M16
Erica tetralix-Sphagnum compactum wet heath
Ericetum tetralicis Schwickerath 1933

Synonymy
Molinietum caeruleae Rankin 1911*b*, Tansley 1939 *p.p.*; *Molinia* consocies Summerhayes & Williams 1926; Submoorland heath Muir & Fraser 1940 *p.p.*; *Gentiana pneumonanthe* localities Simmonds 1946; Damp heath Rose 1953; Wet heath Rose 1953, Rutter 1955, Newbould 1960, Ivimey-Cook & Proctor 1967; Three-species heath Williams & Lambert 1959; *Calluna-Erica tetralix* wet heath Gimingham 1964 *p.p.*, Bannister 1966 *p.p.*; *Ericetum tetralicis boreoatlanticum* Ivimey-Cook *et al.* 1975; *Campylopo-Ericetum tetralicis* Birse & Robertson 1976 *p.p.*; Mire noda 1–5 Daniels 1978 *p.p.*; *Narthecio-Ericetum tetralicis* Moore (1964) 1968 *sensu* Birse 1980 *p.p.*

Constant species
Calluna vulgaris, *Erica tetralix*, *Molinia caerulea*, *Sphagnum compactum*.

Rare species
Erica ciliaris, *Gentiana pneumonanthe*, *Lepidotis inundata*, *Rhynchospora fusca*.

Physiognomy
The *Ericetum tetralicis* is characteristically dominated by mixtures of *Erica tetralix*, *Calluna vulgaris* and *Molinia caerulea*, but the proportions of these are very variable, being influenced by differences in the water regime and trophic state of the soils, and also by grazing and burning, the last factor being able to transform the appearance of particular stands over short periods of time and producing great structural diversity within a small compass (e.g. Williams & Lambert 1961). *E. tetralix* often grows very vigorously here, typically on these wetter soils adopting a semi-prostrate habit (Bannister 1966). *Calluna*, on the other hand, is often subordinate and of somewhat weak growth (Gimingham 1972), though it can become abundant in drier stands or where there has been deliberate encouragement by controlled burning. In other situations, *Molinia* is very much the dominant, with the ericoids reduced to sparsely-scattered bushes among dense tussocks of the grass, such that some accounts of the community have grouped it within a broadly-defined *Molinietum* (Rankin 1911*b*, Summerhayes & Williams 1926, Tansley 1939).

Typically, however, no other sub-shrubs attain high frequency through the community as a whole, though some can be of local importance. Thus, *Erica cinerea* and *Ulex gallii* figure occasionally, and sometimes with local abundance, in transitions to drier heaths in south-west England, and *E. cinerea* and *U. minor* can occur in similar situations further east. More strikingly, around Poole Harbour and in Cornwall, the *Ericetum* provides one of the loci for the nationally-rare *E. ciliaris* and its hybrids with *E. tetralix* (= *E.* × *watsonii* Benth.: Chapman 1975). *U. europaeus* can also be found occasionally on less impoverished soils and can spread within the community in drier, disturbed situations.

As defined here, the *Ericetum tetralicis* includes vegetation in which there are no species other than the three vascular constants or very few sporadic associates. Such impoverished heaths are of wide distribution through lowland Britain and, though difficult to place on floristic grounds alone, have often been fairly obviously derived from this community by, for example, frequent uncontrolled burning and/or draining. However, although the *Ericetum* is at best only moderately species-rich, there are typically some additional plants. Most characteristic of these are the two Sphagna, *S. compactum*, which is a fairly strong preferential for the community and particularly associated with drier situations, and *S. tenellum*, less diagnostic and usually marking out wetter places. In some stands, these occur as scattered cushions; in others, they can form a virtually continuous carpet between the *Molinia* and ericoids, though they do not accumulate thick peat. *S. subnitens* and *S. cuspidatum* also occur very occasionally throughout and *S. molle*, though not common, shows fairly high fidelity to this community which provides its main locus in south-

eastern Britain. Then, in different kinds of *Ericetum*, there can be some *S. auriculatum*, *S. papillosum* or *S. capillifolium*. The abundance of all these species is strongly influenced by burning but, in stands not recently fired, the balance between them can be of some value in setting the limits of the community: in transitions to the *Narthecio-Sphagnetum*, which is often surrounded by the *Ericetum* in lowland valley mires, there is generally an obvious switch to a luxuriant dominance of *S. papillosum* and *S. auriculatum* or *S. recurvum* (seen especially well in the tables of Newbould 1960 and Ivimey-Cook *et al.* 1975; see also Rose 1953).

No other bryophytes are as common throughout the community as the two characteristic Sphagna but there are occasional records for *Hypnum jutlandicum*, *Leucobryum glaucum*, *Campylopus paradoxus*, *C. pyriformis*, *Pohlia nutans*, *Pleurozium schreberi*, *Gymnocolea inflata*, *Cephalozia connivens*, *C. bicuspidata*, *Odontoschisma sphagni* and *O. denudatum*, in wetter situations for *Kurzia pauciflora* and *Campylopus paradoxus*, and in drier stands for *Dicranum scoparium* and *Racomitrium lanuginosum*. *Hypnum imponens* and *Dicranum spurium* are two mosses of rather local distribution in Britain which can sometimes be found here. Intermixed with bryophytes, there are also quite frequently some lichens, especially larger *Cladonia* spp. *C. impexa* and *C. uncialis* are the commonest of these but one or more of the following occur quite often: *C. arbuscula*, *C. floerkeana*, *C. squamosa*, *C. furcata* and *C. verticillata*.

The canopy of the three vascular constants, generally a few decimetres high at most and often rather open, and the ground cover of bryophytes and lichens, make up the more consistent structural elements of the vegetation, but there are frequently some herbaceous associates. *Scirpus cespitosus* is the commonest of these overall and the *Ericetum* provides the major locus for this plant in south-east Britain, as it does for *Eriophorum vaginatum*, though this is much scarcer in the community. *E. angustifolium* and *Narthecium ossifragum* also occur quite frequently and *Drosera rotundifolia* (sometimes accompanied by *D. intermedia*) can be found in wetter hollows, these species providing a strong floristic link with the *Narthecio-Sphagnetum*. Then, there is occasionally some *Polygala serpyllifolia*, *Potentilla erecta*, *Carex panicea*, *C. echinata*, *Juncus squarrosus*, *Pedicularis sylvatica* and *Dactylorhiza maculata* with, in some of the sub-communities, distinctive enrichment with preferential herbs. *Gentiana pneumonanthe*, a nationally rare species with a disjunct distribution through southern Britain, is almost always found in this community in this country (in contrast to the European mainland where it has more catholic affinities), seeming to prefer growing among bushes of *E. tetralix* and low *Calluna* and avoiding dense, tussocky *Molinia* (Simmonds 1946). *Rhynchospora fusca* and *Lepidotis inundata* are two other rarities which occur in one particular kind of *Ericetum*.

