W11

Quercus petraea-Betula pubescens-Oxalis acetosella woodland

Synonymy

Caithness birchwoods Crampton 1911 *p.p.*; *Betuletum tomentosae* Moss 1911 *p.p.*; Scottish beechwoods Watt 1931 *p.p.*; Highland birchwoods Tansley 1939 *p.p.*; Highland oakwoods Tansley 1939 *p.p.*; Heathy birchwood Pigott 1956; *Betuletum Oxaleto-Vaccinietum* McVean & Ratcliffe 1962 *p.p.*; *Betula*-herb nodum McVean & Ratcliffe 1962 *p.p.*; *Vaccinium*-rich birchwood association McVean 1964*a p.p.*; Herb-rich birch and oakwood association McVean 1964*a p.p.*; *Blechno-Quercetum* (Br.-Bl. & Tx. (1950) 1952) Klötzli 1970 *p.p.*; *Oxalido-Betuletum* Graham 1971 *p.p.*; Loch Lomond oakwoods Tittensor & Steele 1971 *p.p.*; *Betula pubescens-Vaccinium myrtillus* Association Birks 1973 *p.p.*; *Corylus avellana-Oxalis acetosella* Association Birks 1973 *p.p.*; Hazel-ash woodland Peterken 1981 *p.p.*; Oak-lime woodland Peterken 1981 *p.p.*; Birch-oak woodland Peterken 1981 *p.p.*; Birch woodland Peterken 1981 *p.p.*; Woodland plot types 21, 22, 23, 26 & 29 Bunce 1982; *Trientali-Betuletum pendulae* Birse 1982 *p.p.*; *Luzulo-Betuletum odoratae* Birse 1984 *p.p.*; *Blechno-Quercetum* (Br.-Bl. & Tx. (1950) 1952) Birse 1984 *p.p.*; *Lonicero-Quercetum* (Birse & Robertson 1976) Birse 1984 *p.p.*

Constant species

Betula pendula/pubescens, *Agrostis capillaris*, *Anthoxanthum odoratum*, *Deschampsia flexuosa*, *Galium saxatile*, *Holcus mollis*, *Oxalis acetosella*, *Potentilla erecta*, *Pteridium aquilinum*, *Viola riviniana*, *Hylocomium splendens*, *Pseudoscleropodium purum*, *Rhytidiadelphus squarrosus*, *Thuidium tamariscinum*.

Physiognomy

The *Quercus petraea-Betula pubescens-Oxalis acetosella* woodland is almost invariably dominated by either oak or birch or various mixtures of the two. Of the oaks, *Quercus petraea* is very much the more frequent and characteristic species and it can be an abundant component of this community in south-west England, Wales, the Lake District and into southern and central Scotland. Sometimes, it forms a high forest canopy of tall, well-grown trees; in other stands, it dominates in oak coppice with a fairly low cover of thin or multi-stemmed and often crookedly-growing individuals.

Moving north-westwards, *Q. petraea* becomes rarer and increasingly confined to lower altitudes: in the southern and east-central Highlands, it can dominate in this community up to about 275 m, but in the far west, its general limit is around 150 m (McVean 1964*a*). However, there is every indication that oak has been extensively removed from woodlands towards the north-western limit of this community, so its absence there is probably partly artificial (McVean & Ratcliffe 1962, McVean 1964*a*). Sylvicultural activity may also be involved in the low frequency of *Q. petraea* in stands in the eastern lowlands of Scotland. Here, oak is quite common in high-forest and coppice stands of this community, but it is often *Q. robur* or, more frequently, hybrid (Birse 1982, 1984) and this may reflect the preference for *Q. robur* as the plantation oak that grew up in the past two centuries (Anderson 1967, Gardiner 1974).

In oak-dominated stands such as these, birch is often only a low-cover canopy component or a gap-coloniser; and, in coppice, it was often weeded out. Sometimes, though, it was itself cropped to provide bobbin-wood or brushwood for besoms and, with the felling of oak and the abandonment of oak-coppicing, it has spread considerably to become the dominant in neglected and run-down stands. And, at high altitudes and to the far north-west, it is usually the predominant tree. Overall, it is now the most frequent woody species of the community. *Betula pubescens* is the typical birch here and in locally exposed situations towards the lowlands and more consistently at higher latitudes (north-west from Inverness-shire), the trees have the distinctly shorter and bushier stature of ssp. *carpatica* (Walters 1964, Forbes & Kenworthy 1973). But *B. pendula* also occurs, though its predominance is very much concentrated geographi-

https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press

cally in eastern Scotland. Here, it can be as common as *B. pubescens* and shows a fairly precise altitudinal switch to ssp. *carpatica* (as in the Dee valley woods described by Forbes & Kenworthy 1973 where one taxon gave way to the other at about 350 m: see also Hulten 1950, Birse & Dry 1970). Throughout the community, birches intermediate in character between *B. pubescens* and *B. pendula* can be found and these seem to be genuine hybrids (Kennedy & Brown 1983).

When birch dominates here, it can form quite dense thickets but usually the cover is rather open, sometimes very much so, with widely-spaced, rather moribund trees showing signs of early damage by fire or from browsing. The height of the canopy is very variable, though rarely tall: *B. pubescens* ssp. *pubescens* and *B. pendula* commonly attain 15 m but, where *B. pubescens* ssp. *carpatica* predominates, there is generally a bushy cover about 10 m high, quite often lower. Frequently, the birch canopy looks uniform with no great mixture of age-classes: the usual picture is of a single generation of taller individuals and a very few young saplings or seedlings; more rarely, older pioneer birch can be surrounded by a second generation of trees (McVean & Ratcliffe 1962).

