H12
Calluna vulgaris-Vaccinium myrtillus heath

Synonymy
Heather Moor Smith & Rankin 1903, Smith & Moss 1903 *p.p.*; *Callunetum* Lewis & Moss 1911; *Calluno-Vaccinietum* Lewis & Moss 1911; *Calluna* heath Ratcliffe 1959 *p.p.*; *Callunetum vulgaris* McVean & Ratcliffe 1962 *p.p.*; *Calluna*-heath moss sociation Edgell 1969; *Calluna-Vaccinium* heath Gimingham 1972 *p.p.*; *Callunetum vulgaris typicum* Evans *et al.* 1977; *Calluna vulgaris-Vaccinium vitis-idaea* nodum Huntley & Birks 1979; *Calluna vulgaris-Anemone nemorosa* nodum Huntley & Birks 1979; *Calluna vulgaris-Deschampsia flexuosa* nodum Huntley 1979; *Vaccinio-Ericetum cinereae* Birse 1980 *p.p.*; *Calluna vulgaris-Vaccinium myrtillus* nodum Hughes & Huntley 1986; *Calluna vulgaris-Hypnum cupressiforme* nodum Hughes & Huntley 1986.

Constant species
Calluna vulgaris, *Deschampsia flexuosa*, *Vaccinium myrtillus*, *Dicranum scoparium*, *Hypnum jutlandicum*, *Pleurozium schreberi*.

Rare species
Diphasium × *issleri*.

Physiognomy
The *Calluna vulgaris-Vaccinium myrtillus* heath is generally dominated by *Calluna vulgaris*, often overwhelmingly so: indeed, this community includes the bulk of the Calluneta so widely described from the less oceanic parts of the sub-montane zone, through which the regular burning of grouse-moor and hill-grazings that encourages a predominance of species-poor building-phase heather is still commonly practised. But older stands, with a more open cover of degenerate *Calluna*, can often be found and there is structural variety, too, in response to differences in grazing intensity and local climate, both of which can affect the height and extent of the sub-shrub canopy. More distinctly, wherever there is some opportunity for a contribution to the cover from other ericoids, capitalising upon the more open ground in the early or late stages of the heather growth cycle, or persisting in usually smaller amounts among the maturing bushes, the potential diversity of this element of the vegetation is quite high.

As in the *Calluna-Erica* heath, *Erica cinerea* can figure among these associates, recovering particularly well from burning on drier slopes and able to persist patchily beneath quite dense heather (Gimingham 1949, 1972, Bannister 1965). But it is much more uneven in its occurrence in this community, rarely of high cover and, in the colder and wetter climatic conditions characteristic of much of the range of this kind of heath, it fares rather badly. *Vaccinium myrtillus*, by contrast, which is only occasional within the *Calluna-Erica* heath, is a constant here and, though generally subordinate to the heather, it can show temporary abundance after fires and being also a shade-tolerant plant, it is able to survive in a sparse lower tier beneath the closing *Calluna* canopy. Out of reach of any grazing animals, and especially in the humic soils that accumulate among boulders or over exposed crags, it can grow with particular vigour and the community includes stands in such situations where *V. myrtillus* is co-dominant with heather in transitions to *Vaccinium-Deschampsia* heath (Smith & Moss 1903, Smith & Rankin 1903, Lewis & Moss 1911, Moss 1913). Very commonly, too, in this community, and especially around the Scottish Highlands where this Arctic-Alpine species has its centre of distribution in Britain, *V. vitis-idaea* can be found, sometimes with local prominence following burning and often persisting best of all the woody associates among denser and taller heather (Ritchie 1955*a*, Gimingham 1972). Then, *Empetrum nigrum* ssp. *nigrum* is much more frequent through the *Calluna-Vaccinium* heath as a whole than it is in the *Calluna-Erica* heath, although the dense prostrate mats that can develop after fire here are generally overwhelmed fairly quickly by the heather, the *Empetrum* cover being attenuated to far-creeping and sparse-branching shoots which, where they are

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supported by the *Calluna*, are able to put up scattered sprigs of foliage at the same level.

Among other sub-shrubs, *Empetrum nigrum* ssp. *hermaphroditum* occurs only very occasionally and *Arctostaphylos uva-ursi* is rare, although over less markedly impoverished soils in eastern Scotland, the distinction between this community and the *Calluna-Arctostaphylos uva-ursi* heath, where the bearberry is a constant, is probably at least partly mediated by fire (see below). In such situations around the eastern Highlands, too, small, scattered bushes of *Juniperus communis* ssp. *communis* can sometimes be found here. In other stands, where the *Calluna-Vaccinium* heath extends a little way on to soils with somewhat less free drainage, *Erica tetralix* may occur at low covers but this is an exceptional plant here, and its appearance generally marks a decisive shift to Ericion wet heath (Edgell 1969, Birse 1980).

In very many stands of the community, the contribution of herbs to this vegetation is negligible. Of these, only *Deschampsia flexuosa* is at all frequent throughout and, though it is able to spread quite extensively after burning, particularly where there is also grazing, it is often reduced to sparse scattered tufts beneath dense heather. In other cases, however, and especially where grazing is a more consistent part of the treatment, the herbaceous element is more diverse, with species such as *Festuca ovina*, *Agrostis capillaris*, *A. canina*, *Nardus stricta*, *Potentilla erecta* and *Galium saxatile* becoming preferentially frequent in a distinctly grassier kind of heath. In the less oceanic climate characteristic of the range of this community, however, *Molinia caerulea* and *Carex binervis* hardly ever figure and *Blechnum spicant*, which is quite a frequent plant in some kinds of *Calluna-Erica* heath, is at most occasional. *Juncus squarrosus* can sometimes be found with some frequency and there are scattered records for *Pteridium aquilinum*, *Luzula pilosa*, *Trientalis europaea*, *Listera cordata* and *Lycopodium clavatum*. The rare *Diphasium* × *issleri*, now reckoned to be a hybrid between *D. alpinum* and *D. complanatum* (the latter not known from Britain) (Jermy *et al.* 1978), has been recorded from this community in the Morrone area of eastern Scotland (Huntley & Birks 1979*a*).

As in the *Calluna-Erica* heath, the ground layer of the vegetation is often prominent, with distinct patterns of colonisation in relation to the maturity of the heather and other sub-shrubs. Encrusting lichens, *Polytrichum piliferum* and *P. juniperinum* can be locally very abundant in the early years following burning, but again more characteristic of the community as a whole are bulky mosses such as *Dicranum scoparium*, *Pleurozium schreberi*, *Hypnum cupressiforme s.l.* (often obviously *H. jutlandicum*) and *Hylocomium splendens* which, together with larger *Cladonia* spp., make their maximum, and then often very luxuriant, contribution as the heather canopy opens up with age. Where there is atmospheric pollution, such species can become very sporadic in their occurrence, even where the sub-shrub cover is not dense, and the community includes some stands where there are minor losses of this kind, but, in the southern Pennines, where such pollution is particularly severe, impoverished stands of *Calluna* and the Vaccinia are best placed in the *Calluna-Deschampsia* heath where tolerant acrocarps such as *Pohlia nutans* and *Orthodontium lineare* make up the bulk of an often very sparse ground cover.