Finally, the community can have some representation of taller woody species. *Myrica gale* occurs occasionally, sometimes with local abundance and, where *Molinia* is also prominent beneath, the vegetation can take on the appearance of a '*Molinia-Myrica* mire': some stands of this kind were perhaps included in the *Myricetum gale* of Wheeler (1980*c*) and the *Molinia/Myrica/Erica tetralix* bog of the NCC New Forest Bogs Report (1984). Then, there can also be some seedlings and saplings of *Betula* spp., usually *B. pubescens* but with *B. pendula* on drier substrates, and of *Pinus sylvestris*, often spreading from nearby plantations.

Sub-communities

Typical sub-community: *Molinietum caeruleae* Rankin 1911*b*, Tansley 1939 *p.p.*; *Molinia* consocies Summerhayes & Williams 1926; *Gentiana pneumonanthe* localities 1–7, 13, 18–19 Simmonds 1946; Damp heath Rose 1953; Wet heath Rose 1953, Rutter 1955, Newbould 1960, Ivimey-Cook & Proctor 1967 *p.p.*; Three-species heath Williams & Lambert 1959; *Ericetum tetralicis boreoatlanticum* Ivimey-Cook *et al.* 1975; Mire noda 1, 2 & 4 Daniels 1978 *p. p.* In this, the most widespread form of the *Ericetum tetralicis* throughout the southern part of the range of the community, all the variations in the proportions of *Molinia*, *E. tetralix* and *Calluna* can be found, so the gross appearance of the vegetation is very diverse (e.g. Rose 1953, Williams & Lambert 1959, 1961). Where stands have not been recently burned but have a fairly open cover of the dominants, *Sphagnum compactum* and *S. tenellum* can both be very frequent and often abundant, sometimes with a little *S. cuspidatum*, *S. auriculatum*, *S. papillosum* and *S. subnitens* and, more locally, *S. molle* in wetter places. *Hypnum jutlandicum* and *Kurzia pauciflora* are the commonest species among the other bryophytes though, in some areas, *Campylopus brevipilus* becomes very consistent (as in the samples from Aylesbeare Common in Devon included in Ivimey-Cook *et al.* 1975). Lichens, particularly *Cladonia impexa*, can also be frequent and, where the vegetation around lowland valley mires is strongly zoned, there is sometimes a tendency for this element to become more abundant and diverse in moving towards the drier heaths around the *Ericetum*, a feature seen in the data of Ivimey-Cook *et al.* (1975) and recognised in Rose's (1953) separation of 'wet' and 'damp' heaths.

In such transitions, there can also be a modest enrichment of the sub-shrub cover by scattered bushes of *Erica cinerea*, *Ulex gallii* and *U. minor* but, typically, the most frequent vascular associates of the dominants are *Scirpus cespitosus*, usually occurring as scattered tussocks

and, becoming more frequent towards the wetter transitions to valley mire proper, *Narthecium ossifragum* and *Eriophorum angustifolium*. *E. vaginatum* is found very occasionally too, and there can be scattered plants of *Potentilla erecta* and *Juncus squarrosus* and sparse records for some of the preferentials of the next sub-community.

There is a continuous transition between this typical kind of *Ericetum* and the more impoverished wet heaths where bryophytes and lichens in particular are very much reduced, where herbaceous associates become very sporadic in their occurrence and where dominance sometimes passes very obviously to one or other of the vascular constants depending on the particular treatment history. Such stands could be included here, when they would markedly reduce the frequency of *Sphagnum compactum* and *S. tenellum*, or be treated as a separate species-poor sub-community.

***Succisa pratensis-Carex panicea* sub-community:** *Gentiana pneumonanthe* localities 11–12 & 15–17 Simmonds 1946. Although *E. tetralix* and *Calluna* retain high frequency here, there is a tendency for *Molinia* to predominate and the vascular component of the vegetation is considerably richer than in the Typical sub-community. *Potentilla erecta* and *Succisa pratensis* become constant and other fairly frequent preferentials are *Polygala serpyllifolia*, *Carex panicea*, *Danthonia decumbens*, *Salix repens*, *Cirsium dissectum* and *Serratula tinctoria*, with *Myrica gale* sometimes showing local abundance. More occasionally there can be small amounts of *Juncus acutiflorus* or *J. effusus* or some *Agrostis curtisii*, *Festuca rubra* and *Luzula multiflora*. Of scarcer occurrence, but still showing some preference to this sub-community, are *Carex hostiana*, *C. pulicaris*, *Dactylorhiza maculata* and *Platanthera bifolia*. By contrast, some of the community associates such as *Scirpus cespitosus*, *Narthecium ossifragum* and *Eriophorum angustifolium* are of rather reduced frequency here.

Bryophytes and lichens, too, tend to be less common among the more complete cover of angiosperms, with both *Sphagnum compactum* and *S. tenellum* occurring only occasionally. Unusually, however, *S. auriculatum* is more frequent here than in any other kind of *Ericetum* and it can be locally abundant.

***Rhynchospora alba-Drosera intermedia* sub-community:** *Gentiana pneumonanthe* localities 8–10 Simmonds 1946; Wet heath Rose 1953, Newbould 1960 both *p.p.* *Molinia* and *E. tetralix* both remain very frequent here but *Calluna* is a little less common than usual and, more obviously, the cover of all three is reduced. In the network of intervening open areas, there is typically an extensive cover of *Sphagnum compactum* and *S. tenellum* with frequent scattered plants of *Kurzia pauciflora*, occasional *Hypnum jutlandicum*, *Odontoschisma sphagni*, *Campylopus brevipilus*, *Cephalozia* spp. and *Gymnocolea inflata* and locally prominent *Cladonia* spp., particularly *C. impexa*.

Scattered in this ground, there are frequent small tussocks of *Scirpus cespitosus* and often some *Narthecium* and sparse *Eriophorum angustifolium* and occasional *Eleocharis multicaulis*. More distinctive is the preferential occurrence here, often concentrated around wetter hollows and runnels, of *Drosera rotundifolia* and the rarer *D. intermedia*, *Rhynchospora alba* and, at some sites in Dorset and Hampshire and a few isolated stations elsewhere, *R. fusca*. Another rare species, very characteristic of this sub-community and typically occurring on bare peaty patches, is *Lepidotis inundata*, often associated with crusts of the purple alga *Zygogonium ericetorum s.l.* *Pinguicula lusitanica* can also be found in this vegetation at some sites in the south-west. Some of these species provide a strong floristic link between the *Ericetum* and the *Narthecio-Sphagnetum* and its typical *Sphagnum auriculatum* pools, but transitional stands can usually be separated by the scarcity here of *S. papillosum* and *S. auriculatum*.