Apart from oak and birch, other trees are scarce in the community as a whole. *Fraxinus excelsior*, which becomes a distinctive component of the *Quercus-Pteridium-Rubus* woodland towards the north-western limit of its range, does not extend far into this community. It is preferential for more southerly stands on deeper and less-leached soils and, even then, is no more than occasional. And *Acer pseudoplatanus*, despite the high rainfall and free-draining character of many of the soils here, is very rare. *Tilia cordata* survives on some cliffs and in gorges in close association with the community towards the very limit of its distribution in Cumbria (Pigott & Huntley 1978): such vegetation would fall within Peterken's (1981) oak-lime stand types 5B. Then, there are sparse records for *Fagus sylvatica* and some conifers, planted in as occasionals or seeding in from nearby plantations: some planted stands of *Fagus* (e.g. Watt 1931*a*) and of *Larix* spp. can be accommodated within the community.

More typical than any of these species, are larger specimens of two of the understorey elements which occasionally grow tall enough to find a place in the canopy. *Sorbus aucuparia* is occasional throughout and distinctly preferential for one sub-community but generally it is of low cover in high forest, occurring as scattered trees. In ungrazed stands, it can thicken up considerably and, being shade-tolerant, can gain abundance where birch cannot (Anderson 1950, McVean 1958). Towards the far north-west, it can be co-dominant with birch in low scrubby canopies. Grazing and browsing, which are very prevalent in this community, probably also account for the great scarcity of *Ilex aquifolium*, a tree which one would expect to be prominent here in the rather equable climate experienced by more westerly and low-altitude stands.

The only other common smaller woody species throughout the community is *Corylus avellana* and even this is no more than occasional, but it can become locally prominent in ungrazed tracts over deeper soils and has sometimes been selected as a coppice crop. More often, it occurs as scattered bushes beneath an oak canopy or, to the far north-west, amongst a low cover of birch and rowan (as on Skye: Birks 1973). Hawthorn (always *Crataegus monogyna*) is scarce and very much confined to deeper and less strongly leached soils. Particularly in eastern Scotland, but also locally elsewhere (as in Teesdale: Graham 1971), *Juniperus communis* ssp. *communis* can be found in more open places, its increasing abundance often marking transitions to stands of the *Juniperus-Oxalis* woodland. *Rhododendron ponticum* has sometimes been planted into the *Quercus-Betula-Oxalis* woodland and it can spread to become locally prominent. Finally, there can be a few birch saplings within gaps.

Generally, however, the combined cover of ali these species is low and the striking feature on entering stands of this community is their openness. Quite apart from this typical scarcity of smaller trees and shrubs and the absence of anything more than patchy regeneration, the field layer is often short. Grasses frequently make a major contribution. As in the *Quercus-Pteridium-Rubus* woodland, *Holcus mollis* is characteristic of this community, though it is much more consistently frequent and abundant here and is accompanied by constant *Deschampsia flexuosa*, *Anthoxanthum odoratum* and *Agrostis capillaris*, frequent *A. canina* ssp. *montana* and occasional *Festuca ovina*, *F. rubra* and *Holcus lanatus*. These grasses become especially prominent with their flush of new growth in early summer and they can form an extensive sward, trimmed short where grazing is heavy, so that the vegetation looks more like a *Festuca-Agrostis* grassland with trees than a woodland proper. In other stands, their cover is broken by boulders, when they extend between the rocks or occur more patchily on top of them; or, where *Pteridium* is very vigorous, they can thin out to scattered, rather puny plants.

This predominance of grasses (and the abundance of bryophytes: see below) can give this vegetation a rather uniform appearance throughout the year but, where the soil cover is extensive, the field layer often shows a clear pattern of phenological change. In more westerly stands, *Hyacinthoides non-scripta* is the typical vernal dominant, extending northwards the very characteristic role it plays in more Atlantic woodlands in Britain. Where the soils are moister, with some measure of spring waterlogging, it may be joined or locally replaced by

Anemone nemorosa, but this plant becomes most important here where the community extends into the more continental regions of eastern Scotland. There, *Hyacinthoides* is rare and, in long-established woodlands at least, *Anemone* is the typical vernal dominant, with the Northern Montane *Trientalis europaea* continuing the picture of scattered white flowers into early summer.

Another typical early spring flowerer common throughout the community, though usually at low cover, is *Viola riviniana*. With *Oxalis acetosella*, another constant here, this species already shows a rise in frequency in the more north-westerly stands of the *Quercus-Pteridium-Rubus* woodland but their increased prominence in the *Quercus-Betula-Oxalis* woodland is a very good marker of the consistently moist character of the soils in this wetter part of the country. *Oxalis* is often most conspicuous here in winter, its pale green foliage set off against the darker shades of the grass and bryophyte carpet and, in shadier stands, it may carry out the bulk of its photosynthetic activity in this season, becoming hidden later by herb growth, though often persisting even under a dense canopy of *Pteridium* (Packham & Willis 1977, Packham 1978).

A very distinctive feature of the *Quercus-Betula-Oxalis* woodland is that such species as *Oxalis* and *Viola*, indicative of the moistness of the soils, occur together with Quercion herbs which favour surface-leached profiles. Foremost among these are *Galium saxatile* and *Potentilla erecta* which, in the north-west of Britain, transgress far into more mesophytic woodlands. This feature makes the floristic boundary between this community and the *Quercus-Betula-Dicranum* woodland a rather indistinct one, especially where the soils are transitional or disposed in complex mosaics over heterogenous parent materials and where very heavy rainfall induces strong leaching overall. By and large, the best diagnostic feature is the scarcity in the *Quercus-Betula-Oxalis* woodland of ericoid sub-shrubs but even this criterion may be unreliable where stands of the community include siliceous boulders or drier banks. In such situations, *Vaccinium myrtillus* may make an occasional appearance (as in some of the stands in McVean & Ratcliffe's (1962) *Betuletum Oxaleto-Vaccinietum* or Birks' (1973) *Betula-Vaccinium* Association in the far north-west of Scotland), though *Calluna vulgaris* and *Erica cinerea* are typically absent, even under more open canopies. The fact that grazing tends to produce a floristic convergence of the *Quercus-Betula-Oxalis* and *Quercus-Betula-Dicranum* woodlands (see below) further confounds this boundary.