Sub-communities

***Calluna vulgaris* sub-community:** *Calluna* heath Ratcliffe 1959; *Callunetum vulgaris* McVean & Ratcliffe 1962 *p.p.*; *Calluna*-heath moss sociation Edgell 1969 *p.p.*; *Callunetum vulgaris typicum* Evans *et al.* 1977 *p.p.*; *Calluna vulgaris-Deschampsia flexuosa* nodum Huntley 1979 *p.p.*; *Vaccinio-Ericetum cinereae*, Typical subassociation Birse 1980 *p.p.*; *Calluna vulgaris-Vaccinium myrtillus* nodum Hughes & Huntley 1986. The vegetation here is typically species-poor, with *Calluna* usually overwhelmingly dominant and often regenerating vigorously after burning. Among such dense, and often quite tall, growth, other sub-shrubs are of low cover. *Vaccinium myrtillus* is very frequent and *Erica cinerea* fairly common, but they generally occur only as scattered plants in a sparse second tier to the canopy, and *Empetrum nigrum* ssp. *nigrum* is usually almost totally overwhelmed. *V. vitis-idaea* is also very scarce but it would probably be more frequent, even if not very abundant, were not so many of the stands from lower altitudes.

Other vascular associates are few. *Deschampsia flexuosa* occurs frequently, though typically as scattered and rather drawn-up individuals, and sparse plants of *Potentilla erecta* and *Pteridium aquilinum* are quite common, but other herbs are very infrequent and the grassier physiognomy found in some stands of *Calluna-Vaccinium* heath is never seen here. The ground cover, too, is usually not very extensive, though such typical community species as *Dicranum scoparium*, *Hypnum jutlandicum* and *Pleurozium schreberi* occur frequently as scattered shoots and there is occasionally some *Hylocomium splendens*, *Rhytidiadelphus loreus*, *Ptilidium ciliare* and *Cladonia impexa*.

***Vaccinium vitis-idaea-Cladonia impexa* sub-community:** *Callunetum vulgaris* McVean & Ratcliffe 1962 *p.p.*; *Calluna vulgaris-Vaccinium vitis-idaea* nodum Huntley & Birks 1979*a*; *Vaccinio-Ericetum cinereae*, Typical subassociation Birse 1980 *p.p.* This sub-community includes most of the richer stands of *Calluna-Vaccinium* heath in which heather, though still very much the

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general dominant, is frequently accompanied by *V. myrtillus*, *V. vitis-idaea* and *E. nigrum* ssp. *nigrum*, with occasional *Erica cinerea*. Often, these other sub-shrubs are present in small amounts, with sparse shoots scattered among a fairly uniform canopy of vigorous *Calluna* or with the more shade-sensitive stratified into a second tier, but in recently-burned stands or among degenerate heather which has begun to open up, one or more of them can show local abundance in diverse patchy mosaics of bushes and mats. Very occasionally, too, there can be a little *Arctostaphylos uva-ursi* or *Juniperus*.

As in the *Calluna* sub-community, herbs are usually sparse, with just scattered plants of *Deschampsia flexuosa* and occasional *Potentilla erecta*, *Juncus squarrosus* and *Blechnum spicant*, but bryophytes and lichens are more numerous than there and generally much more abundant. Bulky pleurocarps tend to be especially prominent with *Hylocomium splendens* becoming very common and, along with *Hypnum jutlandicum* and *Pleurozium schreberi*, forming large patches among the sub-shrub stools and over their decumbent branches. *Dicranum scoparium* remains very frequent and there is occasionally some *Rhytidiadelphus loreus*, *R. triquetrus*, *Polytrichum commune*, *Ptilidium ciliare* and *Barbilophozia floerkii*. Among the lichens, clumps of *Cladonia impexa* are particularly distinctive with occasional *C. uncialis*, *C. arbuscula* and *C. crispata* and, among the smaller species, there can sometimes be found *C. pyxidata*, *C. coccifera*, *C. squamosa* and *C. floerkeana*. *Hypogymnia physodes* also occurs quite commonly on old sub-shrub branches.

***Galium saxatile-Festuca ovina* sub-community:** *Callunetum vulgaris typicum* Evans *et al.* 1977 *p.p.*; *Calluna vulgaris-Deschampsia flexuosa* nodum Huntley 1979 *p.p.*; *Calluna vulgaris-Anemone nemorosa* nodum Huntley & Birks 1979; *Vaccinio-Ericetum cinereae*, *Viola riviniana* subassociation Birse 1980. In this sub-community, the dominance of *Calluna* is not nearly so overwhelming as in other kinds of *Calluna-Vaccinium* heath and, though the other sub-shrubs occur at least occasionally in a canopy that can be quite vigorous and tall, the total cover of the bushes is less than usual. Among this more open growth, it is the variety and abundance of herbs that catches the eye. *Deschampsia flexuosa* is frequently joined here by *Festuca ovina*, *Nardus stricta* and *Agrostis capillaris*, with occasional *A. canina*, *F. rubra*, *Anthoxanthum odoratum* and *Danthonia decumbens*, the first two in particular showing locally high cover but more usually occurring in mixtures with one or more of the others, ramifying more diffuse low covers of sub-shrubs or forming stretches of grassy sward between larger bushes. *Galium saxatile* and *Potentilla erecta* occur frequently as scattered plants among this ground and there is occasional *Carex pilulifera*, *Campanula rotundifolia* and *Polygala serpyllifolia*. Where this kind of heath extends on to soils which are somewhat less base-poor and impoverished this element may be further enriched by such species as *Lotus corniculatus*, *Lathyrus montanus*, *Succisa pratensis*, *Viola riviniana* and *Anemone nemorosa*, the local abundance of one or more of which can create a very distinctive effect (e.g. Huntley & Birks 1979*a*, Birse 1980).

Bryophytes remain quite varied in this sub-community, with *Rhytidiadelphus squarrosus* and *Pseudoscleropodium purum* joining the community species as low-frequency preferentials, but they are generally not so abundant as in the last, occurring often as rather open wefts ramifying among the grass culms. Lichens are also rather few and of low cover, with just occasional patches of *Cladonia impexa* and *C. arbuscula*.

Habitat

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

This is the commonest type of heather-dominated vegetation occurring at moderate altitudes outside the more oceanic parts of upland Britain. The community can be found, mostly between 200 and 600 m, throughout the western and northern regions of the country wherever the mean annual maximum temperature falls below 26 °C (Conolly & Dahl 1970) and it makes a locally important contribution to moorland vegetation on Dartmoor, through Wales and on the North York Moors. However, within this broadly-defined zone, the *Calluna-Vaccinium* heath is strongly concentrated in areas where the climate, and particularly the winter climate, is more severe, occurring most extensively through the central and north-east Highlands of Scotland, the central reaches of the Southern Uplands and the Northern Pennines, where, for the most part, mean annual maxima are less than 24 °C (Conolly & Dahl 1970), and February minima usually more than half a degree or so below freezing (Page 1982). Throughout these areas, rainfall is not everywhere very high: mostly, there are from 1000 to 1600 mm precipitation annually (*Climatological Atlas* 1952) with usually 160–180 wet days yr^{-1} (Ratcliffe 1968). But the general conditions are wet and cloudy and, in the harsh winters, there can be more than 40 days with snow lying.

