M19
Calluna vulgaris-Eriophorum vaginatum blanket mire

Synonymy

Eriophoretum vaginati Smith & Moss 1903, Lewis 1904, Lewis & Moss 1911, Moss 1913, Adamson 1918, Watson 1932, Tansley 1939, all *p.p.*; Mixed moor Pearsall 1938; *Sphagnum* community, Type B 'Moss' Pearsall 1941; *Calluna* & *Calluna-Eriophorum* Moss Pearsall 1941; *Betula nana* bogs Poore & McVean 1957; Blanket bogs Ratcliffe 1959; *Calluneto-Eriophoretum* McVean & Ratcliffe 1962, Eddy *et al.* 1969, Birks 1973, Meek 1976, Evans *et al.* 1977; *Empetreto-Eriophoretum* McVean & Ratcliffe 1962; *Vaccinio-Ericetum tetralicis* Moore 1962, Birse & Robertson 1976, Dierssen 1982; *Trichophoreto-Eriophoretum* Eddy *et al.* 1969 *p.p.*; *Eriophorum vaginatum* bog Edgell 1969 *p.p.*; *Erica tetralix-Vaccinium oxycoccos* & *Juncus squarrosus-Deschampsia flexuosa* Series Tallis 1969 *p.p.*; *Rhytidiadelphus loreus-Sphagnum fuscum* Community Birse & Robertson 1976; *Vaccinio-Eriophoretum* Hill & Evans 1978 *p.p.*; Mire noda 10 & 11 Daniels 1978; *Rhytidiadelpho-Sphagnetum fusci* Birse 1980; *Erico-Sphagnetum papillosi* Moore (1964) 1968 *emend.* Birse 1980 *p.p.*; *Calluna-Pleurozium* & *Calluna-Cladonia* noda Bignal & Curtis 1981.

Constant species

Calluna vulgaris, *Eriophorum angustifolium*, *E. vaginatum*, *Rubus chamaemorus*, *Pleurozium schreberi*, *Sphagnum capillifolium*.

Rare species

Arctostaphylos alpinus, *Betula nana*, *Vaccinium microcarpum*, *Kiaeria starkei*.

Physiognomy

The *Calluna vulgaris-Eriophorum vaginatum* mire comprises blanket bog vegetation that is generally dominated by mixtures of *Eriophorum vaginatum* and ericoid sub-shrubs. Sphagna can be prominent over wetter ground but typically this element is not so rich or luxuriant as in the *Scirpus-Eriophorum* or *Erica-Sphagnum* mires. And the true hummock/hollow relief that can commonly be found in those communities is only rarely developed here, though the surface of the ground is often uneven because of the marked tussockiness of *E. vaginatum*, a structural feature of some importance for the strong contingent of hypnoid mosses, which constitute a further distinctive component over drier surfaces.

E. vaginatum is consistently more important here than in the *Scirpus-Eriophorum* and *Erica-Sphagnum* mires: among our Sphagnetalia communities, it shows a peak of abundance in this kind of vegetation and in the *Eriophorum* mire, which seems often to have been derived from it by impoverishment of the associated flora and with which it was often grouped in early schemes under the heading of *Eriophoretum vaginati* (e.g. Smith & Moss 1903, Lewis 1904*a*, *b*, Lewis & Moss 1911, Moss 1913, Adamson 1918, Watson 1932, Tansley 1939). *E. vaginatum* is usually at least a co-dominant here, contributing a dull-green colour to the vegetation through much of the year and giving it a particularly striking aspect in June with its cottony fruits. The tussocks, which grow by intravaginal tillering, acquire a robust hemispherical shape and can come to stand proud of the bog surface by 2–3 dm, crowned by the densely-packed living shoots and the remains of the foliage, which dies back annually by February but persists intact for many years (Goodman & Perkins 1968, Polozova 1970, Wein 1973, Chapin *et al.* 1979). The tussocks thus provide a relatively dry microhabitat, though one which is heavily shaded until senescence sets in, which, under normal circumstances, may not be for many decades (Polozova 1970).

The proportion of *E. vaginatum* to the ericoid sub-shrubs is very variable and, though it shows some consistency in the different sub-communities, it is very much affected by certain kinds of treatment, particularly by burning and grazing which can help convert the vegetation into the *Eriophorum* mire, where the cotton-grass is overwhelmingly dominant and the sub-shrubs of much more patchy occurrence. Variation between the

two communities is continuous and replacement of the richer by the more impoverished can be temporary, so transitions are common. In general, however, the two can be separated by the very frequent occurrence here of *Calluna*, *Vaccinium myrtillus* and *Empetrum nigrum* ssp. *nigrum* and, at higher altitudes, of the Arctic-Alpine *V. vitis-idaea*, *V. uliginosum* and *E. nigrum* ssp. *hermaphroditum*. Overall, *Calluna* is the most common co-dominant of *E. vaginatum*, but diverse mixtures of these species occur very frequently and typically the sub-shrubs are so abundant and so vigorous, especially over the drier ground, as to give the vegetation the appearance of a heathy moorland, an aspect recognised in Pearsall's (1938, 1968) epithet of 'mixed moor' and in the names *Calluneto-Eriophoretum* and *Empetreto-Eriophoretum* coined by McVean & Ratcliffe (1962). Two other woody Arctic-Alpines, *Arctostaphylos alpinus* and *Betula nana*, both national rarities, can also be found here, preferentially among our Sphagnetalia mires, though they are very local and generally both rather inconspicuous, *Arctostaphylos* being a prostrate plant and *Betula* usually growing low and gnarled.

The distinctly montane character of this element in the vegetation provides a sharp contrast with both the *Scirpus-Eriophorum* and *Erica-Sphagnum* mires, something reinforced by the absence here of *Myrica gale*, essentially a lowland plant. One further difference, which perhaps reflects the generally drier nature of the peats in this community, is the rather restricted occurrence of *Erica tetralix*: this is commoner in stands to the west and at usually lower altitudes, as in parts of Wales (Ratcliffe 1959*a*, Tallis 1969, Edgell 1969), south-west Scotland (Birse & Robertson 1976, Birse 1980) and through Strathclyde (Bignal & Curtis 1981), where its frequency helps define the *Erica* sub-community, but it is distinctly local through much *Calluna-Eriophorum* mire.

Further contrasts with these other kinds of ombrogenous mire can be seen among the vascular associates. Compared with the strongly oceanic blanket bog vegetation of the *Scirpus-Eriophorum* mire, *Scirpus cespitosus* often plays a subordinate role here, *Molinia caerulea* is strikingly scarce and herbs such as *Potentilla erecta*, *Polygala serpyllifolia* and *Pedicularis sylvatica* are very infrequent. The first two tend to follow *E. tetralix* in their pattern of occurrence, thus helping to give the *Erica* sub-community a transitional floristic character. It is there, too, that *Narthecium ossifragum* and *Drosera rotundifolia*, which can be so prominent in the wetter lawns of both the *Scirpus-Eriophorum* and *Erica-Sphagnum* mires, have most of their relatively sparse occurrences in this community. *Andromeda polifolia* and *Vaccinium oxycoccos*, both good preferentials for the *Erica-Sphagnum* mire, are very uncommon here, although high-altitude *Calluna-Eriophorum* mire provides the British locus for the rare small cranberry *V. microcarpum*.

On the positive side, the commonest vascular associates in the community are *Eriophorum angustifolium*, a very frequent plant throughout British Oxycocco-Sphagnetea vegetation, and, much more distinctive here, *Rubus chamaemorus*. This Arctic-Subarctic herb is strongly preferential to the *Calluna-Eriophorum* mire, though it is not universally present: it is decidedly scarce in the lower-altitude *Erica* sub-community and sometimes of patchy occurrence elsewhere, being affected by particular treatments. Early or late sampling may also under-estimate its abundance, because it is not evergreen: it passes the winter as dormant buds brought close to the peat surface by rhizome extension, does not put up its shoots until May and shows early senescence of its aerial parts, with their quick death in the first frosts of the autumn. When in bloom, in late May and early June, the large white flowers provide a delightful relief to what is for the most part a rather dreary scene, but flowering is somewhat sporadic and local and, since the flowering period coincides with lactation in deer and hill-sheep, the flowers often get eaten off providing a nutritious bite (Taylor 1971).

Few other features of the vascular flora are distinctive, though *Deschampsia flexuosa* and *Juncus squarrosus* occur occasionally throughout and each can be locally abundant and, at higher altitudes, *Carex bigelowii* becomes frequent. *Nardus stricta*, *Carex nigra*, *Melampyrum pratense* and *Galium saxatile* can be found at low frequencies and the community also provides an occasional locus for the Arctic-Subarctic *Cornus suecica* and the Northern Montane *Listera cordata*. By and large, however, herbs here are few in number and occur as scattered individuals.

The bryophyte flora, by contrast, is rich and often extensive, frequently covering more than 50% of the ground, a further difference between this community and the *Eriophorum* mire. As noted above, though, varied and luxuriant carpets of Sphagna are not the rule in this community. *Sphagnum capillifolium* is sufficiently frequent throughout to qualify as a constant and it can be locally abundant, but even this species is somewhat patchy and others, like *S. papillosum*, *S. subnitens* and *S. tenellum*, prominent in the wet lawns of other ombrogenous mires, and the semi-aquatics *S. cuspidatum* and *S. auriculatum*, which can figure elsewhere in transitions to bog pools, are generally uncommon and rather uneven in their occurrence. Some of these species are better represented in the transitional vegetation of the *Erica* sub-community, where there can be a semblance of hummock/hollow relief; and some higher-altitude *Calluna-Eriophorum* mires also show locally extensive *Sphagnum* carpets, in which the montane *S. fuscum* has its best representation among British Sphagnetalia communities. In some places, too, generally in the *Erica* sub-

community, though also in the *Empetrum* sub-community, *S. recurvum* can be prominent, perhaps in response to some soligenous enrichment.