Other characteristic herbs of the *Quercus-Betula-Oxalis* woodland include *Teucrium scorodonia*, *Stellaria holostea*, *Luzula pilosa*, (with, more occasionally, *L. multiflora*), *Conopodium majus*, *Veronica chamaedrys*, *V. officinalis*, *Hypericum pulchrum* and *Succisa pratensis*. Scattered plants of all these species, flowering under more open canopies, typically occur through the grassy carpet, but they become especially prominent in areas where there is some protection from grazing, as amongst boulders. Here, too, where there is some slight flushing, *Primula vulgaris* and *Lysimachia nemorum* can occur as in some stands distinguished by Tittensor & Steele (1971) and Birse (1984). Where flushing brings a more pronounced measure of base-enrichment, the field layer may acquire some of the characteristics of more calcicolous communities like the *Fraxinus-Sorbus-Mercurialis* or *Alnus-Fraxinus-Lysimachia* woodlands, but more calcicolous herbs are generally absent from the *Quercus-Betula-Oxalis* woodland.

By mid-summer, many stands of the community have a cover of *Pteridium* fronds, though in bouldery woods bracken is restricted by and large to deeper soils in crevices. Quite a common pattern is for bracken to become much more vigorous and extensive where the community extends down from more rocky slopes with very thin soils to deeper creep soils at the slope foot. Being shade-sensitive, it is also more prominent in open areas of the canopy and it can become abundant, too, in stands where there has been some relaxation of grazing or a neglect of coppicing (e.g. Tittensor & Steele 1971). The same is probably true of *Lonicera periclymenum*: this is generally only occasional here with sparse, trailing stems but it can thicken up locally to form a dense tangle. The third member of this trio, *Rubus fruticosus* agg., so conspicuous in sub-scrub throughout the *Quercus-Pteridium-Rubus* woodland, is here very much confined to less heavily grazed stands on less markedly leached soils. However, when all three of these species are present in such situations, succeeding a bluebell carpet and with abundant *Dryopteris dilatata*, *D. filix-mas* and *D. borreri* (as in the *Dryopteris* sub-community), the similarity between the two woodland types is very obvious.

Ferns can be a conspicuous element in other kinds of *Quercus-Betula-Oxalis* woodland, too. *Blechnum spicant* is the most frequent and characteristic of these overall, though it is strongly preferential for one sub-community. *Thelypteris limbosperma* is generally less common, though it is a very good marker of certain sub-communities and often conspicuous around the margins of stands and in transitions to closely-related tall-herb vegetation (as in McVean & Ratcliffe's (1962) 'fern-dominated treeless facies' of their *Betula*-herb nodum). *T. phegopteris* and *Gymnocarpium dryopteris* are somewhat less frequent, though both can become prominent in zonations to the *Juniperus-Oxalis* woodland. *Athyrium filix-femina* is occasional on moister soils and *Polypodium vulgare* agg. (probably *sensu stricto*) can sometimes be found, often epiphytic on oak. Sheltered sites with some slight base-enrichment can provide localities for *Polystichum aculeatum* or *P. setiferum* but the more calcicolous *Phyllitis scolopendrium* is absent.

One other species that can attain great abundance in ungrazed stands is *Luzula sylvatica*, a prominent feature of this kind of woodland on inaccessible slopes and on islands, as in Loch Lomond (Tittensor & Steele 1971) and Windermere, where it can crowd out most of the other herbs (usually not *Oxalis*, however) and bryophytes. More extensive sampling of this kind of *Quercus-Betula-Oxalis* woodland would probably permit the diagnosis of a distinct sub-community, though it seems best to retain such vegetation within the parent community (cf. Birse (1984) who characterised a distinct *Luzulo-Betuletum*).

Other herbs of note which occur very occasionally here are *Rubus saxatilis*, like *Trientalis* a species with northern continental affinities, and, at some of its most far-flung stations, *Convallaria majalis*.

Throughout the *Quercus-Betula-Oxalis* woodland, bryophytes make a consistent and important contribution, thriving among close-cropped grassy swards where competition is reduced and over boulders blown free of litter and only fading in variety and abundance under denser covers of tall herbs and bracken. They are especially extensive in sites which have a degree of shelter additional to that provided by the trees themselves, as on north-facing slopes or where the community extends into ravines, and in the cool and humid climate of the far north-west where they frequently cover more than half of the ground in a thick and luxuriant carpet that is enriched by a variety of more strictly Atlantic species. In more oceanic areas, there can also be specialised epiphytic floras on the trunks, branches and twigs of the trees and shrubs.

Further details of such richer suites are given below but, among the more generally characteristic bryophytes here are *Rhytidiadelphus squarrosus*, *Pseudoscleropodium purum*, *Thuidium tamariscinum*, *Hylocomium splendens* (all community constants), *Pleurozium schreberi*, *Dicranum majus*, *Polytrichum formosum*, *Rhytidiadelphus triquetrus* (all frequent but unevenly represented in different sub-communities) and *Dicranum scoparium*, *Mnium hornum*, *Plagiothecium undulatum*, *Atrichum undulatum* and *Eurhynchium praelongum* (occasional to frequent throughout). Except in more north-westerly stands, hepatics are usually few in number, but *Lophocolea bidentata s.l.* occurs quite commonly and *Plagiochila asplenoides* is occasional. As among the herbs, it may again be noted that the balance among the bryophyte element is towards the calcifugous, with species such as *Thamnium alopecurum* and *Eurhynchium striatum* of restricted occurrence, one further reflection of the prevalence of surface leaching in the soils here.