It is such a regime that favours the rise to prominence here, among the *Calluna*, of the broadly-montane *Vaccinium myrtillus* and *Empetrum nigrum* ssp. *nigrum* (Bell &

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Tallis 1973) and the more specifically Arctic-Alpine *V. vitis-idaea* (Ritchie 1955*a*), sub-shrubs which are of restricted importance among the heaths of the warmer and less humid lowlands of Britain. In fact, even within the community, there is probably an element of climatically-related variation in the representation of these different species, particularly in the case of the more demanding *V. vitis-idaea*, which becomes, more quickly than the others, rather scarce towards lower altitudes and latitudes (as in many stands of the *Calluna* sub-community) but, by and large, it is in the *Calluna-Vaccinium* heath that this suite of species shows its first consistent rise to prominence.

The same species, too, more particularly the Vaccinia, also help distinguish this community, which falls within what Birse & Robertson (1976) called 'Boreal heather moor', from the *Calluna-Erica* heath, equivalent to their 'Atlantic heather moor', a community which largely replaces it through the more humid but equable lowlands and upland fringes of western Scotland. *V. vitis-idaea* is hardly ever found in that kind of vegetation and, though *Erica cinerea* and *V. myrtillus* occur in both communities, the balance between them shifts decisively from the former, which retains a measure of physiological activity through the winter (Bannister 1965, Gimingham 1972), to the latter with the move to a less oceanic climate. Where the two kinds of heath show some geographical overlap, as through parts of the Southern Uplands and the Grampians, they can often be separated altitudinally or by aspect, the *Calluna-Vaccinium* heath typically occupying the higher ground or the more shady north- and east-facing slopes. The same climatic change plays a part in the scarcity here of *Molinia*, generally a plant of the more equable lowlands, of *Blechnum spicant*, which is broadly Atlantic in its distribution, and of the Oceanic West European *Carex binervis*.

With the generally high rainfall and humidity, the soils beneath the *Calluna-Vaccinium* heath are typically kept moist throughout the year, but they are almost always free-draining, the scarcity of such plants as *Erica tetralix* and *Scirpus cespitosus* serving as a good marker of the but rare occurrences of the community over impeded profiles. Characteristically, this is a vegetation type of more acidic soils developed over shedding slopes, extending on to level ground where the substrate is sharply pervious, but occurring very often over hill slopes and valley sides, screes and crags of gentle to steep angle. Sometimes, the soils are strongly humic and, among boulders or rock crevices, they can amount to little more than fragmentary rankers, though such accumulations often provide very congenial conditions for the growth of *V. myrtillus* in this community. Frequently, however, and particularly on gentler slopes, the profiles are more mature, sometimes brown earths or brown podzolic soils, though generally humo-ferric podzols. Superficial pH is usually between 3.5 and 4.5 although in the *Galium-Festuca* sub-community in particular, this kind of heath can extend on to more mesotrophic brown soils when there is some small relief from the prevailingly calcifuge character of the flora. Local flushing of podzols by seepage from nearby base-rich rocks can produce a similar effect (Huntley & Birks 1979*a*, Birse 1980).

The range of soils able to support the *Calluna-Vaccinium* heath occurs widely through the cold, wet submontane zone, developing from a variety of more siliceous parent materials such as Silurian sandstones in Wales and the Southern Uplands, the Devonian Old Red Sandstones along the Welsh borders, Carboniferous sandstone up the Pennines and Oolite grits in the North York Moors, and on such rocks the community often marks out scarps and their associated talus slopes or dips free of impervious drift. It can be found, too, over some intrusive igneous rocks like the Lake District Borrowdale Volcanics and the granites of Dartmoor, Galloway and the Grampians. But in the east-central Highlands, where many of the most extensive tracts of this kind of heath occur, it is coarse glacio-fluvial gravels that provide the most distinctive substrate, particularly on the slopes of the terraced moraines in the haughlands above the limits of cultivation through Speyside and Deeside.

And it is in this region, too, that there has been some of the most widespread and continuous use of burning as a treatment for the regeneration of the vegetation. In the uplands, heather has probably long been an important element in the diet of certain cattle breeds but, over the last 200 years or so, it is sheep that have become the more important stock and, throughout its range, the *Calluna-Vaccinium* heath can be found in rough upland grazings, pastured generally in summer but also, in more sheltered situations, in winter too, when the heather and bilberry provide a valuable bite at a time when herbs are in short supply (e.g. MacLeod 1955). And since probably at least 1800, burning has been practised with varying degrees of regularity to curtail any regression to the scrub or woodland cleared for pasturing and to renew the sub-shrub growth (Gimingham 1972). But, increasingly after 1850 or so, efforts were made to capitalise on the rise in the red grouse population that followed the expansion of heathland and, in the North York Moors, parts of the Pennines, Cheviots and Southern Uplands, but especially through the east-central Highlands, this community forms a major element of grouse-moors that are still actively shot over.

Although heather shoots provide the main food of red grouse (Jenkins *et al.* 1963), such that there is a general relationship between bird density and the extent of vigorous *Calluna*, the factors relating the grouse and its

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environment are complex. Bigger and more successful populations of birds, for example, tend to occur on heaths underlain by less base-poor and oligotrophic substrates (Miller *et al.* 1966, Jenkins *et al.* 1967, Moss 1969) which may, though this is still uncertain, exert an influence by supporting heather of better food value (Moss *et al.* 1975). In fact, on many of the so-called 'rich' moors, it is the *Calluna-Arctostaphylos uva-ursi* heath rather than this community that occupies most of the ground, but among stands of the *Calluna-Vaccinium* heath, it is the *Galium-Festuca* sub-community, with its modest mesophytic element, that extends most often on to these more productive sites (Birse 1980).

However, on 'rich' and 'poor' moors alike, the need for a judicious regime of muirburn, as it is known in Scotland, to maintain high and healthy grouse stocks, was established early (Lovat 1911) and has been since confirmed in the continuing research on the bird and its environment (e.g. Picozzi 1968, Jenkins *et al.* 1970). In Scotland, burning can be carried out between 1 October and 15 April (exceptionally to the end of April in a wet season or to 15 May beyond 457 m) and, though better regeneration has been demonstrated in the north-east after autumn rather than spring burns (Miller & Miles 1970), March and early April have been the traditionally-favoured times in northern Scotland. The usual practice is to burn with the wind, although slower fires can be maintained by back-burning and, of course, the moisture content of the soil and vegetation also affect the intensity of the fire (Gimingham 1972). The size of the burn is of importance too, wider fires tending to be more intense (Hobbs & Gimingham 1984*a*). The crucial thing seems to be to aim for a ground temperature of less than 200 °C if possible, certainly below 400 °C, even short exposures to temperatures above which can be lethal to the heather stem bases (Whittaker 1960), while at the same time keeping the canopy temperature high enough to burn off the bulk of the above-ground material but not so high as to increase greatly the nutrient losses in smoke (Kenworthy 1964, Allen 1964, Evans & Allen 1971): 500 °C seems to be an optimal canopy temperature to satisfy these requirements (Gimingham 1972).