Typically, however, it is hypnaceous mosses which provide the consistency to the bryophyte element in the *Calluna-Eriophorum* mire. Among these, *Pleurozium schreberi*, *Rhytidiadelphus loreus*, *Hypnum cupressiforme/jutlandicum* and *Plagiothecium undulatum* are all very frequent throughout, with *Hylocomium splendens* becoming common at higher altitudes, and mixtures of these can form extensive mats over drier areas of the ground, particularly over the tops of old *E. vaginatum* hummocks and among the stools of sub-shrubs where the bushes have opened up somewhat. Other mosses recorded frequently are *Dicranum scoparium*, *Polytrichum commune* and *Aulacomnium palustre*, with *Racomitrium lanuginosum*, *Polytrichum alpestre* and *Pohlia nutans* attaining occasional levels in some of the sub-communities and *Campylopus paradoxus* and *Rhytidiadelphus squarrosus* being found sparsely throughout. High-altitude stands sometimes have the rare montane moss *Kiaeria starkei*.

Leafy hepatics are typically not so conspicuous as they are in more oceanic ombrogenous mires and some of the most characteristic species there are either absent from this community (*Pleurozia purpurea*) or much less common (*Mylia anomala*, *Odontoschisma sphagni*). But others occur fairly frequently, such as *Lophozia ventricosa*, *Barbilophozia floerkii*, *Diplophyllum albicans*, *Calypogeia fissa*, *C. muellerana*, *C. trichomanis*, *Cephalozia bicuspidata*, *Mylia taylori* and, particularly at higher altitudes, *Ptilidium ciliare*, and some of these can attain a measure of local abundance.

Finally, among the general features of the community, there is the frequent occurrence of lichens, especially in the higher-altitude *Vaccinium-Hylocomium* sub-community. Larger *Cladonia* spp., such as *C. impexa*, *C. uncialis* and *C. arbuscula*, can be particularly abundant crowning the tops of old *Eriophorum* hummocks and among senescent *Calluna*, but peat-encrusting species, such as *C. squamosa*, *C. bellidiflora*, *C. floerkeana* and *C. gracilis*, also occur and there can be records for *Cetraria islandica*, *Hypogymnia physodes* and *Cornicularia aculeata*.

Sub-communities

***Erica tetralix* sub-community:** Blanket bogs Ratcliffe 1959 *p.p.*; *Vaccinio-Ericetum tetralicis* Moore 1962 *p.p.*, Birse & Robertson 1976 *p.p.*; *Eriophorum vaginatum* bog, low-level facies Edgell 1969 *p.p.*; *Erica tetralix-Vaccinium oxycoccos* series, *Plagiothecium-Hylocomium* & *Racomitrium-Cladina* noda Tallis 1969; *Trichophoreto-Eriophoretum* Eddy *et al.* 1969 *p.p.*; *Calluneto-Eriophoretum* Meek 1976; *Calluneto-Eriophoretum typicum* Evans *et al.* 1977; *Erico-Sphagnetum papillosi*, *Rhytidiadelphus loreus* subassociation Moore (1964) 1968 *emend.* Birse 1980 *p.p.*; *Calluna-Pleurozium* & *Calluna-Cladonia* noda Bignal & Curtis 1981. This kind of *Calluna-Eriophorum* mire shows a number of floristic features transitional to more oceanic ombrogenous bogs. Among the vascular plants, for example, *E. vaginatum* can be co-dominant with the sub-shrubs, though it is generally less abundant and less prominent structurally than it is in the other sub-communities. *Calluna* often predominates among the woody species, frequently with some *E. nigrum* ssp. *nigrum* and a little *V. myrtillus*, but *E. tetralix* is strongly preferential and is sometimes of moderately high cover. Then, there is frequently some *Scirpus* and this, too, can be locally abundant with prominent tussocks. *Molinia* also occurs occasionally and there can be scattered plants of *Narthecium* and, more sparsely, of *Drosera rotundifolia* or *Vaccinium oxycoccos*. The great infrequency of *Rubus chamaemorus*, which is very local here, is a further distinctive feature.

The bryophyte element is less strikingly peculiar but Sphagna tend to be more consistently abundant than in many tracts of *Calluna-Eriophorum* mire, certainly than in much of the *Empetrum* sub-community, with *S. capillifolium* being quite commonly accompanied by *S. papillosum* and sometimes by *S. tenellum*, *S. subnitens* or *S. compactum*. And there can be a slight suggestion of the development of hummocks and hollows with these species disposed over stretches of wetter or drier ground. Other stands can have an abundance of *S. recurvum*, sometimes with *S. palustre*, in fairly extensive lawns.

The difference between this kind of vegetation and drier types of *Scirpus-Eriophorum* and *Erica-Sphagnum* mire, where hypnaceous mosses and herbs such as *Juncus squarrosus* and *Deschampsia flexuosa* (all quite common in this sub-community) show some increase, is thus a fine one, and especially hard to discern if individual samples are examined in isolation. The context of the samples, that is the overall character of the mire from which they are taken, sometimes helps but the similarity of the vegetation types is a real reflection of the convergence of ombrogenous mire floristics in certain environmental conditions (see below).

***Empetrum nigrum* ssp. *nigrum* sub-community:** *Eriophoretum vaginati* Smith & Moss 1903, Lewis 1904, Lewis & Moss 1911, Moss 1913, Adamson 1918, Watson 1932, Tansley 1939, all *p.p.*; Mixed moor Pearsall 1938; *Sphagnum* community, Type B 'Moss' Pearsall 1941; *Calluna* & *Calluna-Eriophorum* Moss Pearsall 1941; Blanket bogs Ratcliffe 1959 *p.p.*; *Eriophorum vaginatum* bog, high-level facies Edgell 1969; *Calluneto-Eriophoretum* Eddy *et al.* 1969 *p.p.*, Birks 1973; *Calluneto-Eriophoretum deschampsietosum* & *myrtillosum* Evans

https://doi.org/10.1017/9780521391658.023 Published online by Cambridge University Press

et al. 1977; *Vaccinio-Eriophoretum* Hill & Evans 1978 *p.p.*; Mire noda 10 & 11 Daniels 1978. This sub-community, long familiar as the richer kind of 'Pennine blanket bog', generally preserves all the typical floristic features of the *Calluna-Eriophorum* mire, though it is very variable in the proportions of the major structural elements and thus in its gross appearance, a feature very well described from Moor House in Cumbria (Welch & Rawes 1966, Eddy *et al.* 1969, Rawes & Hobbs 1979). *E. vaginatum* is usually abundant and structurally prominent and, indeed, on uneroded mires, it can be dominant for some time after episodes of burning, and become more permanently ascendant under intensive grazing. Generally, however, sub-shrubs play a fairly consistent part in the vegetation. *Calluna* is usually the leading species among these and, on virgin mires, this forms the bulk of an open canopy, 2–3 dm tall, the bushes alternating with healthy *Eriophorum* tussocks or growing on moribund ones, and the *Calluna* itself sometimes showing its familiar stages of growth from pioneer through to degenerate where burning or grazing are absent (Watt 1955, Gimingham 1972). There is also often some *V. myrtillus* and/or *E. nigrum* ssp. *nigrum* and both of these, particularly the latter, can increase to very great abundance for some time after burning or where grazing has been withdrawn, or more permanently where drier peat surfaces have been bared by erosion: under these last conditions both *E. vaginatum* and *Calluna* can show much less vigorous growth than usual. At the high altitudes characteristic of this vegetation, such erosion, often aggravated by generations of burning and grazing and, more recently, by drainage schemes, is widespread, the peats often deeply scored by systems of haggs, which introduce a characteristic patterning into the vegetation (e.g. Tansley 1939, Tallis 1964*b*, 1965, 1973*b*, 1985*b*). This sub-community also provides some of the more southerly stations for the Arctic-Alpine sub-shrubs *V. vitis-idaea* and *V. uliginosum*, though these become very much more frequent in the *Vaccinium-Hylocomium* sub-community. In sharp contrast to the *Erica* sub-community, *E. tetralix* is very scarce here, and any increase is often an indication of the local occurrence of a tract of that kind of *Calluna-Eriophorum* mire within the *Empetrum* sub-community (as at Moor House: Eddy *et al.* 1969).

Scirpus and *Molinia* both decline here to their usual low levels of frequency in the community and *Rubus chamaemorus* increases greatly, though it is absent from some far-flung localities for this sub-community, as in North Wales (Ratcliffe 1959*a*, Edgell 1969) and on Skye (Birks 1973) and can be decidedly patchy elsewhere, as on Stainmore (Pearsall 1941) and parts of Moor House (Eddy *et al.* 1969), this local variation sometimes being obviously related to treatment. *Eriophorum angustifolium* occurs very commonly, usually at low covers, and there is occasionally some *Deschampsia flexuosa*, but other herbs are few and there are no preferentials among this element.

Bryophytes, too, show little that is distinctive, though there is a typically rather impoverished *Sphagnum* flora. *S. capillifolium* remains frequent and it can be quite abundant on the wetter ground around the *E. vaginatum* and beneath the sub-shrubs, though burning and erosion can have a drastic effect on its extent. *S. papillosum* is especially scarce and *S. subnitens* occurs only very occasionally though, as in the *Erica* sub-community, some stands show a local abundance of *S. recurvum* (as in a facies distinguished by Eddy *et al.* 1969).

Over somewhat drier ground, the hypnaceous mosses are particularly abundant, forming extensive mats over the decumbent branches and litter among older *Calluna* bushes and over the crowns of ageing *Eriophorum* tussocks. Where bare peat is exposed, acrocarpous species such as *Dicranum scoparium*, *Campylopus paradoxus* and *Pohlia nutans* become frequent and these are commonly accompanied by such hepatics as *Mylia taylori*, *Kurzia pauciflora*, *Ptilidium ciliare*, *Cephalozia* spp. and *Calypogeia* spp., together with lichens like *Cladonia impexa*, *C. squamosa*, *C. bellidiflora*, *C. floerkeana*, *Cornicularia aculeata* and *Hypogymnia physodes*.