Sub-communities

***Dryopteris dilatata* sub-community:** *Blechno-Quercetum fraxinetosum* Klötzli 1970 *p.p.*; *Oxalido-Betuletum typicum* Graham 1971; Loch Lomond Community types 4, 8, 9 & 10 Tittensor & Steele 1971; Hazel-ash stand types 3C & 3D Peterken 1981 *p.p.*; Oak-lime stand type 5B Peterken 1981 *p.p.*; Birch-oak stand types 6Ac & 6Bc Peterken 1981 *p.p.*; *Lonicero-Quercetum*, *Endymion* & Typical subassocations (Birse & Robertson 1976) Birse 1984 *p.p.*; *Luzulo-Betuletum*, *Rubus saxatilis* subassociation Birse 1984. Oak, almost invariably *Q. petraea*, is more frequent than birch in this sub-community and quite commonly it dominates in high forest with a tall (sometimes more than 20 m) canopy that is almost closed. In such situations, *B. pubescens* (only rarely *B. pendula* or intermediates) may be relegated to being a coloniser of gaps: a frequent picture is for there to be occasional birch and some large *Sorbus aucuparia* forming a sparse second tier to the canopy below the oak. In disused oak coppices, too, which are quite widespread here, birch may be sparse, though where it does spread in, it sometimes overtops the often quite low and poorly-growing oak. In other stands, birch may be proportionately much more abundant, forming, with occasional *Sorbus*, a patchily dense cover with just a few oaks. *Fraxinus* is occasional in the canopy of this kind of *Quercus-Betula-Oxalis* woodland though its saplings are rare.

Corylus is also preferentially frequent here and it may be plentiful enough to form a distinct understorey in oak high forest, though the bushes are usually fairly small and their total cover low. In some sites, it has clearly been selected for in what is now disused hazel coppice with oak reduced to occasional standards. Elsewhere, *Corylus* joins *B. pubescens* and *Sorbus* as a co-dominant in open scrubby thickets (as in some of the Teesdale stands: Graham 1971). *Crataegus monogyna*, though not nearly so common here as in the *Quercus-Pteridium-Rubus* woodland, is preferential for this sub-community. The most frequent saplings are those of birch.

In the field layer here, at least where the soil cover is moderately deep and not too much broken by boulders, *Hyacinthoides* is a common vernal dominant. As it fades, ferns generally become the most prominent element and by late July, *Pteridium* fronds are fully expanded and the crowns of *Dryopteris dilatata*, *D. filix-mas* and *D. borreri*, all preferential here, have their new foliage. *Pteridium* tends to follow *Hyacinthoides* in favouring more extensive soil covers and then it can produce a dense canopy; the dryopteroids, on the other hand, can extend amongst or on top of moss-covered boulders or grow around the tree bases, a feature well

https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press

seen in Graham's (1971) *Oxalido-Betuletum*, where distinct variants are recognised on this basis. *Gymnocarpium dryopteris*, *Thelypteris phegopteris* and *T. limbosperma* can all be locally prominent here, though the last is not so common or characteristic as in the *Blechnum* sub-community. *Blechnum* itself is also rather infrequent.

Lonicera periclymenum and, especially, *Rubus fruticosus* agg. are both more frequent in this sub-community than in other kinds of *Quercus-Betula-Oxalis* woodland, though their abundance is distinctly patchy. When plentiful, they can provide an important structural element by mid-summer, but quite often they form a rather sparse cover which does not completely mask the herbs that grow between the ferns. Among these, there is a slight shift away from species indicative of more markedly leached soils and a somewhat more luxuriant physiognomy. All the characteristic grasses of the community are well represented with, in addition, *Deschampsia cespitosa* becoming occasional in moister areas but *Galium saxatile* and, more noticeably, *Potentilla erecta* are reduced in frequency. The shade-tolerant *Oxalis* can be very abundant and taller herbs like *Teucrium scorodonia*, *Digitalis purpurea* and the sprawling *Stellaria holostea* are frequent. The small rosettes of *Viola riviniana*, on the other hand, are rather uncommon.

The same trends can be seen among the bryophytes which have consistently lower cover beneath this extensive layer of bulkier herbs. *Hylocomium splendens*, *Pleurozium schreberi*, *Thuidium tamariscinum*, *Dicranum majus* and *Polytrichum formosum*, which are such a prominent component of bryophyte mats in the *Blechnum* sub-community, are all rather infrequent here and sometimes this element of the vegetation is reduced to *Rhytidiadelphus squarrosus*, *Pseudoscleropodium purum*, *Hypnum cupressiforme* and *Eurhynchium praelongum* growing among the herbs and over their litter. More open areas of soil fern stools and tree bases may have *Atrichum undulatum*, *Mnium hornum* and *Dicranum scoparium* and wherever boulders break up the surface, there can be a greater richness and cover among the bryophytes.

***Blechnum spicant* sub-community:** Heathy birchwood Pigott 1956; *Betuletum Oxaleto-Vaccinietum* McVean & Ratcliffe 1962 *p.p.*; *Betula* herb nodum McVean & Ratcliffe 1962 *p.p.*; *Blechno-Quercetum typicum* and *coryletosum* Klötzli 1970 *p.p.*; *Oxalido-Betuletum vaccinietosum* Graham 1971 *p.p.*; Loch Lomond Community types 2, 3 & 4 *p.p.* Tittensor & Steele 1971; *Betula pubescens-Vaccinium myrtillus* Association Birks 1973 *p.p.*; *Corylus avellana-Oxalis acetosella* Association Birks 1973 *p.p.*; Birch-oak stand types 6Ab & 6Bb Peterken 1981 *p.p.*; Birch stand type 12A Peterken 1981 *p.p.*; *Blechno-Quercetum*, Typical subassociation Birse 1984 *p.p. B. pubescens*, often ssp. *carpatica*, is the usual dominant here, forming, with frequent *Sorbus* and occasional *Corylus*, a low and often rather open canopy. Commonly, there is no understorey, though smaller birch and rowan can occur in gaps and may form a scrubby fringe to stands where grazing is less intense. Oak is scarce but the occasional trees that are encountered are almost always *Q. petraea*. *Fraxinus* can be found very rarely.

