal fluctuations (Barry, 1981; Academy of Sciences of the USSR, 1964; Lindsay *et al.*, 1988).

The most recent concerns about global warming (e.g. World Meteorological Organisation, 1990) are highly relevant to future work in montane areas. The montane zone experiences considerable extremes in temperature, precipitation and windiness. It should be sensitive to global climate change, not least from temperature changes in the Atlantic Ocean and from changes in acidic (occult) deposition. Some of the more pessimistic scenarios point to the virtual elimination of alpine areas in central and southern Europe (P. Ozend and L. Borel communication cited in Nilsson and Pitt, 1990). It is too early to provide other than informed speculation on how the montane zone in GB should respond to global warming. A co-ordinated long-term monitoring programme in Norway, Ireland and GB would be a valuable step to improve the quality of available information and to enable the detection of gross environmental changes in montane/arctic-alpine areas.

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Appendix

This comprises summary descriptions of montane vegetation communities according to Birks and Ratcliffe (1981) and Rodwell's (1991, 1992) GB National Vegetation Classification, NVC. There is a brief description below each transposition. For a few communities we give McVean and Ratcliffe's (1962) term where Birks and Ratcliffe's (1981) give no description.

Birks and Ratcliffe (1981)		Rodwell (1991, 1992): GB National Vegetation Classification		Functional Group
A2	alpine willow scrub	W20	*Salix lapponum-Luzula sylvatica* scrub	Chionophilous Species rich
Low growing *Salix lapponum* scrub, often with other montane willows, *Vaccinium myrtillus*, *Luzula sylvatica*, *Deschampsia* sp. and a rich assembly of forbs in a carpet of hypnoid mosses.				
B2A	species-poor prostrate *Calluna* heath	H13	*Calluna vulgaris–Cladonia arbuscula* heath *Cladonia arbuscula-C. rangiferina* sub–community	Chionophobous
A mat of prostrate *Calluna vulgaris* with few other vascular plants apart from *Empetrum nigrum*, and with a sparse cover of *Cladonia* lichens.				
B2B	*Racomitrium*-rich prostrate *Calluna* heath	H14	*Calluna vulgaris–Racomitrium lanuginosum* heath	Chionophobous
A mat of prostrate *Calluna vulgaris* growing in a carpet of *Racomitrium lanuginosum*, with abundant *Empetrum nigrum* and occasional *Erica cinerea*, *Arctostaphylosus uva-ursi* and *Carex bigelowii*.				
B2C	Lichen-rich prostrate *Calluna* heath	H13	*Calluna vulgaris–Cladonia arbuscula* heath	Chionophobous
A mat of prostrate dwarf *Calluna vulgaris* and *Empetrum nigrum*, with co-dominant *Cladonia* spp. and other lichens such as *Ochrolechia frigida*.				
B2D	mixed prostrate dwarf-shrub heath	H15 H17	*Calluna vulgaris–Juniperus communis nana* heath *Calluna vulgaris–Arctostaphylos alpinus* heath	Chionophobous
A mat of prostrate *Calluna vulgaris* and *Arctostaphylos alpinus*, typically with a low constancy of *Loiselurea procumbens* and *Empetrum nigrum*, *Racomitrium lanuginosum* and *Cladonia* lichens.				
B3B	snowbed *Vaccinium myrtillus* heath	H22a	*Vaccinium myrtillus–Rubus chamaemorus* heath, *Polytrichum commune-Galium saxatile* sub-community	Chionophilous
Dwarf shrub heath dominated by *Vaccinium myrtillus* with a lesser cover of *Calluna vulgaris*, *Empetrum nigrum* and *Vaccinium vitis-idaea*. Associated with moderately late snowbeds in heather moors.				
B3C	species-rich *Vaccinium* heath	H18b	*Vaccinium myrtillus–Deschampsia flexuosa* heath, *Alchemilla alpina–Carex pilulifera* sub-community	Anthropogenic