***Juncus squarrosus-Dicranum scoparium* sub-community:** Submoorland heath Muir & Fraser 1940 *p.p.*; *Calluna-Erica tetralix* wet heath Gimingham 1964 *p.p.*, Bannister 1966 *p.p.*; *Campylopo-Ericetum tetralicis* Birse & Robertson 1976; *Narthecio-Ericetum tetralicis* Moore (1964) 1968 *sensu* Birse 1980. In this sub-community, which is the usual kind of *Ericetum* to the north and east of Britain, there are some noticeable shifts in the comparative frequency and abundance of the commonest species of the community. *Molinia*, for example, is rarely of high cover here and is sometimes totally absent and, though *E. tetralix* retains constancy and is often quite abundant, it generally yields dominance to *Calluna*. Then, *Scirpus cespitosus* is more frequent and of consistently higher cover in this sub-community than elsewhere.

The continuing high frequency of *Sphagnum compactum* and *S. tenellum*, and the relative scarcity of *S. capillifolium* and *S. subnitens*, emphasise the close relationships of this vegetation to the other kinds of *Ericetum*. *S. compactum*, in particular, is often abundant here and commonly accompanied by *Hypnum jutlandicum*, *Dicranum scoparium*, *Racomitrium lanuginosum*, *Diplophyllum albicans* and, less frequently, by *Pohlia nutans*, *Pleurozium schreberi* and *Campylopus paradoxus*. Lichens, too, often contribute prominently to the ground cover with *Cladonia impexa* and *C. uncialis* especially common, *C. arbuscula*, *C. floerkeana* and *C. squamosa* more occasional.

The general impression of the vegetation, then, is of a rather drier kind of heath than is usual in the other sub-

https://doi.org/10.1017/9780521391658.020 Published online by Cambridge University Press

communities, though it should be noted that the Oceanic *Erica cinerea*, which would be expected to accompany many of the above bryophytes and lichens in heaths to the west of Britain, is very scarce here. The only distinctive vascular plant is *Juncus squarrosus*, which is much more frequent than in other sub-communities, though rarely abundant. There is commonly some *Narthecium* and occasional plants of *Eriophorum angustifolium*, *Potentilla erecta* and *Polygala serpyllifolia*. Increased frequencies of the last three of these is one other feature of the floristic switch to the *Scirpus-Erica* wet heath in moving to the western uplands of Britain.

Habitat

The *Ericetum tetralicis* is a community of acid and oligotrophic mineral soils or shallow peats that are at least seasonally waterlogged. It is largely confined to the relatively dry lowlands of Britain, being particularly associated with the surrounds of valley mires maintained by a locally-high ground water-table, though in Scotland it extends on to thin ombrogenous peats at higher altitudes. Grazing and burning are important in maintaining the vegetation and, although draining has permitted its migration on to once-wetter peats in some places, many stands have been altered or destroyed by lowering the water-table.

The *Ericetum* occurs typically on acid soils (with a surface pH that is generally between 3.5 and 4.5) that are too dry for the development of Sphagnetalia magellanici bogs and too wet to sustain Calluno-Ulicetalia heaths. The soils here are maintained in a very moist state for much of the year but are not so thoroughly waterlogged to favour the luxuriant growth of the major peat-forming Sphagna. The frequent presence of such plants as *Scirpus cespitosus*, *Narthecium ossifragum* and *Eriophorum angustifolium*, and the occurrence in wetter depressions of *Drosera* spp. and *Rhynchospora* spp., provides some continuity with the vegetation of mire surfaces, but the scarcity of *Sphagnum papillosum* and *S. magellanicum* serves as a good marker of the boundary with the Sphagnetalia, typically a group of mire communities developed on deeper, wetter peats. The *Ericetum* can extend a little way on to the fringes of topogenous mires and, particularly in eastern Scotland, it is found on the thin margins of blanket peats, but mostly it occurs on wet mineral soils with sometimes but a thin humic top. Among the Sphagna which can maintain themselves on such surface-moist profiles are *Sphagnum tenellum* and, much more diagnostic of the community, *S. compactum* and the scarcer *S. molle*.

Towards the opposite extreme, the soil surface beneath the *Ericetum* can dry out intermittently in summer, but waterlogging is too sustained to permit the encroachment far into the community of Calluno-Ulicetalia species. *Erica cinerea*, for example, which is a common plant in heaths over free-draining acid soils throughout much of the range of the *Ericetum tetralicis*, cannot germinate well on the wet surfaces characteristic here (Bannister 1964*a*, 1965) and quickly fails if the water-table is raised (Bannister 1964*d*), perhaps because of the accumulation of ferrous ions (Jones & Etherington 1970, Jones 1971*a*, *b*): valley mires in particular seem to be rich in iron, which is often precipitated locally as ochre. Except in the more continental parts of East Anglia, where *E. cinerea* becomes increasingly scarce (Bannister 1965), the limit of this plant in heath sequences developed over progressively wetter soils provides a good indication of the switch to the *Ericetum*. Over south-eastern England, *Ulex minor*, and, further west, *U. gallii* and *Agrostis curtisii*, show the same behaviour, penetrating into the community only along its drier fringes or where increased through-put enhances aeration and nutrient status, as perhaps occurs in some stands of the *Succisa-Carex* sub-community.

The vascular plant which benefits most obviously from the intermediate wetness of the soils of the *Ericetum* is *E. tetralix* itself. This plant is widely represented on oligotrophic and poorly-aerated soils in Britain (Bannister 1966), extending on to the lawn and hummock component of Sphagnetalia mires and, in the more oceanic climate of south-west Britain, transgressing far into the Calluno-Ulicetalia heaths, but it tends to show a peak of abundance in the transitional zone occupied by the *Ericetum*. It may be able to avoid some of the effects of the waterlogged environment by virtue of its shallow root system (Sheikh 1970), but probably of greater importance is that here it can establish and grow free of some of the competition that limits its contribution on more free-draining and/or richer soils (Bannister 1966, Gimingham 1972). Of continuing importance through much of the *Ericetum*, however, are competitive interactions with *Calluna* and *Molinia*: the relationships between these species give rise to much of the more obvious variation within and between stands and help characterise some of the sub-communities (Rutter 1955).