***Vaccinium vitis-idaea-Hylocomium splendens* sub-community:** *Betula nana* bogs Poore & McVean 1957; *Calluneto-Eriophoretum* McVean & Ratcliffe 1962; *Empetreto-Eriophoretum* McVean & Ratcliffe 1962, Dierssen 1982; *Juncus-Deschampsia* Series Tallis 1969 *p.p.*; *Calluneto-Eriophoretum* Eddy *et al.* 1969 *p.p.* This sub-community embraces all of the high-montane blanket mire first comprehensively described by McVean & Ratcliffe (1962). It preserves all the general floristic features of the community but is especially distinctive in the consistent presence of the Arctic-Alpine sub-shrubs *V. vitis-idaea* and *E. nigrum* ssp. *hermaphroditum*, which are frequent throughout, and *V. uliginosum*, which is of somewhat more restricted occurrence. Various mixtures of these species, usually with abundant *Calluna* and generally smaller amounts of *V. myrtillus*, and sometimes with some *E. nigrum* ssp. *nigrum*, are typically co-dominant with *Eriophorum vaginatum* in the familiar kind of mixed canopy, though one which is often less tall than at lower altitudes. The montane character of the vegetation is reinforced by the occurrence of the rarities *Arctostaphylos alpinus*, *Betula nana* and *Vaccinium microcarpum* in some stands.

Among the vascular associates, *Eriophorum angustifolium* is rather less common here than usual but *Rubus chamaemorus* remains very frequent, *Juncus squarrosus* occurs quite often, usually at low covers, and in many stands there is some *Carex bigelowii*. *Scirpus cespitosus* also shows something of a resurgence in frequency here.

The remaining distinctive features of this sub-community are found among the ground layer. First, Sphagna can be quite prominent, with *S. capillifolium* being accompanied in some stands by *S. papillosum* and *S. subnitens*, in others by *S. fuscum*; *S. russowii* is also found very occasionally. Then, the hypnaceous mosses are consistently joined by *Hylocomium splendens* and there is quite commonly some *Racomitrium lanuginosum* and *Polytrichum alpestre*; and the rare *Kiaeria starkei* can sometimes be found. Among the hepatics, *Ptilidium ciliare* is strongly preferential, and *Mylia anomala* a little more common than usual, with *Anastrepta orcadensis* figuring occasionally. The lichen flora, too, is usually well developed, *Cladonia arbuscula* and *C. uncialis* being especially frequent, *C. impexa*, *C. rangiferina* and *Cetraria islandica* occurring somewhat less commonly. Among the available stands, three variants have been recognised.

***Betula nana* variant:** *Betula nana* bogs Poore & McVean 1957; *Calluneto-Eriophoretum*, shrub-rich facies McVean & Ratcliffe 1962. Superficially, this kind of *Calluna-Eriophorum* mire is virtually identical with the typical *Vaccinium-Hylocomium* form, mixtures of *E. vaginatum* and *Calluna* generally being co-dominant, with smaller amounts of *V. myrtillus*, *V. vitis-idaea*, *E. nigrum* ssp. *nigrum* and/or *E. nigrum* ssp. *hermaphroditum*, and sometimes a little *Erica tetralix*, forming a cover 2 dm or so high. Closer inspection, however, reveals the presence of *Betula nana* generally growing low among or beneath the other woody species, sometimes showing more conspicuously where their cover is a little thinner. Some stands, from north of the Great Glen, can also have small amounts of *Arctostaphylos alpinus* growing low over the ground and others, in the north-west Highlands, contain *Vaccinium microcarpum*. *Rubus chamaemorus* is generally of low cover in this variant but, among the other vascular associates, *Juncus squarrosus* can be locally abundant. *Carex bigelowii*, in contrast to the other variants, is absent here.

Bryophytes have extensive cover but, though *Sphagnum* growth seems vigorous, the carpet is made up almost entirely of *S. capillifolium*, very occasionally with some *S. fuscum*. Hypnaceous mosses are more varied, with *Pleurozium schreberi*, *Hylocomium splendens*, *Plagiothecium undulatum* and *Hypnum cupressiforme/jutlandicum* all well represented. *Ptilidium ciliare* is the commonest hepatic, though *Mylia anomala* and *Lophozia ventricosa* occur occasionally. Lichens tend to be less conspicuous than in the other variants but *C. arbuscula* and *C. impexa* can be locally abundant and *C. rangiferina* is found in some stands.

Typical variant: *Calluneto-Eriophoretum*, *Sphagnum* type and lichen-rich facies McVean & Ratcliffe 1962; *Juncus-Deschampsia* series Tallis 1969 *p.p.*; *Calluneto-Eriophoretum*, *Empetrum* facies Eddy *et al.* 1969 *p.p.* *Calluna* and *E. vaginatum* are generally co-dominant in this variant, with some *V. myrtillus* and *V. vitis-idaea* and, rarely, a little *V. uliginosum*, and *E. nigrum* ssp. *hermaphroditum* usually better represented than *E. nigrum* ssp. *nigrum*. *Rubus chamaemorus* and *Juncus squarrosus* can both be quite abundant and *Carex bigelowii* becomes frequent, though generally at low covers.

Although the contingent of hypnaceous mosses remains an important element in the ground cover, Sphagna can be quite abundant in wetter places, with *S. capillifolium* the best represented species (*S. quinquefarium* sometimes being distinguished) but *S. subnitens* and *S. fuscum* also figuring with local prominence. *Cladonia* spp., too, are common with *C. arbuscula*, *C. uncialis* and *C. rangiferina* occurring throughout and sometimes attaining high cover.

***Vaccinium uliginosum-Polytrichum alpestre* variant:** *Empetreto-Eriophoretum* McVean & Ratcliffe 1962. This is the most distinctive kind of high-montane *Calluna-Eriophorum* mire in which *E. nigrum* ssp. *hermaphroditum* almost totally replaces ssp. *nigrum*, becoming the usual co-dominant of *Eriophorum vaginatum* in place of *Calluna*, which is only very occasional and of low cover. *Vaccinia* are also prominent, with *V. uliginosum* frequently joining *V. myrtillus* and *V. vitis-idaea*. Mixtures of the sub-shrubs and cotton-grass form a very low canopy, often scarcely 1 dm high. Scattered through this are frequent plants of *Rubus chamaemorus* and *Juncus squarrosus* and, now becoming very common, *Carex bigelowii* and *Scirpus cespitosus*. *Vaccinium microcarpum* has also been recorded very occasionally.

In the ground layer, *S. capillifolium* and *S. papillosum* can both have high cover and, less frequently, there can be some *S. fuscum*, *S. subnitens*, *S. tenellum* or *S. russowii*. Hypnaceous mosses are a little less conspicuous, though *Pleurozium schreberi*, *Rhytidiadelphus loreus* and *Hylocomium splendens* all occur quite commonly in small amounts. *Dicranum scoparium* is also frequent, but more striking here is the constancy of *Racomitrium lanuginosum* and *Polytrichum alpestre* and the occasional occurrence of *Kiaeria starkei*. *Ptilidium ciliare* and *Lophozia ventricosa* are the commonest hepatics. Lichens also remain a prominent feature, with frequent records for *Cladonia arbuscula* and *C. uncialis*, and occasional *C. impexa* and *Cetraria islandica*.

Habitat

The *Calluna-Eriophorum* mire is the typical blanket bog vegetation of high-altitude ombrogenous peats that have accumulated in the wet and cold climate of the uplands of northern Britain. The harsh nature of the montane environment is reflected in the floristics of the community, though the vegetation often takes some of its character from the effects of treatments, notably

burning, grazing and draining; and these have contributed, perhaps with climatic change, to its modification and, in some places, to the erosion of the peats.

On the mantle of blanket peat that has developed over gentler slopes in those parts of Britain with more than 1200 mm annual precipitation (*Climatological Atlas* 1952) or in excess of 160 wet days yr^{-1} (Ratcliffe 1968), the *Calluna-Eriophorum* mire is characteristic of higher altitudes where high precipitation/evaporation ratios coincide with low temperatures throughout the year. In fact, the climate is not quite so consistently humid as within the range of the *Scirpus-Eriophorum* mire, which is concentrated within the 2000 mm isohyet, with more than 200 wet days yr^{-1}. The *Calluna-Eriophorum* mire does extend into this zone, in the higher reaches of the north-west Highlands, but, for the most part, annual rainfall is between 1200 and 2000 mm, with 160–200 wet days yr^{-1}. But the greater difference between the distributions of the two communities is in relation to temperature. The *Scirpus-Eriophorum* mire is essentially an oceanic blanket bog community, largely confined to lower altitudes with relatively mild winters and a comparatively small annual temperature range. The *Calluna-Eriophorum* mire, by contrast, is characteristic of areas with harsh winters, with February minima for the most part below freezing, and cool summers. Overall, its range coincides closely with those parts of Britain which have annual accumulated temperatures of less than 830 day-degrees C yr^{-1} (Page 1982), an area which takes in most of the higher ground through the Scottish Highlands, in the Southern Uplands, in the Lake District and down the Pennines, but which excludes most of Wales and also Dartmoor, where the climate is wet enough to support blanket mire development, but insufficiently cool for this community to be more than local. The altitudinal separation between the *Scirpus-Eriophorum* and *Calluna-Eriophorum* mires is fairly well maintained throughout their ranges, though its absolute level depends on the degree of oceanicity. In general, the former is restricted to sites below 500 m, with a mean altitude in the available samples of about 300 m, while the latter is generally found above 300 m, with a mean of 550 m, but in the wetter west of Scotland, the dividing line tends to be set rather higher, whereas, in the more continental east, the *Calluna-Eriophorum* mire extends down virtually to sea-level and the *Scirpus-Eriophorum* mire is almost totally excluded.