As in the *Dryopteris* sub-community, *Hyacinthoides* occurs frequently as a vernal plant and quite commonly here it is preceded by the flowering of *Primula vulgaris* or, in very moist places, *Anemone nemorosa*. But the cover of these species is very much restricted in more bouldery woods to patches of deeper soil and it is a marked feature of many of the more rocky or heavily-grazed stands that there is relatively little seasonal change in the appearance of the vegetation.

Where the soil mantle is more extensive, grasses typically make up the bulk of the field layer, with mixtures of all the characteristic community species forming a varied and fairly open-textured sward. In late spring, there is a flush of new growth but heavy grazing often keeps the cover fairly short and smaller herbs like *Oxalis*, *Galium saxatile* and *Potentilla erecta* occur frequently and with patchy abundance. Less commonly, there can be some *Luzula pilosa*, *Veronica chamaedrys*, *V. officinalis*, *Teucrium scorodonia*, *Conopodium majus*, *Succisa pratensis*, *Melampyrum pratense* and *Stellaria holostea* and, in inaccessible spots, as in boulder crevices, these may thicken up to form a more luxuriant cover.

In many stands, too, ferns add further variety by mid-summer. *Pteridium* is common and, on deeper soils, it can be abundant, taking over dominance from the grasses and herbs by August or permanently extinguishing most of them with its thick accumulations of litter and heavy shade. But more characteristic here is *Blechnum spicant* which is very frequent both in the grassy swards and amongst boulders, and often very luxuriant in the characteritically moist climate in which these woods grow. *Thelypteris limbosperma* is frequent too and *Athyrium filix-femina* occasional and there can be locally abundant *Thelypteris phegopteris*, *Gymnocarpium dryopteris* and *Dryopteris aemula*. Where this sub-community extends over the very broken ground of boulder-choked ravines, all these can occur together creating the feel of an extraordinarily lush hanging garden.

The other component which contributes very greatly to this impression is the bryophytes. Even amongst the grasses, these can be abundant and varied provided, as is

https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press

usually the case, grazing keeps the height of the vascular plants low. Then, *Pleurozium schreberi*, *Rhytidiadelphus loreus*, *Dicranum majus* and *Polytrichum formosum* frequently join the community constants in a diverse patchwork over the ground. But the bryophytes become especially prominent here where the soil cover thins out over stable rock surfaces and they can provide a virtually continuous cover over nidus-capped boulders. On the flat and gently-sloping tops of such rocks, the vegetation is essentially a bryophyte-rich and fragmented version of the field layer, though with a shift towards a more calcifugous composition with the increased acidity of the very shallow and strongly-leached soils. In effect, such a flora represents a local occurrence of one of the suite of species that is fully developed in the *Quercus-Betula-Dicranum* woodland. Most of the grasses, *Deschampsia flexuosa* being the notable exception, fall in frequency and many of the mesophytic herbs disappear, though *Oxalis*, *Potentilla erecta* and *Galium saxatile* can remain common. *Blechnum* occurs occasionally, too, and it is here that *Vaccinium myrtillus* can make an appearance. The bulk of the cover, though, is provided by such mosses as *Hylocomium splendens*, *Rhytidiadelphus loreus*, *Dicranum majus*, *Pleurozium schreberi*, *Polytrichum formosum*, *Thuidium tamariscinum* and sometimes its more Atlantic counterpart *T. delicatulum*. Less frequently, there may be some *Hylocomium brevirostre*, *H. umbratum*, *Isothecium myosuroides*, *Rhytidiadelphus triquetrus*, *Ptilium crista-castrensis* and the hepatics *Diplophyllum albicans* and *Plagiochila spinulosa* (McVean & Ratcliffe 1962, Ratcliffe 1968, Birks 1973).

An increasing prominence of siliceous boulders in this kind of situation, with the progressive extinction of the more mesophytic flora on the drift or downwash soils between them and the appearance of a distinctive suite of bryophytes on the boulder sides, marks a transition to the *Quercus-Betula-Dicranum* woodland. Quite often, though, such zonations are gradual and complex mosaics can occur, a feature well seen in the patterns over drift and Torridonian sandstone in Skye (Birks 1973). In such regions, too, enrichment with more Atlantic bryophytes can occur throughout both communities, exaggerating the convergence between the vegetation types. Full details of the extraordinary abundance and diversity of this flora is given under the *Quercus-Betula-Dicranum* woodland where there is also an account of the specialised suite found on rotting logs and the species epiphytic on birch. On hazel, rather more characteristic of the *Quercus-Betula-Oxalis* woodland, epiphytes include *Ulota crispa* (subsuming *U. bruchii*), *U. phyllantha*, *U. calvescens*, *Frullania dilatata* and *F. teneriffae* on twigs (the *Uloteto-Frullanietum* of Barkman 1958), *Dicranum scoparium*, *Isothecium mysuroides*, *Hypnum mammilatum*, *Neckera complanata*, *Radula complanata* and *Metzgeria furcata* on trunks (the *Scoparieto-Hypnetum* of Barkman 1958) and *Eurhynchium striatum*, *Hylocomium brevirostre* and *Mnium hornum* on the tree bases (the *Eurhynchietum striatae* of Barkman 1958) (Birks 1973). On hazel bark, too, and on the occasional oaks, larger foliose lichens may occur in Lobarion pulmonariae communities (e.g. Rose 1974, James *et al.* 1977).