The interactions with *Calluna* are probably largely related to waterlogging. *Calluna* can germinate and establish over a wider range of soils than *E. tetralix* (Bannister 1964*c*, Gimingham 1972) and, in particular, maintains its representation on substrates where there is some fluctuation in moisture content (Rutter 1955) or a consistently lower water-table, even in more continental areas where *Erica cinerea*, which it often accompanies in drier heaths, cannot thrive. On wetter, humic surfaces, however, *E. tetralix* can outstrip *Calluna* in its germination performance (Bannister 1964*b*) and maintain itself better in mixed populations (Smart in Gimingham 1972): consistent severe waterlogging induces reduced transpiration, chlorosis and failure of the root system in

Calluna (Bannister 1964*c*, *d*). The results of interactions of this kind can be seen in walking upslope through stands of the Typical sub-community around some valley mires, where shifts in dominance from *E. tetralix* to *Calluna* can occur, particularly outside south-western England, where there is no climatic complication of the amplitude of the former. And they are visible, too, in the poorer contribution of *Calluna* to the wet-hollow vegetation of the *Rhynchospora-Drosera* sub-community. The rather consistent way in which *Calluna* tends to exceed *E. tetralix* in the *Juncus-Dicranum* sub-community, on the other hand, is probably related to the treatment the *Ericetum* receives around the upland fringes, where it is often subject to controlled burning (see below).

The relationship between these two ericoids is complicated by interactions with *Molinia*, particularly towards the south-west of Britain where, like *E. tetralix*, it is represented not only through the Sphagnetalia mires but also in the Calluno-Ulicetalia heaths (as well, of course, as in a range of Molinietalia communities). In the *Ericetum*, *Molinia* fares less well on very badly-aerated profiles, but it is probably hindered more strongly by the generally poor trophic state of the soils (Loach 1966, 1968*a*, *b*, Sheikh & Rutter 1969, Sheikh 1969*a*, *b*, 1970). Thus, although *Molinia* maintains high frequency through much of the *Ericetum*, its competitive ability is often reduced, against *E. tetralix* on the more consistently waterlogged soils and against *Calluna* on somewhat drier, impoverished profiles. Where there is some amelioration of edaphic extremes, it can predominate: *Molinia*-dominated stands occur within the Typical sub-community and are especially common in the *Succisa-Carex* sub-community, where the appearance of species such as *Succisa*, *Serratula tinctoria*, *Cirsium dissectum*, *Juncus* spp. and *Myrica gale* is suggestive of a transition to Junco-Molinion vegetation. This kind of *Ericetum* can mark out areas of more base-rich soil (pH here sometimes exceeds 5) perhaps derived from less acidic parent materials or enriched with sub-surface water-flow.

Environmental conditions favouring the development of the *Ericetum* are of local occurrence in lowland Britain, depending as they do on the maintenance of a high water-table in acidic soils. In southern England, such conditions are generally associated with drainage-impedence over impervious parent materials, like non-calcareous clays, shales and superficials, which give rise to stagnogleys, or with the development of impervious horizons, such as an iron pan or strongly argillic B horizon, in podzolised profiles. These waterlogged, base-poor soils are concentrated on the more acidic components of the complex sequences of younger deposits that make up the landscape of south-eastern England. Here, the *Ericetum* is found over Eocene clays, sands and gravels in south Dorset, Hampshire and Surrey, and over the clays and sands of the Lower Greensand and Hastings Beds in the Weald, and, more locally, in West Norfolk. Further west, in Devon and Cornwall, Triassic sandstones and pebble-beds carry the community and these were probably an important substrate for, now lost, wet heaths of this kind in the Cheshire Plain and east Yorkshire. In parts of the New Forest, the *Ericetum* occurs over Pleistocene gravels.

On such deposits, the community can pick out areas where a perched water-table occurs over stretches of flatter ground with drainage-impedence in podzols, a particularly distinctive habitat on ill-drained terrace fragments in the northern part of the New Forest (Fisher 1975*a*, *b*), or occupy the bottoms of hollows where erosion has cut down to impervious bedrocks, as in some of the Hampshire and Sussex sites described by Rose (1953). More strikingly, it occurs on slopes around more fully-developed mires in shallow valleys, where the water-table comes close to the surface with a switch to impervious strata, but is not yet so high as to encourage the development of Sphagnetalia vegetation, which supervenes below. In such situations, the hydrological regime is essentially topogenous, often with an artesian element maintaining a high-table and producing back-gleying in the mire surrounds. But the hollows are also fed by run-off from higher ground and tracks with more obvious soligenous inflow can sometimes be seen around the margins. The Typical sub-community often makes up the bulk of the cover in these sites, with the *Rhynchospora-Drosera* sub-community marking out wet and often sandy depressions: the latter vegetation can then be seen as transitional to the Rhynchosporion element in the hollows of the mire surface proper. The *Succisa-Carex* sub-community seems to replace the Typical sub-community over richer parent materials or where there is more marked sub-surface water-flow.

In a few remaining sites further north, the *Ericetum* can occur in this kind of setting: in some places on the North York Moors, for example, it fringes valley mires developed in drift-filled hollows cut into Jurassic rocks. But, increasingly in northern Britain, the community is found on gleys and gleyed podzols on drift-smeared slopes around the upland fringes and, particularly in eastern Scotland, it extends on to the drier peats on the edges of ombrogenous bog, extending to altitudes of 500 m or even more (Birse & Robertson 1976, Birse 1980). Here, the *Juncus-Dicranum* sub-community is the usual form of the *Ericetum*, *Molinia* becoming sparser in the continental climate and *Calluna* and Nardo-Callunetea associates increasing, perhaps in response to treatment. It is in Scotland, where the distribution of the communiity has not been too fragmented, that there is the most continuous geographical transition between the *Ericetum* and its north-western counterpart, the

Scirpus-Erica wet heath. The switch between the two communities occurs around the 1600 mm isohyet (*Climatological Atlas* 1952) or 180 wet days yr^{-1} line (Ratcliffe 1968), beyond which shallow ill-drained slopes often carry moderately thick ombrogenous peat with the *Scirpus-Erica* community.

Superimposed upon the natural patterns of variation in the *Ericetum*, developed in relation to the degree of waterlogging and, less so, the trophic state of the soil, are differences produced by biotic factors, most notably grazing, burning and draining. Throughout its range, the community lies within the forest zone and, without any grazing or burning, most stands would probably progress fairly quickly to some kind of woodland. Indeed, this has been the fate of some stands lying within tracts of heath on certain commons in south-east England where traditional management has fallen into disuse. Elsewhere, occasional burning, with grazing in some areas like the New Forest and around the upland fringes, continue to be of importance in maintaining the community. But both treatments, and especially burning, also have a marked effect on floristic variation within the community, particularly on the local pattern of dominance and the richness of the associated flora.