Where weather conditions remain more or less normal, it is the amount and disposition of the fuel that exert the major control over the temperature trends in a burn (Hobbs & Gimingham 1984*a*), both the maxima and the duration of high temperatures increasing with the age of the vegetation (Fritsch 1927, Kenworthy 1963). The biomass per unit area in *Calluna* increases at least until stands are about 20 years old and the material becomes increasingly woody with age (Gimingham 1972). But the vegetative regeneration of *Calluna*, which is generally relied upon as the means of replenishing the supply of food, is much impaired in plants which are more than 15 years old (Lovat 1911, Gimingham 1960, Kayll & Gimingham 1965, Miller & Miles 1970, Mohamed & Gimingham 1970) and there is also the general decline in the density of stems per unit area as stands age (Miller & Miles 1970). Ideally, then, burning is timed towards the close of the building phase in the heather life-cycle, when the regrowth is often 12–15 years old, though longer rotations are necessary in exposed situations or shorter ones in sheltered sites: an average canopy height of 30–38 cm seems to be a good upper limit (Gimingham 1972). And many small burns are better than few large ones, the optimal area being perhaps $\frac{1}{2}$–1 ha, with 2 ha as a maximum, and long thin strips, say 30 m wide, being preferable to rounded or squarish areas (Watson & Miller 1970, Gimingham 1972).

The well-managed grouse-moor thus consists of a mosaic of more or less even-aged stands of heather produced by regular burning to maximise the extent of nutritious pioneer and building regrowth and on many such sites most of the structural and floristic differences among the *Calluna-Vaccinium* heath can be related to this treatment. If vegetative regeneration proceeds well, vigorous sprouting from shoot clusters on the undamaged heather stools (Mohamed & Gimingham 1970) can establish a virtually complete cover by the fourth or fifth season after burning, occasionally even as early as the third (Gimingham 1972) and, as this thickens up to form a dense and even canopy, there is increasingly little opportunity for anything but a very limited contribution from other plants. The *Calluna* sub-community with its patchy lower tier of other shade-tolerant sub-shrubs, puny herbs and rather sparse bryophytes, includes many stands of this kind.

In the early stages of heather regeneration, however, and particularly where this phase is prolonged, the characteristic associates of the community can play a more prominent role. Where older stands have been burned, for example, the more intense heat produced by the combustion of much very woody material, and the inherently poorer sprouting capacity of the aged stools (Mohamed & Gimingham 1970), makes for very slow vegetative recovery. And, though *Calluna* could be said to have fire-adapted sexual regeneration, benefiting from the light and open compacted surface, and perhaps also from the heat-treatment of the seeds previously stored in the congenially humid litter and soil (Gimingham 1972), recolonisation by seeding alone can be very slow (Hobbs & Gimingham 1984*b*). As in other heath communities, damp peaty surfaces may develop first a covering of algae and then a thin skin of *Lecidea uliginosa* and *L. granulosa*, followed by *Cladonia* spp. and locally extensive patches of *Polytrichum piliferum* and *P. juniperinum*. But often very noticeable here is the rapid spread of the Vaccinia and *Empetrum*, whose

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buried rhizomes can largely escape the effects of fire, the intense heat from which may scarcely penetrate the soil (Hobbs & Gimingham 1984*a*). So, much more variegated covers of sub-shrubs can develop, only slowly becoming stratified and patchy as the heather gradually assumes dominance once more. And, over the accumulating litter, there spread patches of the bulky pleurocarpous mosses and *Cladonia impexa*. It is stands such as this which predominate in the *Vaccinium-Cladonia* sub-community, together with older tracts of *Calluna-Vaccinium* heath where degeneration of the heather bushes has allowed a resurgence of these associates in the gaps.

A different trend of development involves a marked spread of *Deschampsia flexuosa* in the early post-burn succession and, particularly where the humic top-soil is very thin or has been totally burned off, this may be accompanied by other grasses like *Festuca ovina*, *F. rubra*, *Agrostis capillaris*, *A. canina* and *Danthonia*, and herbs such as *Potentilla erecta* and *Galium saxatile*, with the sub-shrubs eventually spreading among them, creating the characteristic flora of the *Galium-Festuca* sub-community, further enrichment occurring where the soils are a little more fertile than usual or flushed.

Very frequently these processes of recovery are subject to the additional and immediate influence of grazing: most burned stands of the *Calluna-Vaccinium* heath are open to stock and wild herbivores and indeed, though moors are often managed primarily for either grouse-rearing or pasturing, the two activities are frequently combined. Even where stock-rearing predominates, regular burning is often practised because although prudent moderate grazing alone ought to be able to maintain a productive cover of heather in this vegetation, this is hardly ever possible to achieve (Gimingham 1972). It was perhaps more likely in former times when small-scale mixed farming predominated in the uplands, with cattle being pastured instead of or along with sheep. But with the widespread shift to the heavy and more selective grazing of hardy sheep breeds, introduced into Scotland from the late 1700s, the productivity of heath vegetation declined and the occasional fires that had probably long been employed to set back tree invasion were replaced in many areas by more regular burning, often on a ten-year rotation (Gimingham 1972).

Provided it is not too heavy, grazing in the early stages of regeneration can speed the development of a closed canopy, though it certainly has marked effects on its proportional composition. Though *Calluna* is palatable, for example, grazing often induces plagiotrophic growth and the adoption of a semi-prostrate habit which may put it at an advantage here over *Vaccinium myrtillus* or the less common *Erica cinerea* (Gimingham 1949). In other situations, preferential grazing may allow the spread of the less palatable *V. vitis-idaea* or *Empetrum nigrum*, and substantial variations in all these sub-shrubs, developed in response to grazing, can be seen in the *Vaccinium-Cladonia* sub-community.

On less peaty soils, and particularly where these are tending towards podzolised brown earths, grazing often favours the maintenance of the grassy composition typical of the *Galium-Festuca* sub-community and this kind of *Calluna-Vaccinium* heath can also include mosaics of sub-shrubs and sward well on their way towards becoming better quality Nardo-Galion grasslands in a grazing-mediated succession that is generally welcomed by upland farmers. *Calluna-Vaccinium* heaths with quite abundant *Festuca ovina* and *Agrostis canina* can also extend on to podzols, but where heavy grazing follows burning on less fertile soils here, it is *Nardus stricta* or sometimes *Juncus squarrosus* that tend to increase their cover. Stands with moderate amounts of these unpalatable monocotyledons can be grouped in the *Galium-Festuca* sub-community but vegetation in which they become dominant at the expense of the sub-shrubs belongs in the relevant grassland types.