<table>
<tr><td colspan="5">Montane dwarf shrub heath dominated by <i>Vaccinium myrtillus</i> with an abundance of hypnoid mosses, grasses and small herbs, particularly <i>Alchemilla alpina</i>.</td></tr>
<tr><td>B3E</td><td><i>Vaccinium-Empetrum</i> heath</td><td>H18
H20</td><td><i>Vaccinium myrtillus–Deschampsia flexuosa</i> heath
<i>Vaccinium myrtillus–Racomitrium lanuginosum</i> heath</td><td>Weakly Chionophobous</td></tr>
<tr><td colspan="5">Montane dwarf shrub heath dominated by <i>Vaccinium myrtillus</i> and <i>Empetrum nigrum</i> with abundant hypnoid mosses, and with <i>Vaccinium vitis-idaea</i> and <i>V.uliginosum</i> locally dominant.</td></tr>
<tr><td>B3F</td><td>lichen-rich <i>Vaccinium</i> heath</td><td>H19</td><td><i>Vaccinium myrtillus–Cladonia arbuscula</i> heath</td><td>Chionophobous</td></tr>
<tr><td colspan="5">Montane dwarf shrub heath dominated by a low mat of <i>Vaccinium myrtillus</i> and <i>Empetrum nigrum</i>, with an abundance of lichens.</td></tr>
<tr><td>B4B</td><td>high altitude <i>Dryas</i> heath</td><td>CG14</td><td><i>Dryas octopetala–Silene acaulis</i> ledge community</td><td>Chionophilous and Species rich</td></tr>
<tr><td colspan="5">A montane calcicolous heath with abundant <i>Dryas octopetala</i> among many herb species including <i>Silene acaulis</i>, <i>Alchemilla</i> spp., <i>Saxifraga</i> spp.</td></tr>
<tr><td>C1B</td><td><i>Agrostis–Festuca</i> acid grassland</td><td>U4</td><td><i>Festuca ovina–Agrostis capillaris–Galium saxatile</i> grassland</td><td>Chionophobous and Anthropogenic</td></tr>
<tr><td colspan="5">Anthropogenic close-cropped sward with <i>Festuca ovina</i> as the overwhelming dominant. Probably derived from E1A/E1C.</td></tr>
<tr><td>C2B</td><td><i>Nardus stricta</i> snowbed</td><td>U7</td><td><i>Nardus stricta–Carex bigelowii</i> grass heath</td><td>Chionophilous</td></tr>
<tr><td colspan="5">Montane grassland associated with late snow-lie. Generally dominated by tussocky <i>Nardus stricta</i>, with varying amounts of <i>Carex bigelowii</i> and <i>Racomitrium lanuginosum</i>.</td></tr>
<tr><td>C5A</td><td>species-poor <i>Deschampsia cespitosa</i> grassland</td><td>U13a</td><td><i>Deschampsia cespitosa–Galium saxatile</i> grassland <i>Anthoxanthum odoratum–Alchemilla alpina</i> sub-community</td><td>Chionophilous</td></tr>
<tr><td colspan="5">Wet montane stands of tufted <i>Deschampsia cespitosa</i> with a moderate cover of acidophilous grasses, herbs and bryophytes. Often irrigated by melt-water from late snowbeds.</td></tr>
<tr><td>C5B</td><td>species-rich <i>Deschampsia cespitosa</i> grassland</td><td>U17c</td><td><i>Luzula sylvatica–Geum rivale</i> tall herb community, <i>Agrostis capillaris–Rhytidiadelphus loreus</i> sub-community</td><td>Chionophilous and Anthropogenic</td></tr>
<tr><td colspan="5">Wet montane stands of grasses, notably <i>Deschampsia cespitosa</i>, with a rich assembly of herbs such as <i>Geum rivale</i>, <i>Angelica sylvestris</i>, <i>Rumex acetosa</i>, <i>Ranunculus acris</i> and <i>Alchemilla alpina</i>.</td></tr>
<tr><td>C6</td><td><i>Carex bigelowii</i> heaths</td><td>U8</td><td><i>Carex bigelowii–Polytrichum alpinum</i> heath</td><td>Chionophilous</td></tr>
<tr><td colspan="5">Short swards of <i>Carex bigelowii</i> with <i>Polytrichum alpinum</i> and/or <i>Dicranum fuscescens</i> together with <i>Cetraria islandica</i> and <i>Cladonia</i> spp.</td></tr>
</table>