To some extent, the *Ericetum* is protected against the effects of very severe fires by the wetness of the ground, but more superficial fires commonly remove the bulk of the standing vegetation. *Calluna*, *E. tetralix* and *Molinia* are all well able to regenerate after fires, by sprouting from buried stools or basal shoots or, with the ericoids, by the rapid establishment of seedling populations. But the results of any particular burn are very variable, one or other of the species being able to take advantage according to such factors as the previous state of the vegetation, the time since the previous burning, the intensity of the fire and environmental conditions afterwards (Whittaker 1960, Gimingham 1972). Such opportunism creates great local diversity in the proportional contribution of the dominants in individual stands (e.g. Williams & Lambert 1959, 1961) and makes it difficult to discern consistent patterns of response among the species. In wetter habitats, such as are generally characteristic here, *E. tetralix* may be able to regenerate vegetatively better than *Calluna* because its semi-prostrate lower branches are protected to some extent by the *Sphagnum* carpet and litter (Fritsch & Salisbury 1915, Bannister 1966). But *Calluna* can re-establish in abundance from seed and, in somewhat drier situations and in areas with a cooler climate, it may have the edge. More controlled burning, deliberately to maximise the proportion of building-phase *Calluna*, may account for the consistent predominance of this ericoid in the *Juncus-Dicranum* sub-community in north-eastern Britain: this kind of *Ericetum* also has that abundance of *Cladonia* spp. typical of the middle years of regrowth in regularly-burned heaths. More severe burning of the community can destroy both ericoid stools and buried seed and probably gives *Molinia* an advantage in the long term (Tansley 1939, Rose 1953, Ratcliffe 1959*a*). This grass can also benefit by the burning off of choking litter and by the quick release of nutrients from the ash.

More deleterious to the community are the effects of burning on the associated flora, especially the typical bryophytes, which recover only very slowly and which can be virtually eliminated by frequent fires. Such treatment has probably contributed to the widespread impoverishment of the *Ericetum* on heaths throughout southern Britain, and has been especially destructive when combined, as it often has been, with draining. The survival of the community is ultimately dependent on the maintenance of a high water-table and, where this has been lowered, either by direct drainage or by such operations in the mires below, most of the associates are lost. Where the land is not reclaimed, mixtures of the dominants may survive for some considerable time, often with much *Calluna* on poorer soils or with a spread of *Molinia* where surface oxidation of humus has released nutrients. But the woeful effects of drainage on the *Ericetum* can be readily seen in the shrinking distributions of two of its most distinctive rare species, *Lepidotis inundata* and *Gentiana pneumonanthe*, and in losses in south-eastern Britain of *Scirpus cespitosus* and *Eriophorum vaginatum*, common enough to the north and west but very much confined to the community in this region.

Zonation and succession

The *Ericetum tetralicis* occurs as part of zonations related to the height of the water-table in sequences of acid and oligotrophic soils. Locally, these can be complicated by increased soligenous influence on slopes or by variations in the base-richness and trophic state of soil parent materials or waters. Burning can superimpose differences in floristics and structure and frequent firing and/or draining degrades the community. In the absence of grazing and burning, the *Ericetum* progresses to woodland.

When fully developed around lowland valley mires, the pattern of communities in which the *Ericetum* occurs is very striking (e.g. Rose 1953, Wheeler 1983). Downslope, on the deep, wet peats of the bog itself, it gives way to the *Narthecio-Sphagnetum* with the *Sphagnum auriculatum* bog-pool community in deeper hollows, many of the species of the *Ericetum* running on into the lawn and hummock component of the mire surface, but *Sphagnum compactum* and, to a lesser extent, *S. tenellum*, being replaced by *S. papillosum* and *S. magellanicum*. Beyond this, towards the main axis of the mire, there is often a zone of Littorelletea vegetation or Caricion nigrae poor fen and then a central strip of *Salix-Galium* woodland.

In mires with a little more enrichment, the last community may be replaced by the *Alnus-Carex* woodland from which patchy *Caricetum paniculatae* swamp may run out a little way. Upslope from the *Ericetum*, with the passage to drier acidic soils, there is a transition to Calluno-Ulicetalia heath, though the particular community involved varies according to the region in which the site occurs. In the more continental climate of East Anglia, a sharp switch to the *Calluna-Festuca* dry heath is characteristic but, with the shift into the more oceanic south-west, so-called 'humid heaths' are interposed in the sequence, first the *Ulex minor-Agrostis curtisii* heath in sites around the Hampshire basin, and then from there westwards the *Ulex gallii-Agrostis* heath. Increasingly, in such zonations, both *E. tetralix* and *Molinia*, as well as *Calluna*, maintain their representation through these intermediate vegetation types, so it is generally the downslope limit of *E. cinerea*, the *Ulex* spp. and *A. curtisii* that marks the transition to the Ericion wet heath. Above these zonations, pockets of deeper, well-drained soil can have stands of the *Pteridium-Galium* community or, where there has been some enrichment of the ground, the *Rubus-Pteridium* underscrub or *Ulex-Rubus* scrub, the latter especially characteristic of disturbed places, as along trackways.

Complete zonations of this kind can still be seen in and around the series of New Forest valley mires, such as the Denny/Shatterford system and Wilverley, Holmsley and Matley bogs (Rose 1953, Tubbs 1968, Ratcliffe 1977, NCC New Forest Bogs Report 1984) and on some of the south Dorset heaths, like Morden, though there the *Ericetum* is reduced to a narrow zone around a rather flat-bottomed valley (Ratcliffe 1977). Elsewhere, the sequence of communities is incomplete below. At Thursley Common in Surrey, for example, the *Narthecio-Sphagnetum* terminates the zonation below (Rose 1953, Ratcliffe 1977) and, quite often, it is the *Ericetum* itself which occupies the wettest ground, clothing the bottom of shallow valleys and hollows. This is the case on some of the remaining Sussex commons like Ashdown Forest, over the northern New Forest terraces (Fisher 1975*a*, *b*) and on many of the fragments of south Dorset heathland, where there are the additional features of the presence of *Erica ciliaris* in a number of the communities and the close juxtaposition with open-water and maritime vegetation (Chapman 1975, Ratcliffe 1977).