Zonation and succession

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

The clearest soil-related sequences are seen where the free-draining brown earths or podzols which typically underlie the *Calluna-Vaccinium* heath give way to seasonally-gleyed base-poor soils such as stagnopodzols or gley-podzols. Such zonations sometimes reflect the distribution of impervious drift over otherwise fairly uniform ground but they are often disposed over slopes which are increasingly gentle and, in areas of higher rainfall, this kind of sequence can run on over accumulations of ombrogenous peat. In such situations, the shift on to periodically-waterlogged ground is typically marked by a transition to Ericion tetralicis wet heath. Through the heartland of the *Calluna-Vaccinium* heath, in the east-central Highlands, down through south-east Scotland to the North York Moors, such vegetation is generally represented by the *Juncus-Dicranum* sub-community of the *Ericetum tetralicis*, in which the most characteristic changes are the appearance of *Erica tetralix* and *Scirpus cespitosus* with patchy *Molinia caerulea* and, in more intact stands, some *Sphagnum compactum* and *S. tenellum*. In fact, however, many tracts of this vegetation on grouse-moors and within hill-grazings are also subject to burning and pasturing, which can favour

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the extension across the soil-related boundaries of fairly uniform canopies of heather, impoverished throughout, or, where the treatments have been especially frequent or severe, a progressive run-down with a spread of *Juncus squarrosus* among a much-reduced cover of sub-shrubs, patterns well seen over some tracts of the North York Moors. This is sometimes a prelude to the development of wet *Juncus-Festuca* grassland though, in the less oceanic uplands, such vegetation tends to be rather local and often related to the occurrence of modest flushing among sequences of dry and wet heaths.

Mosaics of these communities can sometimes be seen over the redistributed peat washed down from the eroding margins of blanket bogs over the high plateaus and watersheds of the uplands or extending on to the shallow intact peat of the bog plane proper where the fringes have become dry. But more complete sequences run on from impeded peaty soils to ombrogenous peats with Erico-Sphagnion vegetation, typically of the *Calluna-Eriophorum* type with its often rather limited *Sphagnum* cover but continuing strong representation of sub-shrubs and bulky pleurocarps over its drier stretches. This kind of pattern can be seen on the grandest scale in the Cairngorms, with the various vegetation types disposed in roughly altitudinal zones over the massively-domed granite mountains (Watt & Jones 1948) but it is visible too in the Moffat and Moorfoot Hills in the Southern Uplands (Ward *et al.* 1972*b*, Ratcliffe 1977, Hill & Evans 1978), the Cheviots and in the unpolluted parts of the Pennines (Tansley 1911, 1939).

Such zonations form a pattern analogous to that seen in the more oceanic parts of western Britain, where the communities are generally replaced by the *Calluna-Erica* dry heath, the *Scirpus-Erica* wet heath and the *Scirpus-Eriophorum* mire. However, the geographical separation of these sequences is not complete and, where there is some overlap in their ranges, as in parts of the Southern Uplands, the drier sub-shrub communities generally partition according to altitude or aspect. The *Calluna-Vaccinium* heath, for example, can be found within the more oceanic zonation in the Moffat Hills and Galloway on higher crags or over slopes with a northerly or easterly aspect; conversely, the *Calluna-Erica* heath sometimes finds a place in the east-central Highlands on south-facing slopes at lower altitudes. Such shifts are to a great extent a reflection of the competitive balance between *Calluna* and *E. cinerea* or the Vaccinia (Figure 28).

Other topoclimatic shifts can be seen in the east-central Highlands too. Where conditions are particularly cold and humid, as around the steep and largely sunless corries on the northern slopes of the Cairngorms, the *Calluna-Vaccinium* heath is itself replaced by the *Vaccinium-Rubus chamaemorus* heath, a widespread community of the north-west and central Highlands but in the latter area often distinctly chionophilous, growing on humic rankers kept wet by long snow-lie. The appearance of *R. chamaemorus* with scattered *Cornus suecica* among the sub-shrubs and of patchy *Sphagnum capillifolium* are good indicators of this transition. Then, in more exposed situations, where rankers and podzols extend over ridges and summits, the *Calluna-Vaccinium* heath gives way to the *Calluna-Cladonia* heath in which the sub-shrub cover is often very dwarfed and where fruticose *Cladonia* spp., of restricted importance in the *Calluna-Vaccinium* heath, together with other large lichens, can be very varied and abundant.

Arctostaphylos uva-ursi sometimes figures locally in such transitions but it is much better represented in zonations and mosaics with *Calluna-Vaccinium* heath at lower altitudes through the east-central Highlands. There, the *Calluna-A. uva-ursi* heath has a very similar altitudinal and geographical range to this community and it is possible that burning has some role in mediating switches from one vegetation type to the other. But the *Calluna-A. uva-ursi* heath is also more consistently associated with less-impoverished soils, typically acidic but often with moder humus rather than mor (McVean & Ratcliffe 1962, Birse 1980), so a combination of treatment and edaphic factors may be responsible for the distribution of the two.

The other widespread interaction between these variables involves transitions to Nardo-Galion grasslands, which are especially likely to develop where there has been grazing in the early stages of post-burn recovery. Then the appearance of the *Galium-Festuca* sub-community may presage a succession to the *Festuca-Agrostis-Galium* grassland, the major plagioclimax pasture of base-poor soils through the upland fringes. Sub-shrubs typically have low frequency and cover in that vegetation but moderately heavy grazing may produce a more or less permanently-maintained mosaic of patches of heath among a grassy ground, or sporadic pasturing sustain a shifting balance of the elements in a more labile pattern with all shades of intermediate vegetation, something well seen in the accounts of Scottish grazings by King (1962) and King & Nicholson (1964). In many sites, however, continuous heavy grazing has favoured a progressive loss of sub-shrub vegetation to grassland, something which, over more fertile brown soils, is usually welcomed by graziers, though not by those with an interest in grouse, the numbers of which decline as the heather cover is reduced (e.g. Yalden 1972, Hewson 1977, Anderson & Yalden 1981). The constant danger in such situations, however, is the spread of *Pteridium aquilinum* which, particularly where the vigour of *Calluna* is reduced by the burning and grazing of *Calluna-Vaccinium* heath over colluvial soils or well-drained drift, is likely to invade vigorously, producing dense