Birks and Ratcliffe (1981)		Rodwell (1991, 1992): GB National Vegetation Classification)		Functional Group
C7	*Juncus trifidus* heaths	U9	*Juncus trifidus–Racomitrium lanuginosum* rush heath	Chionophobous
A high montane community with an open growth of tussocky *Juncus trifidus* with variable amounts of *Racomitrium lanuginosum* and *Cladonia* spp.				
D1	Tall herb (*Sedum rosea-Alchemilla glabra*) communities	U17	*Luzula sylvatica–Geum rivale* tall herb community	Chionophilous and Species rich
Species-rich tall herb stands of ungrazed ledges. Typically with *Luzula sylvatica*, *Geum rivale*, *Deschampsia cespitosa* and *Sedum rosea*, but with many other species locally dominant.				
D2B	*Cryptogramma–Athyrium* snowbed	U18	*Cryptogramma crispa–Athyrium alpestre* snowbed	Chionophilous
High-altitude fern snowbeds on rocky ground, dominated by *Athyrium distentifolium* (*alpestre*) and *Cryptogramma crispa*, with a variety of associated snow-tolerant herbs, bryophytes and lichens.				
D3	Dwarf herb nodum	CG12	*Festuca ovina–Alchemilla alpina–Silene acaulis* dwarf herb community	Chionophilous and Species rich
A montane dwarf herb community forming a dense low sward with a rich mixture of grasses and forbs, with *Silene acaulis* the most frequent dominant.				
D3x	*Alchemilla alpina-Sibbaldia procumbens* snowbed	U14	*Alchemilla alpina–Sibbaldia procumbens* dwarf herb community	Chionophilous and Species rich
Late-lie snow-beds of *Alchemilla alpina-Sibbaldia procumbens* among the mosses *Polytrichum alpinum*, *Racomitrium fasciculare* and *R. canescens* with tufts of *Nardus stricta*, *Agrostis* spp. and *Festuca* sp.				
D5	*Saxifraga aizoides* banks	U15	*Saxifraga aizoides–Alchemilla glabra* banks	Species rich
Hanging banks of *Saxifraga aizoides* on wet, base-rich rocks, typically with *S. oppositifolia*, *Alchemilla alpina*, *A. glabra*, *Deschampsia cespitosa* and a rich variety of herbs and bryophytes.				
D6	*Luzula sylvatica–Dryopteris* treeless communities	U16 U19	*Luzula sylvatica–Vaccinium myrtillus* community *Thelypteris limbosperma–Blechnum spicant* community	Chionophilous and Species rich
Tall-herb vegetation on acid rock ledges dominated by *Luzula sylvatica* and/or *Thelypteris* (*Oreopteris*) *Limbosperma* and *Dryopteris* spp., with small herbs and *Vaccinium myrtillus*.				
D6A	*Betuletum Oxaleto–Vaccinetum*, treeless facies (McVean & Ratcliffe, 1962)	U16	*Luzula sylvatica–Vaccinium myrtillus* community	Chionophilous and Species rich

Tall *Luzula sylvatica* stands, sometimes with co-dominant *Vaccinium myrtillus*, with a constant but low cover of *Deschampsia flexuosa* and *Galium saxatile*, *Oxal is are tosella* and *Blechnum spicant*.				
D6B	*Betula*-herb nodum, treeless facies (McVean & Ratcliffe, 1962)	U19	*Thelypteris limbosperma–Blechnum spicant* community	Chionophilous and Species rich
Tail fern beds of dense *Oreopteris limbosperma*, with a constant but low cover of *Blechnum spicant*, *Potentilla erecta*, *Galium saxatile* and *Oxalis acetosella*, low-growing grasses and bryophytes.				
E1A	species-poor *Racomitrium lanuginosum* heath	U10b	*Carex bigelowii–Racomitrium lanuginosum* moss heath, typical sub-community	Chionophobous
A montane summit heath with scattered low-growing vascular plants, especially *Carex bigelowii* and *Vaccinium myrtillus*, rooted in a near-continuous carpet of *Racomitrium lanuginosum*.				
E1B	species-rich *Racomitrium lanuginosum* heath	U10c	*Carex bigelowii–Racomitrium lanuginosum* moss heath, *Silene acaulis* sub-community	Chionophobous and Species rich
A *Racomitrium lanuginosum* carpet with a variable cover of cushion herbs, including base-demanding species such as *Silene acaulis*, *Armeria maritima* and *Polygonum viviparum*.				
E1C	*Festuca ovina-Deschampsia flexuosapRacomitrium lanuginosum* heath	U10a	*Carex bigelowii–Racomitrium lanuginosum* moss heath, *Galium saxatile* sub-community	Chionophobous and Anthropogenic
A grassy summit heath where *Festuca ovina/vivipara*, *Deschampsia flexuosa*, *Carex bigelowii* and *Vaccinium myrtillus* share dominance with *Racomitrium lanuginosum*.				
E1D	*Empetrum nigrum hermophoditum–Racomitrium lanuginosum* heath	H20	*Vaccinium myrtillus–Racomitrium lanuginosum* heath	Chionophobous
Montane moss/dwarf heath dominated by *Racomitrium lanuginosum* with *Empetrum nigrum hermaphroditum* and/or *Vaccinium myrtillus* and hypnaceous mosses, grasses and sedges.				
E1E	*Juncus trifidus-Racomitrium lanuginosum* heath	U10c	*Carex bigelowii–Racomitrium lanuginosum* moss heath, *Silene acaulis* sub-community	Chionophobous
An open, wind-ablated montane community with a variable cover of *Racomitrium lanuginosum* with *Juncus trifidus*, *Deschampsia flexuosa*, *Festuca ovina/vivipara* and small herbs, e.g. *Silene acaulis*.				
E2	*Rhytidiadelphus loreus–Deschampsia cespitosa* heath	U13b	*Deschampsia cespitosa–Galium saxatile* grassland, *Rhytidiadelphus loreus* sub–community	Chionophilous
Late snowbed moss heath dominated by *Rhytidiadelphus loreus*, *Hylocomnium splendens* and *Polytrichum alpinum*, with frequent *Deschampsia cespitosa*, *Ptilidium ciliar* and *Carex bigelowii*.				