Anemone nemorosa **sub-community:** Caithness birchwoods Crampton 1911 *p.p.*; Scottish beechwoods, *Holcus* type Watt 1931*a*; Birch stand type 12A Peterken 1981 *p.p.*; *Trientali-Betuletum*, typical subassociation Birse 1982 *p.p.* Either oak or birch, or mixtures of the two, can dominate here but, in this eastern Scottish sub-community, there is a clear shift in the taxa represented. In contrast to more western stands of the *Quercus-Betula-Oxalis* woodland, when oak is present here it generally shows some obvious *robur* characteristics though pure *Q. robur*, like pure *Q. petraea*, is rare. And, though *B. pubescens* remains quite frequent, it is not as common, especially in the lower-altitude stands, as *B. pendula*. The structure of the woodland varies: sometimes oak is predominant as a fairly tall and quite closed canopy with birch occasional in gaps; in other cases birch is much the more abundant, forming a cover that can be quite open. Other trees are rare, though *Fagus* can sometimes be found and certain of the beech plantations described by Watt (1931) are essentially this kind of *Quercus-Betula-Oxalis* woodland in which there has been a canopy replacement.

Typically, shrubs and saplings are very sparse and rarely is there a true understorey. *Corylus* occurs very occasionally and sometimes there is a little *Sorbus aucuparia* and some young birch.

Although the field layer here preserves the general characteristics of the community as a whole, it has a number of distinctive features. First, by contrast with western stands, *Hyacinthoides* is rare and the most prominent plant in early spring, even on drier ground, is usually *Anemone nemorosa*. Then, as this finishes flowering, another good preferential, *Trientalis europaeus*, often becomes obvious. Among the carpet of grasses and herbs that gives the vegetation its typical early summer appearance, there are some further species which show a slight rise in frequency here. *Luzula pilosa* is especially common and there is occasionally some *Melampyrum pratense*, *Lathyrus montanus* and *Rubus idaeus*. *Veronica chamaedrys*, *V. officinalis*, *Hypericum pulchrum* and *Ajuga reptans* can also be found, though they are more strongly preferential for the *Stellaria-Hypericum* sub-community. Some stands have *Rubus saxatilis*. A further striking feature is that, apart from *Pteridium* which quite commonly assumes dominance by August, ferns are scarce: *Blechnum spicant* is found

https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press

only occasionally, *Thelypteris limbosperma* is only very locally prominent and dryopteroids are generally very infrequent.

Bryophytes in this sub-community can be quite extensive, though in the markedly drier climate of the region, they do not show the variety or luxuriance characteristic of western stands. But all the community species remain frequent, *Pleurozium schreberi* and *Dicranum majus* are also common and, in addition, there is often an abundance of *Rhytidiadelphus triquetrus*. As usual in the *Quercus-Betula-Oxalis* woodland, when the flush of spring and summer growth among the herbs is over, it is the bryophyte carpet which continues to give this vegetation its verdure throughout the winter.

***Stellaria holostea-Hypericum pulchrum* sub-community:** *Trientali-Betuletum*, typical subassociation Birse 1982 *p.p.*; *Lonicero-Quercetum*, *Endymion* and typical subassociations (Birse & Robertson 1976) Birse 1984 *p.p.* The general character of the woody cover here is very similar to that of the *Anemone* sub-community, though the shift among the oak and birch taxa is a little more pronounced. *Quercus* hybrids and pure *Q. robur* tend greatly to outnumber *Q. petraea* and the birch is generally *B. pendula* with *B. pubescens* only occasional. Again, the structure is variable, with either oak or birch predominating but typically the canopy is open and quite low. Some stands are abandoned oak coppice but, even among those which have a high forest physiognomy, shrubs are sparse with only occasional *Corylus* and very scarce *Crataegus monogyna*.

In the field layer, there is generally no marked vernal aspect to the vegetation, though *Anemone* does occur occasionally and locally it can be abundant. *Trientalis*, too, shows a depressed frequency compared with the previous sub-community. More obviously distinctive here is a shift in the character of the grass and herb sward towards a somewhat more mesophytic composition. Species such as *Anthoxanthum odoratum*, *Agrostis tenuis* and, more especially, *A. canina* ssp. *montana* and *Deschampsia flexuosa*, are less generally prominent here; even where they remain frequent, their cover is patchy or consistently reduced. By contrast, *Holcus mollis* is often abundant and *Festuca rubra* and *Holcus lanatus* become preferentially frequent. Among the dicotyledons, *Potentilla erecta* is somewhat less common than in the *Blechnum* and *Anemone* sub-communities and there is a pronounced rise in *Veronica chamaedrys*, *V. officinalis*, *Ajuga reptans*, *Cerastium fontanum* and, especially characteristic here, *Stellaria holostea* and *Hypericum pulchrum*. *Luzula multiflora* tends to replace *L. pilosa* and there is occasionally some *Rumex acetosa* and *Angelica sylvestris*.

The bryophyte carpet too, though it can retain the high cover typical of the community, reflects this trend. *Hylocomium splendens*, though frequent, is distinctly patchy in its abundance and species such as *Pleurozium schreberi*, *Dicranum majus*, *Polytrichum formosum* and *Rhytidiadelphus loreus* are very rare or totally absent. *R. triquetrus*, as in the *Anemone* sub-community, is constant but here its most consistent companions are *R. squarrosus*, *Pseudoscleropodium purum*, *Thuidium tamariscinum*, *Eurhynchium praelongum* and, good preferentials here, *Plagiomnium undulatum* and *Lophocolea bidentata s.l.*

Habitat

The *Quercus-Betula-Oxalis* woodland is typically a community of moist but free-draining and quite base-poor soils in the cooler and wetter north-west of Britain. Grazing by stock and deer contributes greatly to the character of the field layer and affects the physiognomy of the woody cover of the community by hindering regeneration. Many stands have been treated as coppice and there is evidence of widespread timber removal and some planting.