At these higher altitudes in northern Britain, the *Calluna-Eriophorum* mire is confined to deeper peats, usually more than 2 m thick (at least when uneroded) and sometimes considerably more, on flat or gently-sloping ground, generally 0–10° (mean 4°), though extending on to somewhat steeper slopes in places. It is thus most extensively developed on high-level plateaus and broad watersheds, such as dominate much of the landscape of the eastern Highlands, in the Monadhliath, the Forest of Atholl and the Angus Hills (McVean & Ratcliffe 1962), parts of the Southern Uplands (Birse & Robertson 1976, Birse 1980) and the high Cheviot, and the Pennine summits right down to north Derbyshire (e.g. Moss 1913, Tansley 1939, Pearsall 1941, Eddy *et al.* 1969), with a few outlying stands in Wales (Ratcliffe 1959*a*, Edgell 1969, Tallis 1969). In more rugged country, where the climate is suitable but the terrain often too steep for the development of this kind of vegetation, its occurrence is more restricted: although the community is the major kind of blanket bog at higher altitudes in the western Highlands, it is thus rather patchy there, and it is decidedly scarce in the Lake District.

The peats are usually well-humified, at least above, highly acidic (with a surface pH often less than 4) and very oligotrophic. But, typically, they are not so thoroughly or consistently waterlogged as in the *Scirpus-Eriophorum* mire and, indeed, can become surface-dry and oxidised in the summer. This is probably partly due to the drier climate characteristic of the *Calluna-Eriophorum* mire over most of its range, but it is also perhaps accentuated by the fact that the community often occurs on broadly convex summits and slopes which shed water quite readily. Very frequently, too, such drainage has been sharpened by various kinds of treatment (see below). Thus, although the *Calluna-Eriophorum* mire is clearly a Sphagnetalia community, floristically distinct from the Ericetalia wet heaths of thinner, drier peats, Sphagna are less varied and luxuriant than in the *Scirpus-Eriophorum* or *Erica-Sphagnum* mires, the major peat-builders *S. papillosum* and *S. magellanicum* especially being of restricted occurrence. And the *Calluna-Eriophorum* mire only rarely shows the development of the hummock/hollow structure associated with active differentiation of surface relief within wet *Sphagnum*-dominated carpets. The nearest the community comes to this kind of composition and physiognomy is in the *Erica* sub-community, where lawn species like *E. tetralix*, *Narthecium*, *Drosera rotundifolia* and *Vaccinium oxycoccos* are preferential, and this kind of *Calluna-Eriophorum* mire is characteristic of habitats that are climatically or topographically transitional to those typical of our other ombrogenous mires. It is concentrated towards the more oceanic west, often at lower altitudes (mean about 400 m), including most of the stands of the community in Wales (Ratcliffe 1959*a*, Edgell 1969, Tallis 1969) and in Strathclyde (Bignal & Curtis 1981) and it occurs at higher levels where blanket mire of this general kind extends over flat or concave areas of relief (Tallis 1969, Eddy *et al.* 1969) where a higher water-table can be maintained. The more consistent occurrence of *Scirpus* in the *Erica* sub-community may also reflect the frequency of surface-waterlogging

there: it occurs patchily in some other kinds of *Calluna-Eriophorum* mire, but in stands on more surface-dry peats is often only abundant along tracks, where aeration is reduced by trampling.

In the *Erica* sub-community, *Eriophorum vaginatum* often shows some reduction in abundance and vigour but, for the most part, it is the prominence of this species, rather than the luxuriance of Sphagna, which gives the *Calluna-Eriophorum* mire its Sphagnetalian character. The combination of a generally cool climate with a firm, acidic peat substrate, kept generally moist below but not surface-waterlogged, seems to provide this plant with very favourable conditions for its ascendancy (Tansley 1939, Godwin 1975). It can therefore be a major contributor to the accumulating peats under this vegetation, though it has not always been pre-eminent in their development. Its fibrous tussock bases are very resistant to decay and tend to survive in disproportionate abundance as fibrous clods, but earlier views that the deposits here are mainly *E. vaginatum* peat (e.g. Woodhead & Erdtman 1926) have not been borne out by subsequent studies: very often profiles show a transition to peat with abundant *Sphagnum* remains below and layers rich in *E. vaginatum* frequently occur in situations suggestive of climatic or edaphic dryness, so the cottongrass has probably waxed and waned in abundance since the inception of the development of this kind of blanket mire (e.g. Conway 1954, Tallis 1965, Godwin 1975).

The present climatic and soil conditions experienced by the *Calluna-Eriophorum* mire are reflected in other major features of the vegetation. First, the very poor representation here of *Molinia*, which is virtually confined to the transitional *Erica* sub-community and, even there, not very prominent, and the absence or scarcity of *Myrica*, *Potentilla erecta*, *Polygala serpyllifolia* and *Pedicularis sylvatica*, betoken the shift away from the lowland oceanic environment of the *Scirpus-Eriophorum* mire, where they are all well represented, to a harsher montane habitat. Second, there is the complementary increase in associates whose European distribution is either Arctic-Subarctic, like *Rubus chamaemorus*, or Arctic-Alpine, as with *Vaccinium vitis-idaea*, *V. uliginosum*, *Empetrum nigrum* ssp. *hermaphroditum* and *Carex bigelowii*, all of which occur frequently, and *Betula nana* and *Arctostaphylos alpinus*, which are less common but preferential to this community among our Sphagnetalia mires. The more structurally important of these species are, incidentally, all plants which thrive on acidic but well-drained substrates (e.g. Ritchie 1955*a*, Taylor 1971, Gimingham 1972) and their prominence here, together with *Calluna*, *Vaccinium myrtillus* and *Empetrum nigrum* ssp. *nigrum*, which have a wider representation on ombrogenous mires, is further testimony to the freedom from surface-waterlogging in the peats.

Much of the floristic variation between the sub-communities and variants of the *Calluna-Eriophorum* mire can be related to the different sensitivities of these species to the temperature regimes within the range of altitudes occupied by the community as a whole. At lower levels, this kind of blanket mire extends some way into areas where the climate is a little more equable, with February minima sometimes above freezing and mean annual maxima over 25 °C. In the *Erica* sub-community, therefore, the montane contingent is very poorly represented and the sub-shrub canopy consists largely of more broadly temperature-tolerant species such as *Calluna*, the cool oceanic *E. nigrum* ssp. *nigrum* and the Continental Northern *V. myrtillus*, though these show somewhat depressed vigour on the wetter peats, with *E. tetralix* being correspondingly more frequent. The woody element thus approaches that found in more oceanic ombrogenous mires, reinforcing the transitional character of the *Erica* sub-community with its more luxuriant *Sphagnum* component, frequent *Scirpus* and occasional *Molinia*.

With the shift to higher altitudes and a cooler climate, the *Empetrum* sub-community becomes the usual form of *Calluna-Eriophorum* mire, sporadically in Wales, but very extensively all up the Pennines, over the Cheviot and in south-east Scotland and into the eastern Highlands. The mean altitude of this sub-community is around 600 m and, at these levels, the winters are harsher and the mean annual maximum temperature generally between 21 and 25 °C. The sub-shrub component remains much as before, except that *E. tetralix*, which retains some measure of physiological activity in the winter (Gimingham 1972), is now much reduced in occurrence, with balance shifting to the other species, all of which perform well on the somewhat drier peats. More strikingly, *Rubus chamaemorus* appears as a constant: the British range of this plant coincides closely with the distribution of the more montane kinds of *Calluna-Eriophorum* mire and is closely confined within the 25 °C mean annual maximum isotherm (Taylor 1971).

V. vitis-idaea has a very similar range in Britain to *R. chamaemorus* (Ritchie 1955*a*) and it, too, shows a modest rise in frequency in the *Empetrum* sub-community, but it becomes really common with a further rise in altitude and drop in temperatures in the *Vaccinium-Hylocomium* sub-community. This kind of *Calluna-Eriophorum* mire occurs almost exclusively in Scotland, being especially extensive in the Central Highlands with more patchy occurrences in the more rugged country of the north-west Highlands, but it has outliers on the high Cheviot and in the Pennines and transitional stands can be found on the Berwyns. The mean altitude in this sub-community is almost 700 m and virtually everywhere the mean annual maximum temperature is less than 21 °C.

The area bounded by this isotherm coincides closely with the distribution of *E. nigrum* ssp. *hermaphroditum*, which becomes frequent here and gradually replaces ssp. *nigrum* with increasing altitude: the exact upper limit of the latter is hard to fix because of confusion between the two when in the vegetative state, but it is probably around 750 m (Bell & Tallis 1973). Certainly, in the *Vaccinium-Polytrichum* variant, which attains the highest altitudes reached by the *Calluna-Eriophorum* mire, occurring on summits in the Central Highlands with a mean height of over 850 m, it is very much the predominant sub-species and quite often the leading sub-shrub, being frequently co-dominant with *E. vaginatum*, itself a circumpolar plant that retains its abundance and vigour fairly well throughout the whole altitudinal range. Here, too, *V. uliginosum*, another species generally confined within the 21 °C isotherm, becomes constant with the other Vaccinia, and *Calluna* is almost extinguished, reaching its altitudinal limit as a vigorous plant at around 850 m (Gimingham 1960).

In the very harsh climate experienced by the *Vaccinium-Hylocomium* sub-community, the woody cover can be reduced to a very low canopy and the vegetation provides a locus for some other high-montane species. *Carex bigelowii* has a geographical distribution which closely matches those of *E. nigrum* ssp. *hermaphroditum* and *V. uliginosum*, and it follows them here in becoming gradually more prominent in moving to the higher altitudes of the *Vaccinium-Polytrichum* variant. *Vaccinium microcarpum* and *Sphagnum fuscum* occur occasionally in both this and other variants, and with *Betula nana* bring the composition of the vegetation close to that of the North European Sphagnion fusci mires. *B. nana*, however, and *Arctostaphylos alpinus*, seem both to be better represented at not quite the highest altitudinal extreme of the *Vaccinium-Hylocomium* sub-community: they help characterise a lower-level *Betula* variant which is found patchily through the central and north-west Highlands, and where *E. nigrum* ssp. *nigrum* and *Calluna* still retain a frequent presence. The floristic differences between this *Betula* variant and the typical variant may be due partly to treatment (Poore & McVean 1957): the possibility of soligenous influence in the *Betula* variant (Poore & McVean 1957) was discounted by McVean & Ratcliffe (1962).