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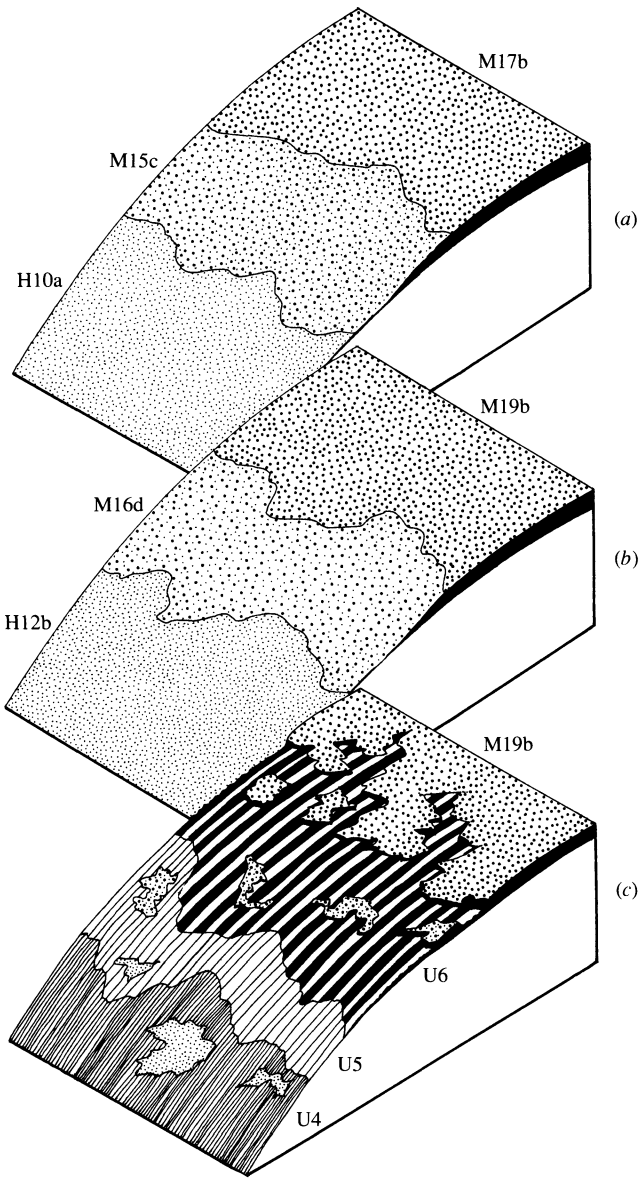
Figure 28. Heath/mire zonations on the drier fringes of blanket bogs in (*a*) more atlantic north-west of Britain and (*b*) more boreal eastern Highlands of Scotland, with (*c*) the fragmentation of heath and mire in the latter with erosion and grazing.
H10a *Calluna-Erica* heath, Typical sub-community
H12b *Calluna-Vaccinium* heath, *Vaccinium-Cladonia* sub-community
M15c *Scirpus-Erica* wet heath, *Cladonia* sub-community
M16d *Ericetum tetralicis*, *Juncus-Dicranum* sub-community
M17b *Scirpus-Eriophorum* mire, *Cladonia* sub-community
M19b *Calluna-Eriophorum* mire, *Empetrum* sub-community
U4 *Festuca-Agrostis-Galium* grassland
U5 *Nardus-Galium* grassland
U6 *Juncus-Festuca* grassland



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stands of the *Pteridium-Galium* community within which sparse sprigs of the shade-tolerant Vaccinia may represent the limit of sub-shrub survival.

Over less fertile peaty podzols, heavy grazing may result in the no less difficult problem of the expansion of *Nardus stricta* and the development of the *Nardus-Galium* grassland with its poor grazing potential. The kind of pattern seen so well in the map of Moor House in Cumbria (Eddy *et al.* 1969) is now very typical of many upland areas outside the grouse-moors: there, the zonation runs down from blanket bog on the high watershed, impoverished *Eriophorum* mire in many places, through a mosaic of *Nardus-Galium* and *Juncus-Festuca* grasslands, to *Festuca-Agrostis-Galium* swards, with ericoids making only a sparse appearance over inaccessible crags and screes. In extreme situations, heavy grazing may prevent the establishment of any vegetation cover on burned tracts of the *Calluna-Vaccinium* heath and where, by accident or mismanagement, fires have got out of hand and burned deep into the surface humus or even down to the mineral horizons beneath, such a combination of circumstances may be disastrous, triggering erosion by rain run-off or gully-erosion (Gimingham 1972, Maltby 1980, Maltby & Legg 1983).

Burning and grazing are so widespread throughout the range of the *Calluna-Vaccinium* heath that, alone or in combination, they effectively maintain this kind of sub-shrub vegetation as a deflected climax which has little opportunity to progress to woodland, though there is little doubt that, except where it attains higher altitudes or occurs in rather more exposed situations, this would be the natural trend. And, in the centre of its range, through the east-central Highlands, such developments would be likely to involve the invasion of pine and birch, often with juniper as a precursor or coincidental colonist. All these species are well able to take advantage of the open conditions established after fires, or even of scuffed areas in broken stretches of turf among the *Calluna-Vaccinium* heath, but the seedlings are very palatable and, where they are not eaten off, are soon crowded out by the regenerating sub-shrubs or herbs and any further germination, a light-dependent process in these plants, precluded (Miles & Kinnaird 1979, Gilbert 1980). With the widespread clearance of woodland, there is also often the problem of the remoteness of seed-parents, particularly critical in the case of pine. Nonetheless, fragments of woody vegetation survive quite widely on crags or in ravines within tracts of the *Calluna-Vaccinium* heath and over the terraced slopes through Speyside and Deeside there can be found some more extensive mosaics of the community with *Juniperus-Oxalis* scrub and *Pinus-Hylocomium* woodland (McVean & Ratcliffe 1962, Ratcliffe 1974, Huntley & Birks 1979*a*, *b*): indeed, it is patchworks of these vegetation types, often with *Calluna-A. uva-ursi* heath, that comprise the 'Caledonian pine forest' in its broad landscape sense. In such patterns, the floristic similarities of the communities are eminently clear and, in many respects, the heath represents the field layer of more open stretches of scrub and woodland without the shrubs and trees. In this part of Britain at least, the *Calluna-Vaccinium* heath seems to have been derived by clearance of mixed forest of pine, birch and juniper whose elements are now to be seen in largely fragmentary form (McVean & Ratcliffe 1962, O'Sullivan 1977). And the increased and long-continued abundance of *Calluna* in the vegetation which has largely replaced this forest has probably contributed to enhanced podzolisation in the soils (Gimingham 1972, Fitzpatrick 1977), a further factor perhaps in the difficulty of re-establishment of the original kind of climax vegetation.

Elsewhere through the range of the *Calluna-Vaccinium* heath, the community is sometimes found in association with *Juniperus-Oxalis* scrub but, wherever there is any opportunity for seral progression, it is generally birch, usually *Betula pubescens* but locally with *B. pendula*, that is the leading colonist and this can quickly form dense thickets from which the less shade-tolerant heath plants are soon extinguished. Where more mature woodland is able to develop, among which oak can eventually find a place, usually *Quercus petraea* but with *Q. robur* sometimes seeding in from planted stock, it is typically of the *Quercus-Betula-Dicranum* type, with the *Quercus-Betula-Oxalis* woodland locally represented over less infertile soils. Conifers often invade neglected heaths from plantations and can figure in such woodlands and, in places such as the North York Moors, many of the slopes which might carry *Calluna-Vaccinium* heath have been afforested with softwoods or, where unburned, have become covered by scrub in which such trees predominate.