In other sites, the basic sequence of communities is complicated by the interpolation of other vegetation types related to base- or nutrient-richness in the substrates or waters. In some of the New Forest mires, like Cranesmoor for example (Newbould 1960), on Hartland Moor in Dorset (Ratcliffe 1977) and at Aylesbeare Common in Devon (Ivimey-Cook *et al.* 1975), the *Schoenus-Narthecium* community figures prominently along the axes of soligenous water movement and, in the last site, there are also extensive stands of Junco-Molinion vegetation, continuing the floristic trend seen within the *Ericetum* itself in the *Succisa-Carex* sub-community. Then, in some of the 'mixed mires' developed on north Norfolk commons like Roydon, there can be a much more striking switch to a more calcicolous series of vegetation types, including the *Cirsio-Molinietum*, the *Schoenetum*, tall-herb Phragmitetalia fen and carr (Rose 1953, Daniels & Pearson 1974, Wheeler 1975).

Further north in Britain, these kinds of valley mire zonations become rare and the *Ericetum* often occurs in what is essentially a reverse sequence of communities, giving way above to ombrogenous mire on deeper, wetter blanket peat, generally within the range of the *Ericetum*, the *Calluna-Eriophorum* mire; and passing below to a variety of northern dry heaths, throughout which burning has often resulted in a fairly uniform predominance of *Calluna*, or which have run down to Nardo-Galion grasslands with much *Juncus squarrosus* and *Nardus stricta*.

Where relaxation of burning and grazing allows invasion of shrubs and trees, the *Ericetum* is probably rapidly converted to woodland. Although this process has not been followed in detail, the most natural successor to the community is likely to be the *Betula-Molinia* woodland, *Betula pubescens* and *Salix cinerea* leading the colonisation and *Pinus sylvestris* sometimes making a prominent local contribution where it can readily seed in from nearby plantations. *Molinia* continues to play a major role in the field layer of this woodland, though the ericoids persist only patchily in areas with a more open canopy. Draining can probably speed up this succession, though it may allow a phase of strong *Molinia*-dominance to supervene between the heath and the woodland. In time, the *Betula-Molinia* woodland may give way to the *Quercus-Betula-Deschampsia* woodland.

Combinations of frequent burning, draining and damage due to other operations like military manoeuvres and mineral extraction have led to an irretrievable loss of the *Ericetum* in many areas (Rose 1953, Ratcliffe 1977). Even where stands survive intact, the characteristic zonations in which the vegetation occurs have been truncated and the community can now often be found closely hemmed in by coniferous plantations or intensive agricultural land (e.g. Moore 1962).

Distribution

The *Ericetum* is largely confined to the south and east of Britain though, particularly in lowland England, its distribution has been much fragmented by heathland reclamation. The Typical sub-community is found throughout the south of the country, being especially well represented on the heaths of south-east and south-

west England and, increasingly to the north, occurring as impoverished stands. The *Rhynchospora-Drosera* sub-community is much more local, being concentrated in the New Forest and around Poole Harbour, the *Succisa-Carex* sub-community a little less so, occurring through south-west England and perhaps elsewhere. In northern Britain, the *Ericetum* is represented by the *Juncus-Dicranum* sub-community which can be seen as a transition to the *Scirpus-Erica* wet heath, which replaces the *Ericetum* in the sub-montane north and west.

Affinities

The *Ericetum tetralicis* has long been familiar from descriptive accounts as various kinds of 'wet heath' (Rose 1953, Rutter 1955, Williams & Lambert 1959, Newbould 1960, Gimingham 1964*b*, Bannister 1966, Ivimey-Cook & Proctor 1967). As defined here, the community corresponds well, in general terms, with these vegetation types, and with their phytosociological definition in Ivimey-Cook *et al.* (1975), but it also takes in part of certain *Molinieta* (Rankin 1911*b*, Summerhayes & Williams 1926, Tansley 1939) and some wet moorland vegetation described from Scotland (Muir & Fraser 1940, Birse & Robertson 1976, Birse 1980).

The community has close relationships with the base-poor *Sphagnum* mires of the Sphagnetalia, particularly the lowland valley bog, the *Narthecio-Sphagnetum*, and is best included with them in the Oxycocco-Sphagnetea. Wet heath of this kind has traditionally been placed in a distinct order, the Sphagno-Ericetalia Br.-Bl. 1948 (= Ericetalia Moore (1964) 1968) with a single alliance, the Ericion tetralicis Schwickerath 1933, within which species such as *Erica tetralix*, *Gentiana pneumonanthe*, *Polygala serpylifolia*, *Sphagnum compactum*, *S. tenellum*, *S. molle* and *Zygogonium ericetorum* show a peak of occurrence. Very similar vegetation has been characterised from neighbouring parts of the Continent as the *Ericetum tetralicis* Schwickerath 1933, some of the sub-associations of which closely parallel types recognised here (e.g. Tüxen 1937, LeBrun *et al.* 1949, Westhoff & den Held 1969). The distinctive vegetation with *Rhynchospora alba*, *Drosera intermedia* and *Lepidotis inundata* has sometimes been separated off from the *Ericetum*, as in the *Lycopodio-Rhynchosporetum albo-fuscae* (Paul 1910) Allorge & Gaume 1925 (Westhoff & den Held 1969). In the north, the community grades, through the *Juncus-Dicranum* sub-community, to its sub-montane counterpart, the *Scirpus-Erica* wet-heath: Birse (1980) united some stands of both these vegetation types in his amended version of the *Narthecio-Ericetum tetralicis* Moore (1964) 1968.

Particularly in the strongly oceanic climate of south-west England, the *Ericetum* shows close affinities with various Calluno-Ulicetalia heaths, into which *E. tetralix* and *Molinia* penetrate far. Through the *Succisa* sub-community, it also grades into the vegetation of the Junco-Molinion. Under certain treatments, these communities and the *Ericetum* can converge into very species-poor *Molinia* vegetation, the phytosociological placement of which presents something of a challenge.

Floristic table M16

	a	b
Erica tetralix	V (3–9)	V (1–7)
Calluna vulgaris	V (1–9)	V (3–7)
Molinia caerulea	V (3–9)	V (2–8)
Sphagnum compactum	V (2–8)	II (1–6)
Potentilla erecta	II (1–3)	V (1–4)
Succisa pratensis	I (3–4)	V (1–5)
Polygala serpyllifolia	I (1–3)	III (1–4)
Carex panicea	I (1–3)	III (2–5)
Sphagnum auriculatum	I (1–4)	III (4–7)
Salix repens	I (1–4)	III (1–5)
Danthonia decumbens		III (2–6)
Sphagnum papillosum	I (1–5)	II (2–5)
Juncus acutiflorus	I (1–4)	II (2–3)
Myrica gale	I (3–7)	II (5–7)
Cirsium dissectum	I (3)	II (3–5)
Ulex gallii	I (3–7)	II (4–7)
Serratula tinctoria		II (3–5)
Ulex europaeus		II (2–4)
Agrostis curtisii		II (1–7)
Festuca rubra		II (3–4)
Juncus effusus	I (3)	II (1–3)
Luzula multiflora	I (2)	II (2–3)
Kurzia pauciflora	II (1–4)	
Drosera intermedia	I (3)	
Rhynchospora alba		
Drosera rotundifolia	II (1–3)	
Campylopus brevipilus	I (2–7)	
Lepidotis inundata		
Eleocharis multicaulis		
Cephalozia macrostachya		
Pinguicula lusitanica		