Treatments, particularly burning and grazing, are of considerable importance in influencing the composition and structure of the *Calluna-Eriophorum* mire throughout its range and particularly where stands form part of unenclosed hill-grazings or grouse-moors. Thus, although the qualitative differences between the sub-communities are set largely by climatic variation, the actual appearance of the vegetation within each altitudinal zone is often the result of human activity. Since all the major structural components of the community, *E. vaginatum*, the sub-shrubs, *R. chamaemorus*, the bryophytes and the lichens, can be affected by such treatments, and often affected in rather different ways, the range of quantitative variation is considerable. And, because treatments have often been applied in complex combinations within a small compass, spatial diversity in individual stands is frequently high. This is shown very clearly in the accounts of the *Calluna-Eriophorum* mire from Moor House, where apparently uniform tracts of the community are revealed on closer inspection to comprise much smaller and quite varied blocks. (e.g. Eddy *et al.* 1969, Rawes & Heal 1978, Rawes & Hobbs 1979). This kind of pattern is typical of many stretches of this type of blanket mire.

It is from Moor House that we have the most detailed studies of the impact of burning and grazing on the *Calluna-Eriophorum* mire and, although work there has been largely on the *Empetrum* sub-community (which, with the impoverished *Eriophorum* mire, makes up the bulk of the blanket bog on the reserve), the general results of the investigations are of some significance for the community as a whole. With burning, the immediate effects are to destroy a proportion of the above-ground parts of the vegetation, produce fertilising ash and increase light penetration (Rawes & Hobbs 1979). Intense fires may consume all standing material, living or dead, but, if burning occurs in the winter, plants with some measure of dormancy, like *E. vaginatum* and *R. chamaemorus*, may escape the worst effects and the ground layer be better protected against severe damage by the increased wetness of the peat surface. And, indeed, it is *E. vaginatum* that typically shows the first response when the sub-shrubs have been burned off, coming to dominate for up to two decades after a fire (Eddy *et al.* 1969, Rawes & Hobbs 1979). *R. chamaemorus*, too, can become very abundant in these early stages, increasing its standing crop and fruit production (Taylor 1971, Taylor & Marks 1971). Over this period, however, the sub-shrubs gradually recover (provided there is no grazing): at Moor House, the mean age of stems of *Calluna*, the usual woody dominant in the blanket bog there, increased through the first decade after a burn and then levelled out. New growth from stools and seed diversified the age-structure of the population with time, though the degenerate phase of growth did not develop because of a smothering of the older stems by the *Sphagnum* carpet (Rawes & Hobbs 1979). *E. nigrum* ssp. *nigrum* and *V. myrtillus*, typical sub-shrubs of the *Empetrum* sub-community, did not figure prominently in post-burn seres at Moor House, but both they and, at higher altitudes, *V. vitis-idaea*, can attain great abundance after fires, provided burning has not been so intense as to destroy their rhizomes: each of these species can thus dominate for some time before being overtopped by *Calluna* (Ritchie 1955*a*, Ratcliffe

1959*a*, Gimingham 1964*b*, 1972, Bell & Tallis 1973). Recovery of *Calluna*, both vegetatively and from seed, proved better at Moor House under short-rotation (10-year) burning than long-rotation (20-year). Indeed, Rawes & Hobbs (1979) reported that most bog species seemed to benefit from the former kind of regime, which appeared to maintain some sort of steady state. Very frequent burning, however, leads to degeneration of the vegetation (see below).

Moderate levels of grazing, too, can maintain a stable diversity in the *Calluna-Eriophorum* mire. The major herbivores on this kind of blanket bog are sheep, with some contribution from deer (mostly red) and smaller mammals (rabbits, hares and voles) and, of particular importance for *Calluna*, grouse and, at higher altitudes, ptarmigan. At Moor House, Rawes & Hobbs (1979) considered that the community could support about 1 sheep per 2.5 ha, without any burning, and continue to produce sufficient food for both stock and grouse.

The most obvious effect of grazing is on the balance between *E. vaginatum* and the palatable ericoids *Calluna* and *V. myrtillus*. *E. vaginatum* is eaten, but its growing points are well protected within the tussocks (Wein 1973), whereas the sub-shrubs can be grazed to extinction under sustained heavy stocking levels (Eddy *et al.* 1969, Rawes & Hobbs 1979) or, conversely, encouraged by enclosure (Rawes 1981, 1983). *R. chamaemorus* also benefits greatly from protection from grazing provided the surrounding vegetation does not become too dense (Taylor 1971, Rawes & Hobbs 1979, Rawes 1983). Less palatable sub-shrubs, on the other hand, like *E. nigrum* ssp. *nigrum* (Bell & Tallis 1973) and *V. vitis-idaea* (Ritchie 1955*a*), can continue to make a more persistent contribution to the cover on grazed *Calluna-Eriophorum* mire. On shallower peats grazing may also increase the proportion of *Juncus squarrosus* and, where trampling decreases aeration along pathways, *Scirpus cespitosus* may spread. Trampling can also disrupt the *Sphagnum* cover, destroy larger *Cladonia* spp. and favour an increase in encrusting lichens, acrocarpous mosses like *Campylopus flexuosus* and some leafy hepatics on exposed peat surfaces. Such developments produce considerable fine variation between stands of the community and, where grazing is particularly heavy and long-sustained, presage a more substantial change in the character of the vegetation (see below).

It is also possible for episodes of burning and grazing to contribute to the development of erosion within stretches of *Calluna-Eriophorum* mire, a process which can ultimately destroy the vegetation and its substrate, but which, in its less severe manifestations, introduces a further measure of patterning into the community. In fact, erosion of the kind of blanket peat of which the *Calluna-Eriophorum* mire is characteristic is a complex of processes, probably with varied causes (e.g. Johnson 1957, Radley 1962, Tallis 1964*b*, *c*, 1965, 1985*b*). At the higher altitudes to which the community penetrates, wind, rain and frost contribute to an element of natural climatic erosion on exposed summits and ridges, producing networks of bare areas, sometimes showing colonisation by encrusting lichens and bryophytes (Radley 1962, Tallis 1965). More dramatic is the marginal fretting of these bogs, in which extensive systems of gullies run back into the peat, separating upstanding remnant haggs, and sheet-erosion with extensive wastage of the upper layers (e.g. Lewis & Moss 1911, Tansley 1939, McVean & Ratcliffe 1962, Tallis 1965, Eddy *et al.* 1969). Severe erosion of this kind can be seen throughout the range of the *Calluna-Eriophorum* mire, being much more generally widespread than in the *Scirpus-Eriophorum* mire, where the bog margins are not so exposed, but it is especially pronounced through the southern Pennines, affecting about 75% of the blanket peat there (Anderson & Tallis 1981; see also Bower 1960, 1961).

This kind of erosion, too, may have a natural and long-standing component. In a detailed study of a small, but probably quite typical, area, Tallis (1985*b*) developed an original suggestion of Conway (1954) that mass movement might occur around the bog margins, restoring stability where accumulation had reached some kind of critical limit but exposing bare peat for removal with enhanced local drainage. With the early initiation of peat development in the southern Pennines, such a stage might have been reached a considerable time ago (Conway 1954, Tallis 1985*a*, *b*). More recently, erosion seems to have been markedly exacerbated by a variety of biotic influences responsible for the exposure of areas of bare peat, over which surface run-off can be channelled, with increased erosive power. Burning, particularly deep, catastrophic fires, and heavy grazing can both contribute to such developments (Radley 1962, Shimwell 1974, Tallis 1981, Tallis & Yalden 1984) and sheep-tracks (Tallis 1973*b*) and footpaths (Shimwell 1981) may also disrupt the cover of surface vegetation. In the southern Pennines, too, atmospheric pollution from the great industrial conurbations of Lancashire and Yorkshire (Conway 1949, Tallis 1964*b*, *c*, Ferguson & Lee 1983) has undoubtedly played a major part, together with enhanced drying of the peats as a result of water extraction, in the loss of *Sphagnum* from blanket mire vegetation there over the past two centuries, and this must also have exposed extensive areas of bare peat (Tallis 1985*b*).

Quite often, the bog vegetation in such severely-eroded areas has become itself so impoverished as to fall within the *Eriophorum* mire, but eroded tracts can retain sufficient floristic richness as to still qualify as *Calluna-Eriophorum* mire. Typically, however, they exhibit a distinctive mosaic with *R. chamaemorus* often especially

abundant around the gully heads, and *E. nigrum* ssp. *nigrum* and *V. myrtillus* becoming more prominent along the sides of the gullies, over the deeply-fretted haggs and on tumbling masses of peat around the bog margins. More gently-sloping gullies with a measure of stagnation may show a regeneration of the mire vegetation but commonly other communities appear here and over thin redistributed peat and any exposed underlying drift (see below).

Zonation and succession

The *Calluna-Eriophorum* mire is characteristically found in zonations and mosaics with wet and dry heaths and grasslands over sequences of increasingly better-drained soils, with soligenous mires often interrupting the patterns where there is local flushing and sometimes relieving the prevailingly calcifuge nature of the vegetation cover. Almost universally, such transitions have been affected by treatments, which can blur the boundaries between the vegetation types, encourage some successional changes among them and introduce new elements of variation, particularly striking where these factors contribute to gross erosion of the peat.