Distribution

The *Calluna-Vaccinium* heath is widely distributed through the less oceanic parts of the sub-montane zone, being particularly extensive in the east-central Highlands but also important in south-east Scotland, the Lake District, parts of Wales and the South-West Peninsula and the North York Moors. It would probably be more extensive in drier areas like the last, and certainly through the Southern Pennines, had not pollution been so severe: here it is largely replaced by the *Calluna-Deschampsia* heath.

Affinities

In many descriptive accounts (e.g. Smith & Rankin 1903, Smith & Moss 1903, Lewis & Moss 1911, Ratcliffe 1959*a*, McVean & Ratcliffe 1962, Evans *et al.* 1977), this vegetation has been grouped in a compendious *Callunetum*, with often only tentative separation from its oceanic equivalent, the *Calluna-Erica* heath, and of course

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with regular burning both communities tend to converge into species-poor stands of heather. But the distinction between these two noted by Muir & Fraser (1940) and Gimingham (1972) seems to be a valid one, both in terms of the floristics of more species-rich stands and their habitat relationships: the *Calluna-Vaccinium* heath belongs fairly clearly among Böcher's (1943) Scano-Danish (Scotch) series and can be included within the 'Boreal heather moor' of Birse (1980).

In Birse's scheme, however, this last vegetation type also takes in some of what is in this scheme separated off into the *Calluna-A. uva-ursi* heath. Certainly, as McVean & Ratcliffe (1962) acknowledged, the relationship between the communities is very close and perhaps partly treatment-mediated. But, on balance, it seems best to retain separate units for these vegetation types while placing them both as close relatives within the Myrtillion boreale alliance.

Floristic table H12

	a	b	c	12
Calluna vulgaris	V (8–10)	V (6–10)	V (4–10)	V (4–10)
Vaccinium myrtillus	V (1–4)	V (1–8)	V (1–6)	V (1–10)
Hypnum jutlandicum	V (1–8)	V (1–8)	V (1–8)	V (1–8)
Dicranum scoparium	V (1–5)	V (1–6)	IV (1–6)	IV (1–6)
Pleurozium schreberi	IV (1–8)	IV (1–8)	IV (1–6)	IV (1–8)
Deschampsia flexuosa	IV (1–4)	IV (1–4)	IV (1–6)	IV (1–6)
Hylocomium splendens	II (1–8)	IV (1–9)	III (1–9)	III (1–9)
Cladonia impexa	II (1–4)	IV (1–8)	II (1–4)	III (1–8)
Vaccinium vitis-idaea	I (1–3)	IV (1–6)	III (1–4)	III (1–6)
Ptilidium ciliare	I (1–3)	II (1–4)	I (1)	II (1–4)
Cladonia pyxidata	I (1–3)	II (1–4)	I (1–3)	II (1–4)
Cladonia uncialis	I (1–3)	II (1–4)	I (1–6)	II (1–6)
Polytrichum commune	I (1–4)	II (1–4)	I (1–4)	II (1–4)
Cladonia coccifera	I (1–3)	II (1–3)	I (1–3)	I (1–3)
Cladonia squamosa	I (1–3)	II (1–4)	I (1–3)	I (1–4)
Juniperus communis		II (1–3)	I (1–3)	I (1–3)
Scirpus cespitosus	I (1–4)	II (1–4)		I (1–4)
Potentilla erecta	III (1–4)	II (1–4)	IV (1–4)	III (1–4)
Galium saxatile	I (1–3)	I (1–3)	IV (1–3)	II (1–3)
Festuca ovina	I (1–3)	I (1–3)	IV (1–6)	II (1–6)
Nardus stricta	I (1–4)	I (1–4)	III (1–4)	II (1–4)
Agrostis capillaris	I (1–4)	I (1–3)	II (1–4)	I (1–4)
Carex pilulifera	I (1–2)	I (1–3)	II (1–4)	I (1–4)
Festuca rubra	I (1–4)	I (1–3)	II (1–6)	I (1–6)
Agrostis canina	I (1–3)	I (1–3)	II (1–4)	I (1–4)
Rhytidiadelphus squarrosus	I (1–4)	I (1–3)	II (1–4)	I (1–4)
Campanula rotundifolia	I (1–3)	I (1–3)	II (1–3)	I (1–3)
Pseudoscleropodium purum	I (1–4)	I (1–3)	II (1–4)	I (1–4)
Danthonia decumbens	I (1–3)		II (1–4)	I (1–4)
Polygala serpyllifolia	I (1–3)		II (1–3)	I (1–3)
Anthoxanthum odoratum	I (1–3)		II (1–6)	I (1–6)
Lotus corniculatus	I (1)		II (1–4)	I (1–4)
Succisa pratensis	I (1–3)		II (1–4)	I (1–4)
Viola riviniana	I (1–3)		II (1–3)	I (1–3)
Lathyrus montanus	I (1)		II (1–4)	I (1–4)
Erica cinerea	III (1–6)	II (1–6)	III (1–6)	III (1–6)
Empetrum nigrum nigrum	I (1–6)	III (1–6)	II (1–4)	III (1–6)

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Floristic table H12 *(cont.)*

	a	b	c	12
Juncus squarrosus	I (1–4)	II (1–4)	II (1–4)	II (1–4)
Hypogymnia physodes	I (1–3)	II (1–4)	II (1–6)	II (1–6)
Rhytidiadelphus loreus	II (1–4)	II (1–4)	I (1–4)	II (1–4)
Cladonia arbuscula	I (1–4)	II (1–8)	II (1–4)	II (1–8)
Blechnum spicant	I (1–3)	II (1–3)	II (1–4)	II (1–4)
Pteridium aquilinum	II (1–6)	I (1)	I (1)	I (1–6)
Barbilophozia floerkii	I (1–3)	II (1–4)		I (1–4)
Cladonia crispata	I (1)	I (1–4)	I (1)	I (1–4)
Rhytidiadelphus triquetrus	I (1–3)	I (1–4)	I (1–6)	I (1–4)
Pohlia nutans	I (1–4)	I (1–4)	I (1–3)	I (1–4)
Lophocolea bidentata	I (1–4)	I (1–3)	I (1–3)	I (1–4)
Lycopodium clavatum	I (1–3)	I (1–3)	I (6)	I (1–6)
Luzula pilosa	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Cladonia floerkeana	I (1)	I (1–3)	I (1)	I (1–3)
Trientalis europaea	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Calypogeia muellerana	I (1)	I (1–3)	I (1–3)	I (1–3)
Plagiothecium undulatum	I (1–6)	I (1–4)	I (1–3)	I (1–6)
Lophozia ventricosa	I (1–3)	I (1–3)	I (1)	I (1–3)
Thuidium tamariscinum	I (1–4)	I (1–3)	I (1–4)	I (1–4)
Listera cordata	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Sorbus aucuparia seedling	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Erica tetralix	I (1–4)	I (1–4)	I (1–4)	I (1–4)
Cladonia chlorophaea	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Cladonia gracilis	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Molinia caerulea	I (1–4)	I (1–3)	I (1–6)	I (1–6)
Empetrum nigrum hermaphroditum	I (1–4)	I (1–4)		I (1–4)
Eriophorum vaginatum	I (1)	I (1–4)		I (1–4)
Polytrichum alpestre	I (1–3)	I (1–3)		I (1–3)
Dicranum fuscescens		I (1–4)	I (1–3)	I (1–4)
Cladonia rangiformis		I (1–3)	I (1–3)	I (1–3)
Arctostaphylos uva-ursi		I (1–3)	I (1–3)	I (1–3)
Anemone nemorosa	I (1)		I (1–4)	I (1–4)
Number of samples	56	167	78	311
Number of species/sample	14 (9–28)	21 (4–42)	19 (5–36)	17 (4–42)
Shrub/herb height (cm)	31 (9–75)	23 (8–60)	21 (7–50)	25 (7–75)
Shrub/herb cover (%)	97 (85–100)	92 (70–100)	88 (40–100)	92 (40–100)
Ground layer height (mm)	36 (10–90)	35 (10–100)	39 (10–150)	37 (10–150)
Ground layer cover (%)	18 (0–100)	65 (0–100)	43 (0–100)	60 (0–100)
Altitude (m)	353 (77–724)	494 (274–910)	412 (105–845)	446 (77–910)
Slope (°)	21 (0–45)	13 (0–85)	23 (0–80)	18 (0–85)
Soil pH	4.4 (3.5–6.0)	4.4 (3.3–6.0)	4.5 (3.4–6.1)	4.4 (3.3–6.1)