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c	d	16
V (3–7)	V (1–7)	V (1–9)
IV (2–6)	V (1–9)	V (1–9)
V (4–6)	III (2–8)	IV (2–9)
V (2–8)	V (1–8)	IV (1–8)
	II (1–4)	II (1–4)
	I (2–3)	I (1–5)
II (1–2)	II (1–3)	II (1–4)
II (1–2)	II (1–3)	II (1–5)
I (2–4)		I (1–7)
I (2)		I (1–5)
		I (2–6)
I (1)	I (3)	I (1–5)
		I (1–4)
I (3)	I (6)	I (3–7)
		I (3–5)
		I (3–7)
		I (3–5)
		I (2–4)
		I (1–7)
		I (3–4)
		I (1–3)
		I (2–3)
IV (2–3)	I (1–2)	I (1–4)
IV (1–3)		I (1–3)
IV (2–4)		I (2–4)
III (1–4)	I (1)	I (1–4)
II (2–3)		I (2–7)
II (3)		I (3)
II (1–2)		I (1–2)
II (2–3)		I (2–3)
I (3)		I (3)

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Hypnum jutlandicum	II (1–4)	II (3–6)
Cladonia impexa	II (1–7)	
Juncus squarrosus	II (1–5)	
Dicranum scoparium	I (1–4)	I (1)
Cladonia uncialis	I (1–5)	
Racomitrium lanuginosum		
Diplophyllum albicans		
Pohlia nutans	I (1–2)	I (1–3)
Pleurozium schreberi	I (1–5)	I (2)
Campylopus paradoxus	I (1–3)	
Cladonia arbuscula		
Sphagnum capillifolium		
Cladonia floerkeana		
Cladonia squamosa		
Mylia taylori		
Pleurozia purpurea		
Lophozia ventricosa		
Kurzia trichoclados		
Sphenolobus minutus		
Huperzia selago		
Sphagnum tenellum	IV (1–10)	II (3–5)
Scirpus cespitosus	III (1–5)	I (3–4)
Narthecium ossifragum	II (1–5)	I (3)
Eriophorum angustifolium	II (1–8)	
Odontoschisma sphagni	I (1–5)	
Pinus sylvestris seedling	I (1–3)	I (3)
Cephalozia connivens	I (1–3)	I (1)
Cephalozia bicuspidata	I (2–3)	I (1–4)
Ulex minor	I (2–5)	I (9)
Carex echinata	I (2–6)	I (4)
Pedicularis sylvatica	I (1)	I (2)
Dactylorhiza maculata	I (1)	I (1)
Leucobryum glaucum	I (1–6)	I (1)
Sphagnum subnitens	I (1–6)	I (3–8)
Nardus stricta	I (4)	I (1–2)

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II (1–5)	IV (1–9)	II (1–9)
III (1–5)	IV (1–9)	II (1–9)
I (1–2)	IV (1–6)	II (1–6)
I (3)	III (1–5)	II (1–5)
I (1)	III (1–4)	II (1–5)
I (1)	III (1–8)	II (1–8)
	III (1–4)	I (1–4)
	II (1–6)	I (1–6)
	II (1–6)	I (1–6)
	II (1–5)	I (1–5)
I (5)	II (1–9)	I (1–9)
I (3)	II (1–8)	I (1–8)
I (1)	II (1–3)	I (1–3)
I (1–3)	II (1–3)	I (1–3)
	II (1–7)	I (1–7)
	II (1–6)	I (1–6)
	II (1–4)	I (1–4)
	I (1–4)	I (1–4)
	I (1–4)	I (1–4)
	I (1–2)	I (1–2)
V (3–7)	III (1–7)	III (1–10)
III (3–4)	V (1–8)	III (1–8)
III (1–6)	III (1–6)	II (1–6)
III (1–3)	II (1–5)	II (1–8)
II (2–3)	I (1–3)	I (1–5)
II (1–2)	I (1–5)	I (1–5)
I (1)	I (1–2)	I (1–3)
I (1)	I (1–3)	I (1–4)
I (1)		I (1–9)
	I (1–3)	I (1–6)
	I (1–2)	I (1–2)
	I (1–3)	I (1–3)
	I (1–7)	I (1–7)
	I (1–5)	I (1–8)
	I (1–4)	I (1–4)

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Floristic table M16 *(cont.)*

	a	b
Gymnocolea inflata	I (2–3)	
Cladonia furcata	I (1–3)	
Sphagnum cuspidatum	I (2–6)	
Betula pubescens seedling	I (1–2)	I (3–4)
Cladonia verticillata	I (1–3)	
Sphagnum molle	I (1–5)	
Eriophorum vaginatum	I (2–7)	
Odontoschisma denudatum	I (1–3)	
Campylopus pyriformis	I (1)	
Aulacomnium palustre	I (1–6)	
Number of samples	45	14
Number of species/sample	13 (8–24)	17 (8–27)

a Typical sub-community
b *Succisa pratensis-Carex panicea* sub-community
c *Rhynchospora alba-Drosera intermedia* sub-community
d *Juncus squarrosus-Dicranum scoparium* sub-community
16 *Ericetum tetralicis* (total)

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c	d	16
I (3)	I (1–7)	I (1–7)
I (1–2)	I (2)	I (1–3)
I (2)	I (1)	I (1–6)
		I (1–4)
I (3)		I (1–3)
I (1–2)		I (1–5)
	I (1–4)	I (1–7)
	I (1–3)	I (1–3)
	I (1)	I (1)
	I (1–3)	I (1–6)
10	41	110
17 (10–28)	19 (13–24)	16 (8–28)

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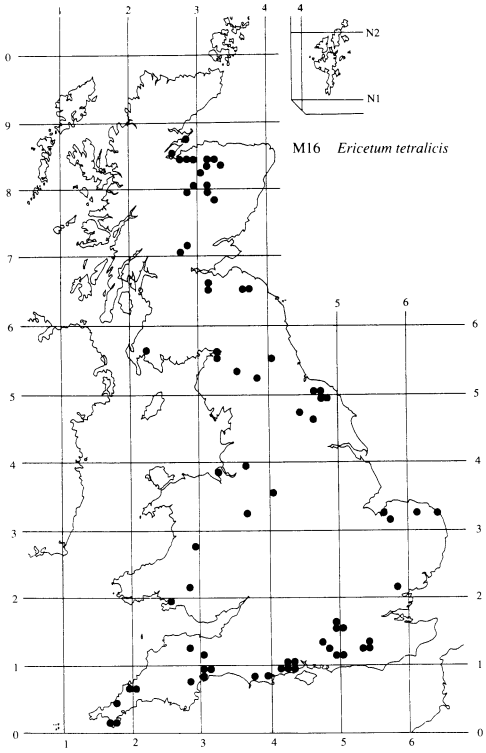