Birks and Ratcliffe (1981)		Rodwell (1991, 1992): GB National Vegetation Classification		Functional Group
E3	*Dicranum starkei* snow-bed heaths	U11 U12	*Polytrichum norvegicum–Kiaeria starkei* snow-bed *Salix herbacea–Racomitrium heterostichum* snow-bed	Chionophilous
	Late snowbeds dominated by a variety of bryophytes, most often *Kiaeria starkei*, *Polytrichum sexangulare* (*norvegicum*) and *Racomitrium heterostichum*, and *Salix herbacea*.			
G5	*Empetrum Nigrum-Eriophorum vaginatum* mire	M19C	*Calluna vulgaris–Eriophorum vaginatum* blanket mire *Vaccinium vitis–idaea–Hylocomium splendens* sub–community	Mire
	High altitude ombrogenous blanket mire with *Empetrum nigrum* ssp. *hermaphroditum*, *Vaccinium vitis–idaea* and *V. uliginosum* replacing *Calluna vulgaris* as the dominant sub-shrubs.			
H3H	Montane *Carex echinata–Sphagnum recurvum* mire	M7	*Carex curta–Sphagnum russowii* mire	Mire
	Montane, oligotrophic soligenous mire of sedges, including *Carex curta*, *C. echinata*, *C. bigelowii*, *C. echinata* and *C. rariflora*, above a Sphagnum carpet which typically has *S. russowii*.			
H31	Montane *Carex nigra*-brown moss mire	M10	*Carex dioica–Pinguicula vulgaris* mire	Mire
	Mesotrophic, species-rich calcareous flush with a short mixed sward of sedges, herbs and bryophytes including montane species such as *Polygonum viviparum*, *Thalictrum alpinum* and *Tofieldia pusilla*.			
H3J	Montane *Carex saxatilis* mire	M12	*Carex saxatilis* mire	Chionophilous, Species rich and mire
	High altitude soligenous flush dominated by a short sward of *Carex saxatilis* with a rich complement of other sedges and herbs e.g. *Carex nigra*, *C. demissa*, *Thalictrum alpinum* and *Aneura pinguis*.			
I1C	Montane *Carex-Saxifraga aizoides* flush	M11A	*Carex derissa – Saxifraga aizoides* mire *Thalictrum alpinum – Juncus tinglumis* sub-community	Mire and species rich
	Montane calcareous flushes of stony ground with constant *Carex demissa* and *Saxifraga aizoides*, small herbs and sedges which include *Thalictrum alpinum* and *Juncus triglumis*.			
I4B	*Anthelica julacea* springs	M31	*Anthelia julacea-Sphagnum auriculatum* spring	Chionophilous and mire
	Montane springs always dominated by hard mats of *Anthelia julacea*, with few other species apart from scattered plants of *Marsupella emarginata*, *Sphagnum auriculatum* and *Deschampsia cespitosa*.			
I4C	*Pohlia wahlenbergii* var. *glacialis* springs	M33	*Pohlia wahlenbergii* var. *glacialis* springs	Chionophilous and mire
	A high-montane bryophyte spring fed by melting snow dominated by *Pohlia wahlenbergii* var. *glacialis* and *Pohlia ludwigii*.			