The basic edaphically-related pattern is best seen where there is a gradual thinning of the ombrogenous peat cover to a humic top over gleyed podzols and then a thin layer of mor over freely-draining podzols, where the *Calluna-Eriophorum* mire gives way first to Ericetalia heath, then to Calluno-Ulicetalia heath and/or Nardetalia grasslands. Typically, such sequences are disposed over ground of progressively increasing slope, running downhill where the blanket bog occupies the summits of hills (a frequent occurrence here), running uphill where it clothes valley bottoms and plateaus which give way above to a fringe of steeper ground. The transitions may be on a grand scale, where more or less flat land is a prevailing element in the scenery, as is the case in parts of the Central Highlands, over the rounded summits of the Cheviot and on the high Pennines, where the communities can show a crude altitudinal pattern of replacement one by the other. But, in more rugged terrain, the zonations are on a finer scale, with repeated sequences over the stepped landscapes of grits and shales, for example, or complex mosaics disposed over craggy ground with small boulders. And, as in similar transitions with the *Scirpus-Eriophorum* mire, regional and local climate can influence the proportions of the communities that are represented, with the wetter elements of the sequence extended on to somewhat steeper slopes in areas with higher rainfall or on northern aspects, but contracted in drier sites.

The particular kinds of *Calluna-Eriophorum* mire found in these zonations, and the types of heath and grassland, vary with altitude and, where the bog gives way both above and below to such sequences, different heaths and grasslands may be represented in each, though the general physiognomic character of the transitions is very similar. The shift to Ericetalia wet heath is thus usually marked by a fairly rapid loss of *E. vaginatum* and a further reduction in the often already low cover of Sphagna such as *S. papillosum* in the ground carpet. Where the *Calluna-Eriophorum* mire extends to lower altitudes in the *Erica* sub-community, such transitions can be fairly gradual and very like those found around the *Scirpus-Eriophorum* mire, with the *Sphagnum* sub-community of the *Scirpus-Erica* wet heath forming a marginal zone. But, at higher altitudes, where the *Calluna-Eriophorum* mire is represented by other sub-communities, it is usually drier forms of Ericetalia heath that replace the community as the peat cover thins: often, in such situations, the *Vaccinium* sub-community of the *Scirpus-Erica* wet heath can be found, but at lower altitudes in eastern Scotland, the *Juncus-Dicranum* sub-community of the *Ericetum tetralicis* can mark the transition. In these vegetation types, the most obvious floristic changes, apart from the reduction in *E. vaginatum* and the Sphagna, are increased vigour among the sub-shrubs, an abundance of *Juncus squarrosus* and/or *Nardus stricta* and the frequent occurrence of acrocarpous mosses such as *Dicranum scoparium* and *Campylopus paradoxus*, with *Racomitrium lanuginosum* and lichens often prominent on bare peat.

Sometimes, this wet-heath zone is of considerable extent but quite frequently, where the margin of the bog is steep, it is reduced in width or totally absent, with an abrupt switch to dry heath, with overwhelming dominance of *Calluna*, or one of the Empetra or Vaccinia. Usually, such vegetation can be included within the *Calluna-Vaccinium* or *Vaccinium-Deschampsia* heaths, but, at higher altitudes, the *Calluna-Cladonia* or *Calluna-Arctostaphylos* heaths can replace the *Calluna-Eriophorum* mire on steeper, drier slopes, and these in turn may give way to lichen- or moss-dominated vegetation on very exposed summits. At lower altitudes, the zonation often continues beyond the heaths into some kind of Nardetalia grassland and, quite often, there are direct transitions from the community to these vegetation types with the increasing influence of pastoral agriculture (see below).

General patterns of the kinds described above are frequently complicated by the local occurrence of soligenous mires, and sometimes small topogenous basins associated with them. Again, the particular character of this vegetation varies with altitude. At lower levels, through the range of the *Erica* and *Empetrum* sub-communities, various kinds of *Carex echinata-Sphagnum* mire, dominated by small sedges or Junci, can be found around flushes and along water-tracks through the bog and into the zones of fringing vegetation. At higher altitudes, this community is replaced in analo-

gous situations by the *Carex-Sphagnum russowii* mire. Where the flushing waters are somewhat less base-poor, the *Carex-Sphagnum warnstorfii* mire occurs, or where there is a marked enrichment, as where the blanket bog has encroached over calcareous substrates, the *Pinguiculo-Caricetum*, *Carici-Saxifragetum* or *Caricetum saxatilis* can mark out sites with soligenous influence, with the *Carex-Calliergon* mire in small waterlogged hollows.

Such variegation often provides the floristically most interesting element of internal patterning on the *Calluna-Eriophorum* mire, because true hummock/hollow relief, with its distinctive zoning of plants and transitions to Rhynchosporion pools, is only rarely encountered. It is sometimes developed in the *Erica* sub-community, which can occur within tracts of the *Empetrum* type where a higher water-table is locally maintained, and then the Rhynchosporion component is generally represented by the *Sphagnum cuspidatum/recurvum* community. In other cases, the *Carex rostrata-Sphagnum recurvum* or *Eriophorum angustifolium* communities can mark out pools.

Much more commonly, internal variation within tracts of the *Calluna-Eriophorum* mire comprises quantitative differences in the major structural elements developed in response to burning and grazing. If such treatments are drastic and frequent or long-maintained, they can induce more substantial qualitative changes in the vegetation: in some cases, such changes can be reversed but they may initiate a run-down of the community and contribute to the destruction of the underlying peats.

Most obviously, frequent burning and heavy grazing contribute to the conversion of the *Calluna-Eriophorum* mire into the *Eriophorum* mire, where ericoids, Sphagna and hypnaceous mosses are of very patchy occurrence and *E. vaginatum* overwhelmingly dominant. Locally-extensive tracts of this impoverished vegetation can be found through much of the range of the *Calluna-Eriophorum* mire, though reversion to the richer blanket bog has been demonstrated after only 15 years of enclosure and freedom from burning at Moor House (Rawes 1983). In the southern Pennines, however, where injudicious treatments have been combined with draining and aerial pollution over the past two centuries, the degeneration of the *Calluna-Eriophorum* mire is particularly widespread and perhaps irremediable. Here, too, erosion of the peats is especially severe, with much bare peat even among the remnants of the richer blanket bog, patchy *Eriophorum angustifolium* pools occurring where water collects and soligenous vegetation approximating to the *Carex echinata-Sphagnum* mire marking out gullies with some moderate water movement. Similar mosaics are very well seen in the map of Moor House in Eddy *et al.* (1969).

In other cases, treatments can convert the *Calluna-Eriophorum* mire into heath or grassland. The peats here are already fairly dry, so it is often a small step, with artificial drainage, to encourage a succession to wet heath, a change marked most obviously by a reduction in the vigour of *E. vaginatum*, and then to dry heath, with its overwhelming dominance of ericoids. Combined with grazing, such treatment can produce a Nardetalia sward or, with liming and fertiliser application, even something approximating to a Cynosurion pasture. With less assiduous improvement, *Juncus squarrosus* often gains an opportunity to spread in such situations, though enclosure of a *Juncus*-dominated pasture at Moor House showed that such a trend could be reversed, the vegetation beginning to develop into *Calluna-Eriophorum* mire after 25 years (Rawes 1981). The recent subsidising of improvement of hill-grazings has greatly speeded the reclamation of this kind of blanket bog for agriculture and rendered such changes more permanent. In other places, draining has been a prelude to afforestation.

Distribution

The *Calluna-Eriophorum* mire is centred on the higher ground in the Pennines and the Central Highlands of Scotland. The *Empetrum* sub-community is especially extensive in the former area, extending northwards through Cheviot and the Borders into eastern Scotland, but most stands in the Highlands are of the *Vaccinium-Hylocomium* sub-community, which extends to the altitudinal limit of this kind of blanket bog in central Scotland as the *Vaccinium-Polytrichum* variant, with the *Betula* and Typical variants represented at somewhat lower levels and penetrating patchily into the north-west Highlands. At lower altitudes, with a rather more oceanic climate, as through Wales and Strathclyde, the *Erica* sub-community is the usual form.

Affinities

The *Calluna-Eriophorum* mire in this scheme unites the richer kinds of *Eriophoretum vaginati* or 'Pennine blanket bog' (e.g. Smith & Moss 1903, Lewis 1904*a*, *b*, Lewis & Moss 1911, Moss 1913, Adamson 1918, Watson 1932, Tansley 1939) with the *Calluneto-Eriophoretum* common in Scotland (Poore & McVean 1957, McVean & Ratcliffe 1962, Birks 1973, Evans *et al.* 1977), also taking in related forms of blanket mire described from Wales (Ratcliffe 1959*a*, Edgell 1969, Tallis 1969) and south-west Scotland (Meek 1976, Birse & Robertson 1976, Birse 1980, Bignal & Curtis 1981) under a variety of names. The essential differences between these types are preserved here in the *Empetrum*, *Vaccinium-Hylocomium* and *Erica* sub-communities, though the first includes what Eddy *et al.* (1969) described as *Calluneto-Eriophoretum* (and some of their *Trichophoro-Eriophoretum*). The *Vaccinium-Hylocomium* sub-community also sub-

sumes the *Empetreto-Eriophoretum* of McVean & Ratcliffe (1962) and Dierssen (1982) as a distinctive variant.

In the scheme proposed by Moore (1968) for the classification of European mires, this kind of vegetation was termed *Vaccinio-Ericetum tetralicis* (see also Moore 1962) and Birse & Robertson (1976) adopted this name for their lower altitude blanket bog of this kind. But Moore's account was very much based on Irish stands, with some of Pearsall's (1941) data from Stainmore, and the character of this vegetation was prevailingly of the type included here in the *Erica* sub-community. In Birse's (1980) account of Scottish vegetation, his *Vaccinio-Ericetum* became subsumed in the *Erico-Sphagnetum*, though he retained a separate *Rhytidiadelpho-Sphagnetum fusci* for the high-montane vegetation contained in this scheme in the *Vaccinium-Hylocomium* sub-community.