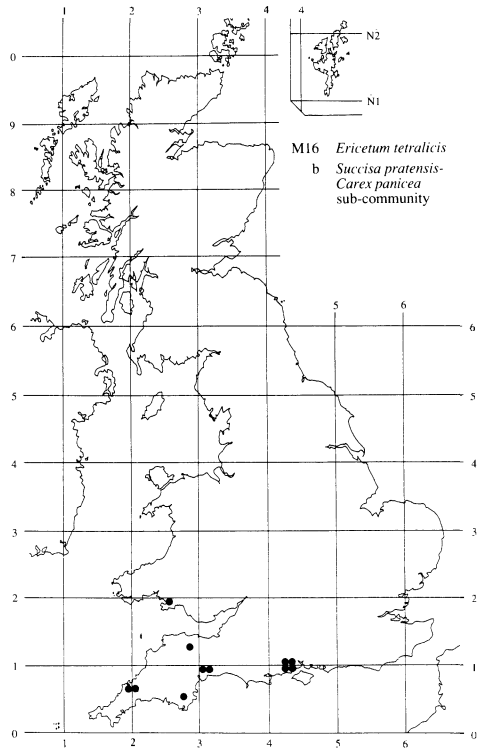

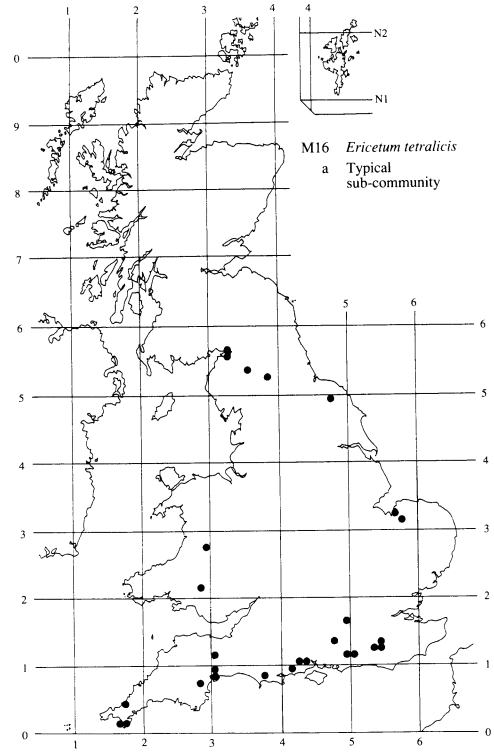

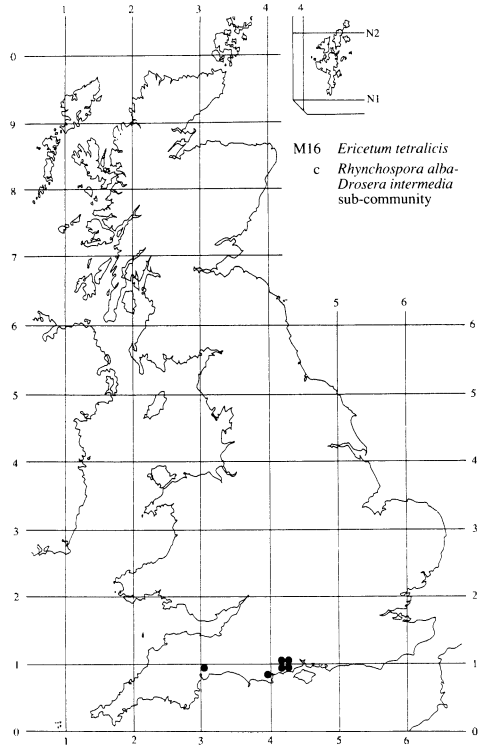

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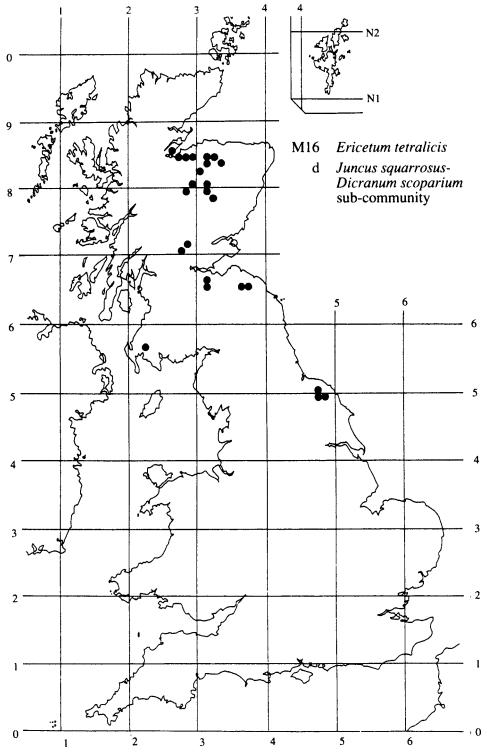

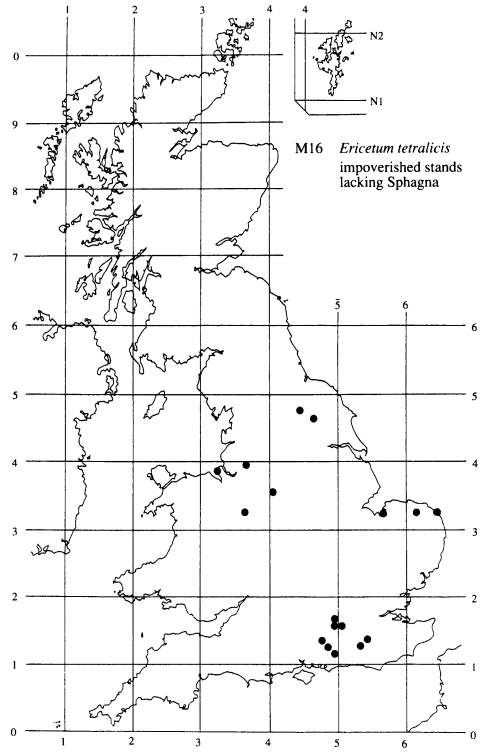

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