a *Calluna vulgaris* sub-community
b *Vaccinium vitis-idaea-Cladonia impexa* sub-community
c *Galium saxatile-Festuca ovina* sub-community
12 *Calluna vulgaris-Vaccinium myrtillus* heath (total)

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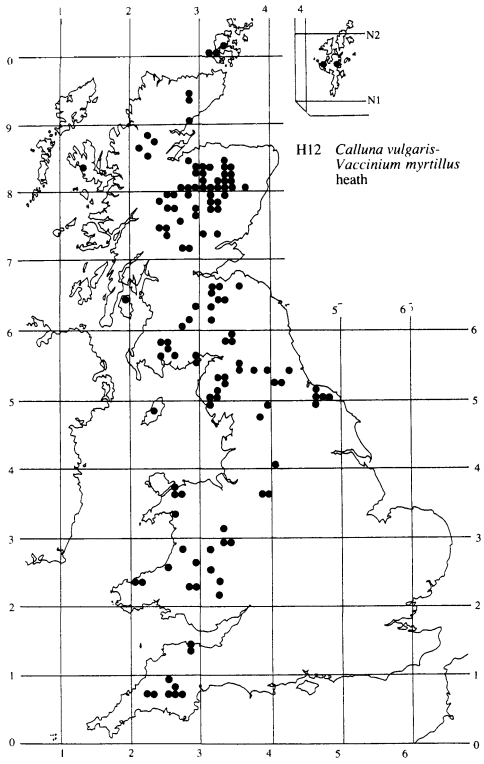

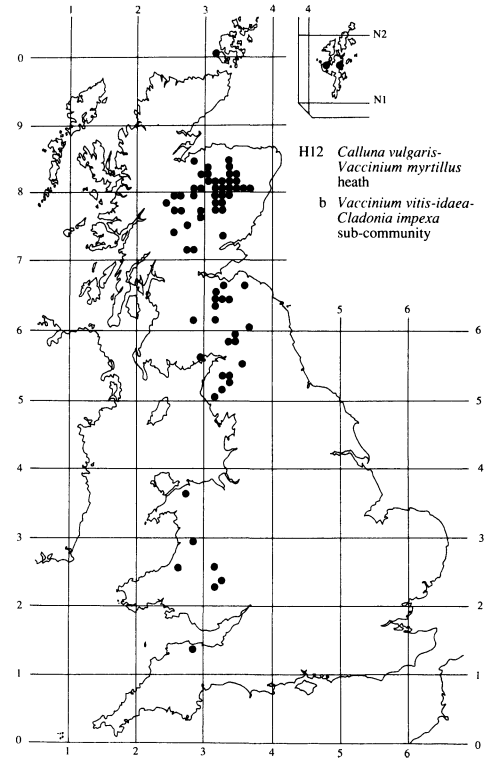

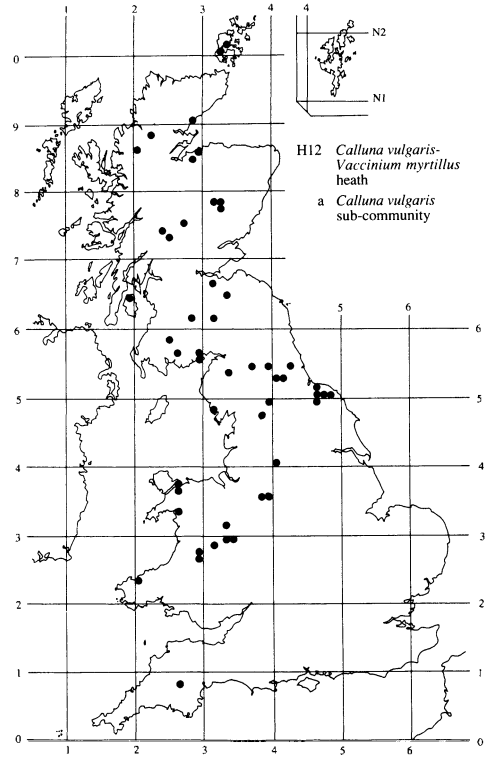

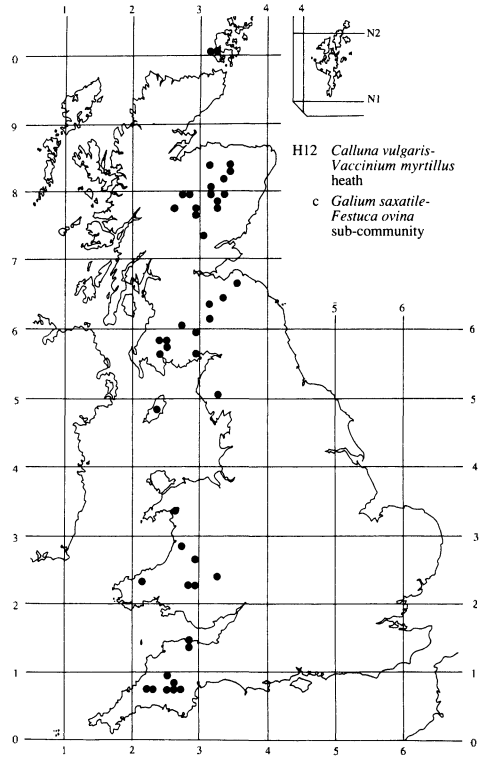

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