The *Quercus-Betula-Oxalis* woodland is confined to those parts of Britain where the annual rainfall exceeds 1000 mm (*Climatological Atlas* 1952), and where there are over 160 wet days yr^{-1} (Ratcliffe 1968). Indeed, except in eastern Scotland, precipitation is generally more than 1200 mm yr^{-1} (with about 180 wet days) and, in the far west, often approaches 3000 mm (with more than 220 wet days). Mean annual maximum temperatures over most of the region are less than 25 °C, in much of Scotland less than 23 °C (Conolly & Dahl 1970). Within the areas characterised by this kind of climate, the *Quercus-Betula-Oxalis* woodland is typically found on the slopes of the upland fringes, extending up to more than 450 m in some places, but generally below 180 m.

Within this zone, it is characteristic of substrates that are neither markedly calcareous nor strongly acidic: it is absent from limestones, even in the very wet far north-west, and does not extend far on to sandstones and grits or pervious and acidic igneous or metamorphic rocks unless there is a mask of superficial deposits or some moderate degree of base-enrichment from downwash waters or by diffuse flushing along seepage lines. It occurs widely on argillaceous rocks like Ordovician and Silurian shales in south-west Scotland, the Lake District and north Wales and, more locally, on Upper Carboniferous shales in the northern Pennines. It also picks out interbedded or intruded rocks of less extreme character occurring within masses of predominantly acidic deposits like the Lewisian gneiss along the north-west seaboard of Scotland, Palaeozoic plutonic rocks in Aberdeenshire, the Borrowdale Volcanics of the Lake District and the Devonian Old Red Sandstone around the Moray Firth and, more locally, in southern Perthshire. Colluvium, head, till and, especially in eastern

https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press

Scotland, fluvioglacial deposits, also provide substrates.

Typically, the soils developed from such deposits show no more than incipient podzolisation under this deciduous woodland. The surface pH is usually in the range 3.5–5.0 but the humus is very often of the transitional moder type and the profile generally a brown earth or brown podzolic soil (Avery 1980). There is typically a weathered B horizon with some accumulation of iron, manganese and organic matter but usually no distinct iron pan or humus-rich B_h (e.g. McVean & Ratcliffe 1962, Tittensor & Steele 1971, Birks 1973, Birse 1982, 1984). In soils derived from shales or colluvium or superficials that are neither too heavy-textured nor excessively free-draining, there is often a somewhat better structure with the profile approaching a mull brown earth, conditions often associated here with the *Dryopteris* sub-community. To the other extreme, as often in the *Blechnum* sub-community, this woodland can extend over areas where there are accumulations of siliceous boulders which carry thin and fragmentary rankers.

The general confinement of the community to base-poor but not excessively-leached brown soils gives the *Quercus-Betula-Oxalis* woodland much of its floristic character and helps to define its limits against its north-western counterparts on more calcareous or more strongly-podzolised profiles, distinctions which are very well seen in the range of communities defined from Loch Lomond by Tittensor & Steele (1971) and, on a finer scale, in the mosaics described from Skye by Birks (1973). On the one hand, calcicoles are fairly rigidly excluded from this community and the nearest approach to the *Fraxinus-Sorbus-Mercurialis* woodland is seen where species characteristic of more enriched mull soils appear in the *Dryopteris* sub-community or, less consistently, in other sub-communities where there is some local flushing.

On the other hand, edaphically-related distinctions between the *Quercus-Betula-Oxalis* woodland and the *Quercus-Betula-Dicranum* woodland, which replaces it on rankers and podzols, are much less sharp. The balance in the floristic composition here, among the grasses, dicotyledons, ferns and bryophytes, is clearly towards the calcifugous (much more so than in its southern analogue, the *Quercus-Pteridium-Rubus* woodland), and towards the very wet far north-west, it becomes increasingly difficult to define the limits of the community, a very real reflection of the overwhelming tendency towards leaching of all but the most calcareous lithomorphic soils in moving towards this region. In such extreme situations, the distinction between the *Quercus-Betula-Oxalis* and the *Quercus-Betula-Dicranum* woodlands is the scarcity here of *Vaccinium myrtillus* and *Calluna vulgaris*, the persistence of less markedly calcifuge grasses like *Anthoxanthum odoratum* and *Agrostis capillaris* and, more especially, of *Hyacinthoides*. It should be noted, though, that grazing, which is very widespread in both communities, can reduce *Hyacinthoides* here and eliminate *Vaccinium* from the *Quercus-Betula-Dicranum* woodland, so tending to make the two vegetation types converge.

The other floristic boundary directly affected by soil conditions is that with wetter woodlands. Typically, the profiles here are kept moist throughout the year, a feature which is important to the maintenance of high frequencies of *Oxalis acetosella* and *Viola riviniana* and to the abundance of bryophyte mats. But they are characteristically free-draining, sometimes excessively so where the community runs some way on to pervious rocks over steeper slopes. This probably plays some part in the general scarcity here of *Q. robur*, at least in the west (e.g. Jones 1959), and the confinement of more mesophytic ferns and dicotyledons to the *Dryopteris* sub-community. Occasionally, flushing can be quite pronounced, especially where soil water encounters shale bands or heavy drift, and then the vegetation may take on some of the character of the *Alnus-Fraxinus-Lysimachia* woodland (well seen in the Community type 5 of Tittensor & Steele 1971), but gleying is rare.

As well as affecting the vegetation through variation in the soils, climate is directly important to the composition of the *Quercus-Betula-Oxalis* woodland in a number of ways. In the first place, the generally low summer temperatures virtually exclude any Continental or Continental Southern elements from the flora. Such species are not very numerous even in the southern analogue to this community, the *Quercus-Pteridium-Rubus* woodland, but they hardly penetrate into the range of the *Quercus-Betula-Oxalis* woodland. *Tilia cordata* persists as a relic on some cliffs and ravines within stands of the community in the Lake District (Pigott & Huntley 1978) and such woodland would therefore fall into the oak-lime stand type 5B of Peterken (1981) but species such as *Carpinus betulus*, *Crataegus laevigata*, *Euphorbia amygdaloides* and *Lamiastrum galeobdolon* are generally absent.