Despite these varied treatments of the different types of this kind of blanket bog, there is sufficient in common among them for them to be retained within a single community. It shows obvious similarities to both the *Scirpus-Eriophorum* and *Erica-Sphagnum* mires and is probably best grouped with them in the Erico-Sphagnion (as Moore (1968) proposed). However, among our ombrogenous communities, it comes closest to the Sphagnion fusci bogs of boreal peatlands, particularly in the *Vaccinium-Hylocomium* sub-community, where *Rubus chamaemorus* and *Empetrum nigrum* ssp. *nigrum* are joined by *E. nigrum* ssp. *hermaphroditum*, *Vaccinium vitis-idaea*, *V. uliginosum*, *Betula nana*, *V. microcarpum* and *Sphagnum fuscum*, all of them species which become prominent to varying degrees through Poland, north-east USSR, Finland and Sweden.

Floristic table M19

	a	b	c	19
Eriophorum vaginatum	V (1–9)	V (1–9)	V (1–8)	V (1–9)
Calluna vulgaris	V (1–9)	V (1–9)	V (1–9)	V (1–9)
Pleurozium schreberi	IV (1–6)	IV (1–6)	V (1–5)	IV (1–6)
Sphagnum capillifolium	IV (1–8)	IV (1–7)	IV (1–9)	IV (1–9)
Eriophorum angustifolium	IV (1–8)	V (1–7)	III (1–4)	IV (1–8)
Rubus chamaemorus	I (1–6)	V (1–9)	V (1–4)	IV (1–9)
Erica tetralix	V (1–4)	I (1–4)	I (1–2)	II (1–4)
Scirpus cespitosus	IV (1–6)	II (1–4)	II (1–5)	II (1–6)
Hypnum jutlandicum	IV (1–8)	I (1–4)		II (1–8)
Narthecium ossifragum	II (1–5)	I (1–2)	I (1–2)	I (1–5)
Molinia caerulea	II (1–7)	I (1–4)		I (1–7)
Drosera rotundifolia	I (1–3)			I (1–3)
Sphagnum compactum	I (1–4)			I (1–4)
Vaccinium oxycoccos	I (1–2)			I (1–2)
Empetrum nigrum nigrum	III (1–5)	V (1–6)	II (1–6)	III (1–6)
Mylia taylori	I (1–3)	II (1–3)	I (1–3)	I (1–3)
Pohlia nutans	I (1)	II (1–3)	I (1–2)	I (1–3)
Cladonia impexa	I (1–4)	II (1–6)		I (1–6)
Cephalozia bicuspidata	I (1–3)	II (1–3)		I (1–3)
Calypogeia trichomanis		II (1–3)	I (1–3)	I (1–3)
Hylocomium splendens	I (1–4)	I (1–2)	V (1–6)	II (1–6)
Cladonia arbuscula	I (4)	II (1–3)	IV (1–8)	II (1–8)
Vaccinium vitis-idaea	I (1–4)	II (1–4)	IV (1–4)	II (1–4)
Juncus squarrosus	II (1–4)	I (1–7)	III (1–5)	II (1–7)
Ptilidium ciliare	I (1–4)	II (1–3)	III (1–5)	II (1–5)
Cladonia uncialis	I (1–4)	I (1)	III (1–4)	II (1–4)
Empetrum nigrum hermaphroditum	I (1)		III (1–6)	II (1–6)
Carex bigelowii		I (1–4)	III (1–5)	II (1–5)

https://doi.org/10.1017/9780521391658.023 Published online by Cambridge University Press

Vaccinium uliginosum	I (1)	I (1–2)	II (1–4)	I (1–4)
Racomitrium lanuginosum	I (1–5)	I (1–3)	II (1–6)	I (1–6)
Polytrichum alpestre	I (1)	I (1)	II (1–4)	I (1–4)
Sphagnum papillosum	I (1–4)	I (1–6)	II (1–7)	I (1–7)
Sphagnum subnitens	I (1–6)	I (4–5)	II (1–8)	I (1–8)
Cetraria islandica		I (1–3)	II (1–3)	I (1–3)
Sphagnum fuscum		I (1–3)	II (1–4)	I (1–4)
Betula nana		I (1)	II (1–4)	I (1–4)
Polytrichum alpinum			I (1–4)	I (1–4)
Arctostaphylos alpinus			I (1–4)	I (1–4)
Vaccinium microcarpum			I (1–3)	I (1–3)
Vaccinium myrtillus	III (1–8)	III (1–9)	IV (1–5)	III (1–9)
Dicranum scoparium	III (1–4)	III (1–6)	III (1–5)	III (1–6)
Rhytidiadelphus loreus	II (1–4)	III (1–4)	III (1–8)	III (1–8)
Plagiothecium undulatum	III (1–6)	III (1–5)	II (1–2)	III (1–6)
Hypnum cupressiforme	II (1–6)	III (1–4)	II (1–7)	II (1–7)
Deschampsia flexuosa	II (1–8)	II (1–8)	II (1–3)	II (1–8)
Polytrichum commune	II (1–4)	II (1–4)	I (1–4)	II (1–4)
Aulacomnium palustre	II (1–5)	II (1–4)	I (1)	II (1–5)
Lophozia ventricosa	I (1–2)	II (1–3)	II (1–3)	II (1–3)
Sphagnum recurvum	I (1–6)	I (1–8)	I (4)	I (1–8)
Sphagnum palustre	I (1–5)	I (1–6)	I (1–4)	I (1–6)
Potentilla erecta	I (1–2)	I (1–4)	I (1–4)	I (1–4)
Nardus stricta	I (1–8)	I (1–4)	I (1–6)	I (1–8)
Rhytidiadelphus squarrosus	I (1–3)	I (1–4)	I (1)	I (1–4)
Barbilophozia floerkii	I (1–2)	I (1–4)	I (1–2)	I (1–4)
Diplophyllum albicans	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Listera cordata	I (1–2)	I (1–4)	I (1–2)	I (1–4)
Campylopus paradoxus	I (1–4)	I (1–3)	I (1–2)	I (1–4)
Odontoschisma sphagni	I (1–4)	I (1–3)	I (1–3)	I (1–4)
Carex nigra	I (1–4)	I (1–3)	I (1–3)	I (1–4)
Melampyrum pratense	I (1–2)	I (1–3)	I (1–2)	I (1–3)
Cladonia squamosa	I (1–2)	I (1–3)	I (1–4)	I (1–4)
Sphagnum tenellum	I (1–2)	I (1–2)	I (1)	I (1–2)
Cladonia bellidiflora	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Galium saxatile	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Calypogeia fissa	I (1–3)		I (1–3)	I (1–3)
Pinguicula vulgaris	I (1–2)		I (1–2)	I (1–2)
Calypogeia muellerana	I (1–4)	I (1–3)		I (1–4)
Cladonia coccifera	I (1–2)	I (1–3)		I (1–3)
Hypogymnia physodes	I (1–3)	I (1–3)		I (1–3)
Cladonia floerkeana	I (1–3)	I (1–3)		I (1–3)
Kurzia pauciflora		I (1–3)	I (1–3)	I (1–3)
Cladonia tenuis		I (4)	I (1–3)	I (1–4)
Mylia anomala		I (1–3)	I (1–3)	I (1–3)
Cornus suecica		I (1–3)	I (1–3)	I (1–3)
Festuca vivipara		I (1–6)	I (1–2)	I (1–6)
Huperzia selago		I (1–3)	I (1–3)	I (1–3)
Cornicularia aculeata		I (1–3)	I (1–3)	I (1–3)
Dicranum fuscescens		I (1–3)	I (1–3)	I (1–3)

https://doi.org/10.1017/9780521391658.023 Published online by Cambridge University Press

Floristic table M19 *(cont.)*

	a	b	c	19
Sphagnum robustum		I (1–2)	I (1–4)	I (1–4)
Cladonia gracilis		I (1–3)	I (1–3)	I (1–3)
Blechnum spicant		I (1–2)	I (1–2)	I (1–2)
Dicranum majus		I (4)	I (1–2)	I (1–4)
Carex binervis		I (1–4)	I (1–2)	I (1–4)
Luzula sylvatica		I (1–4)	I (1–3)	I (1–4)
Number of samples	61	53	56	181
Number of species/sample	17 (11–33)	19 (7–33)	20 (10–33)	19 (7–33)
Herb height (cm)	21 (8–40)	23 (11–60)	17 (5–45)	21 (5–60)
Herb cover (%)	83 (6–100)	89 (65–100)	96 (70–100)	89 (6–100)
Bryophyte height (mm)	38 (5–80)	40 (10–100)	33 (10–60)	37 (5–100)
Bryophyte cover (%)	56 (20–100)	39 (2–80)	75 (60–100)	53 (2–100)
Altitude (m)	409 (28–820)	601 (355–978)	691 (457–923)	568 (28–978)
Slope (°)	4 (0–12)	4 (0–18)	6 (0–25)	5 (0–25)
Soil pH	4.3 (3.2–6.2)	3.8 (3.1–4.7)	4.6 (4.1–5.5)	4.2 (3.1–6.2)

a *Erica tetralix* sub-community
b *Empetrum nigrum nigrum* sub-community
c *Vaccinium vitis-idaea-Hylocomium splendens* sub-community
19 *Calluna vulgaris-Eriophorum vaginatum* blanket mire (total)

Floristic table M19c, variants

	ci	cii	ciii
Eriophorum vaginatum	V (1–5)	V (1–8)	V (1–8)
Calluna vulgaris	V (6–9)	V (2–9)	II (1–4)
Pleurozium schreberi	V (1–4)	V (1–5)	IV (1–4)
Sphagnum capillifolium	IV (1–9)	IV (1–6)	IV (1–4)
Eriophorum angustifolium	II (1–4)	II (1–3)	V (1–4)
Rubus chamaemorus	V (1–3)	V (1–4)	V (1–4)
Vaccinium myrtillus	V (1–2)	V (1–5)	V (1–4)
Hylocomium splendens	V (1–6)	V (1–6)	III (1–3)
Vaccinium vitis-idaea	III (1–3)	V (1–3)	IV (1–4)
Cladonia arbuscula	III (1–5)	V (1–8)	IV (1–4)
Betula nana	V (1–4)	I (1)	
Empetrum nigrum nigrum	III (1–4)	II (1–5)	I (1–2)
Hypnum cupressiforme	III (1–4)	II (1–8)	
Arctostaphylos alpinus	III (1–4)	I (4)	
Erica tetralix	III (1–3)		
Cladonia rangiferina	II (1–3)	I (1–3)	
Mylia anomala	II (1–3)	I (1–3)	I (1–3)

https://doi.org/10.1017/9780521391658.023 Published online by Cambridge University Press

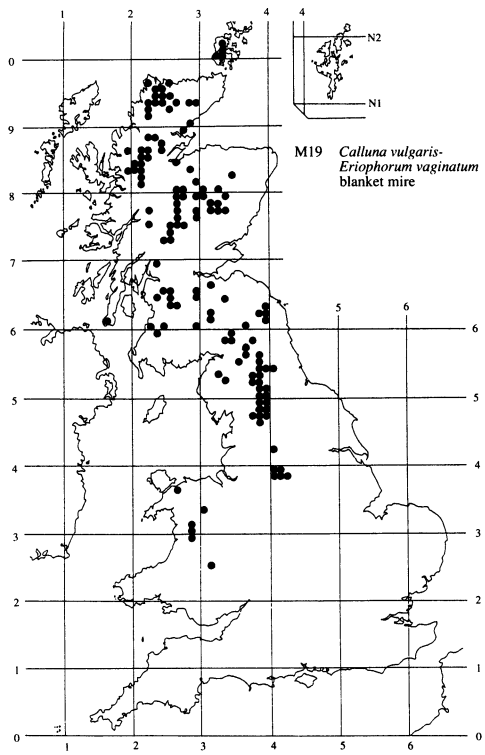
Vaccinium microcarpum	II (1–3)		
Vaccinium uliginosum	I (1–3)	I (2–4)	V (1–4)
Carex bigelowii		III (1–6)	V (1–6)
Racomitrium lanuginosum		II (1–4)	V (1–5)
Polytrichum alpestre		I (1–4)	V (1–4)
Scirpus cespitosus	II (1–2)	II (1–5)	IV (1–4)
Sphagnum papillosum		I (1–4)	III (4–6)
Kiaeria starkei			I (1–2)
Empetrum nigrum hermaphroditum	III (1–3)	III (1–4)	IV (4–6)
Juncus squarrosus	IV (1–5)	II (1–5)	III (1–3)
Rhytidiadelphus loreus	III (1–4)	IV (1–8)	III (1–3)
Ptilidium ciliare	III (1–6)	III (1–2)	III (1–3)
Dicranum scoparium	II (1–3)	III (1–6)	III (1–5)
Cladonia uncialis	I (1–3)	IV (1–4)	IV (1–4)
Cladonia impexa	II (1–2)	II (1–4)	II (1–3)
Lophozia ventricosa	II (1–3)	I (1–2)	II (1–3)
Plagiothecium undulatum	II (1–3)	II (1–3)	
Deschampsia flexuosa		II (1–3)	II (1–3)
Cetraria islandica		II (1–3)	II (1–3)
Sphagnum subnitens		II (1–8)	II (1–4)
Sphagnum fuscum	I (1–2)	II (1–4)	I (4–5)
Anastrepta orcadensis	I (1–3)	II (1–2)	I (1)
Melampyrum pratense	I (1–2)	II (1)	
Rhytidiadelphus squarrosus	I (1–3)		II (1–3)
Polytrichum commune	I (1–2)	I (1–4)	I (1–3)
Diplophyllum albicans	I (1–3)	I (1–3)	I (1–3)
Campylopus paradoxus	I (1–2)	I (1–3)	I (1–2)
Aulacomnium palustre	I (1–2)	I (1–2)	I (1–3)
Pinguicula vulgaris	I (1–2)	I (2)	I (2)
Barbilophozia floerkii	I (1–3)	I (1–3)	I (1)
Cornus suecica	I (1–3)	I (1–3)	I (1–3)
Potentilla erecta	I (1–2)	I (1–4)	I (1)
Erica cinerea	I (1–3)	I (1–3)	I (1–3)
Sphagnum robustum	I (1–4)	I (1–2)	I (1–4)
Cladonia gracilis	I (1–3)	I (1–3)	I (1–3)
Cladonia squamosa	I (1–3)	I (1–4)	I (1–3)
Mylia taylori	I (1–3)	I (1)	
Kurzia pauciflora	I (1–3)	I (1–3)	
Cladonia tenuis	I (1–2)	I (2)	
Listera cordata	I (1–3)	I (1–3)	
Calypogeia fissa	I (1–3)	I (1–3)	
Solidago virgaurea	I (1)	I (1–2)	
Carex binervis	I (1–2)	I (1–3)	
Sphagnum palustre	I (1–3)	I (4)	
Trientalis europaea		I (1)	I (1)
Cladonia bellidiflora		I (1–2)	I (1–3)
Sphagnum tenellum		I (1–3)	I (2)
Cornicularia aculeata		I (1–3)	I (1–3)
Festuca vivipara		I (1–3)	I (1–3)
Galium saxatile		I (1–2)	I (2)

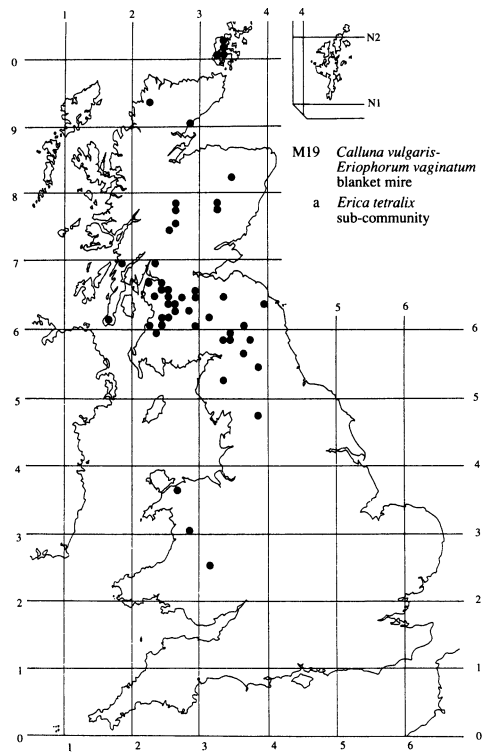
https://doi.org/10.1017/9780521391658.023 Published online by Cambridge University Press

Floristic table M19c, variants *(cont.)*

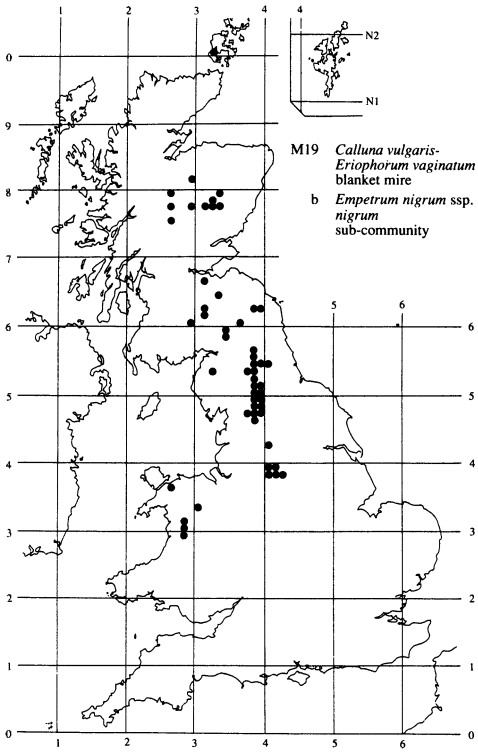
	ci	cii	ciii
Dicranum fuscescens		I (1–3)	I (1–3)
Polytrichum alpinum		I (1–4)	I (1–3)
Number of samples	20	22	12
Number of species/sample	20 (16–27)	21 (12–33)	23 (18–33)
Herb height (cm)	24 (12–45)	15 (5–30)	9 (5–11)
Herb cover (%)	92 (70–100)	98 (85–100)	100
Bryophyte height (mm)		29 (20–40)	40 (10–60)
Bryophyte cover (%)		75	
Altitude (m)	569 (457–766)	705 (495–853)	856 (762–923)
Slope (°)	4 (0–15)	8 (2–25)	5 (2–15)
Soil pH		4.7 (4.1–5.5)	4.3 (4.2–4.3)

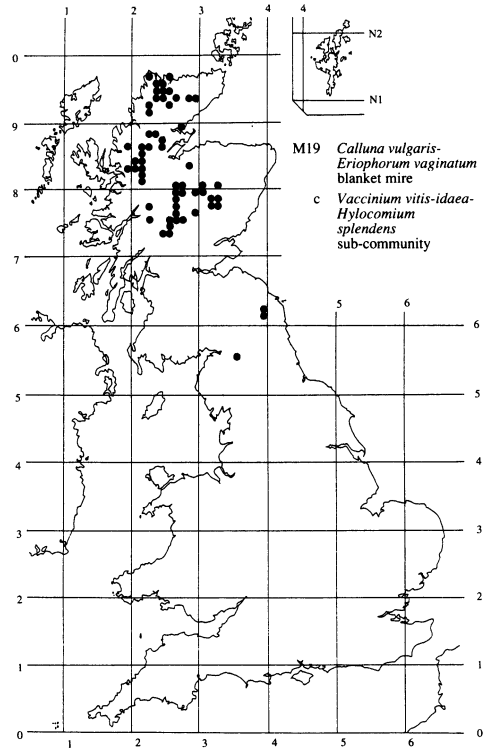
ci *Betula nana* variant
cii Typical variant
ciii *Vaccinium uliginosum-Polytrichum alpestre* variant





https://doi.org/10.1017/9780521391658.023 Published online by Cambridge University Press





https://doi.org/10.1017/9780521391658.023 Published online by Cambridge University Press