On the other hand, the difference between the mean temperatures of the warmest and coldest months of the year within the range of the *Quercus-Betula-Oxalis* woodland is, for the most part, significantly smaller than that of the lowland south and east and this is very much a community of the more equable parts of Britain. This, and the markedly higher rainfall to the north-west, gives the climate a distinctly oceanic character. The impact of this, as might be expected, can be best seen in the two more westerly sub-communities. These can be understood as continuing a floristic trend within British 'bluebell woods', first visible in the *Acer-Oxalis* sub-community of the *Quercus-Pteridium-Rubus* woodland, continuing through the *Dryopteris* sub-community of

https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press

the *Quercus-Betula-Oxalis* woodland and terminating in the *Blechnum* sub-community. In this sequence of woodlands, the maintenance of vernal dominance by *Hyacinthoides* (itself a markedly Atlantic species in Europe: Noirfalise 1968, Roisin 1969), is accompanied by a switch among the oaks and birches to *Q. petraea* and *B. pubescens*, a rise in the prominence of ferns and a lush bryophyte component and, more particularly, an increasing representation of Widespread Atlantic (*sensu* Ratcliffe 1968) mosses and hepatics. Elements of this bryophyte flora can be seen sporadically in *Quercus-Betula-Oxalis* woodlands of north Wales and north-west England but, along the north-west seaboard of Scotland, with its relatively mild, extremely wet and very cloudy climate, these species become a very prominent feature, especially where local topographic variation (like north-facing slopes or deep ravines) accentuates the shelter even further. Exactly what it is among the complex of factors involved in oceanicity that favours these plants is probably quite varied and still uncertain, but the constancy of the humid conditions is probably of major importance, ameliorating desiccation by wind and sun and muting the effects of frosts (Ratcliffe 1968). Most of the species are not strictly associated with this community, or even with woodland in general, but the fact that the *Quercus-Betula-Oxalis* woodland provides an insulating canopy over diverse topography in the far north-west is probably of considerable importance in maintaining the conditions that encourage a rich and diverse flora of this kind.

On moving to the east of Scotland, climatic differences produce some obvious effects in the community. Compared with much of the lowland south-east, the climate here is still very wet but much less so than at identical latitudes on the west coast, with annual rainfall and the number of wet days more like the levels reached along the Lakeland fringes and the foothills of Snowdonia. Furthermore, though the summers are warmer than to the west, the winters are considerably colder, so the regional climate has an element of continentality. This may play a part in the rise to prominence of *B. pendula* in the *Anemone* and *Stellaria-Hypericum* sub-communities here and is certainly involved in the scarcity of *Hyacinthoides*, here replaced by *Anemone*, not in the sort of edaphic shift common in the south-east, but in some kind of response to climate. The appearance of the Northern Montane *Trientalis* is probably also related to the cooler conditions. Although the longer snow cover in this region (Manley 1940) may help some more drought-sensitive bryophytes to persist (Ratcliffe 1968), most of the Atlantic species of the *Blechnum* sub-community are absent. What factor lies behind the striking rise in *Rhytidiadelphus triquetrus* in these two sub-communities (and in eastern Scottish types of *Quercus-Betula-Dicranum*, *Pinus-Hylocomium* and *Juniperus-Oxalis* woodlands) is unclear.

Despite these internal variations within the *Quercus-Betula-Oxalis* woodland in relation to climate and soils, it is of general significance that it replaces the *Quercus-Pteridium-Rubus* woodland in the north-west, where predominantly non-calcareous parent materials have weathered to produce base-poor soils in a cool and wet climate. But there is a further factor of great importance to the floristic distinctions between these two kinds of woodland, the intensity of which roughly corresponds to this major climatic and edaphic divide: it is grazing. Very often, stands of the *Quercus-Betula-Oxalis* woodland are open to stock: many occur on the slopes which lie towards the upper limit of enclosure on upland farms and they provide grazing, mostly for sheep but also sometimes for cattle, especially in winter, when they also give shelter in the frequently inclement weather. They are also extensively grazed by deer, mainly red and roe deer in northern England and Scotland, with naturalised fallow deer (*Cervus dama*) in north Wales and locally elsewhere (around Loch Lomond, for example, where feral goats are also present: Tittensor & Steele 1971). The effects of grazing and browsing can be seen throughout the community, though they are particularly obvious in the *Blechnum*, *Anemone* and *Stellaria-Hypericum* sub-communities: it is likely that the distinctive features of the *Dryopteris* sub-community can sometimes reflect lighter or less consistent grazing or, at least, that relaxation of grazing favours its development on less strongly leached soils (e.g. Tittensor & Steele 1971).

The activities of these larger herbivores are probably partly responsible, first, for the general scarcity of saplings and shrubs in most *Quercus-Betula-Oxalis* woodlands (cf. Yapp 1953). Even given the fact that many stands have been kept clean of shrubs for oak-coppicing and remembering that birch regenerates with difficulty even under its own canopy, the typically sparse understorey here is likely to depend to some extent on the continual devouring of seedlings and the browsing of such saplings as do get away. Young trees of *Q. petraea*, for example, which seem to be better able to regenerate within closed woodland than *Q. robur* (e.g. Jones 1959) are very sparse; saplings of birch, *Sorbus* and, when it is present, *Fraxinus* are often very slow to appear in gaps or around the fringes of stands; and *Corylus* thickens up to form a distinct understorey only in the *Dryopteris* sub-community. Furthermore, when access to stock and deer is restricted, as where stands occur on islands or are fenced, there is often a clear response among the woody species, notably in the shade-tolerant *Sorbus* within the woods and in birch in the adjacent unwooded areas (e.g. McVean 1958).

Second, grazing is certainly of prime importance in maintaining the high frequency and abundance of such grasses as *Anthoxanthum odoratum*, *Deschampsia flex-*

https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press

uosa, *Agrostis* spp. and *Festuca* spp. in the field layer and in restricting the prominence of tall luxuriant herbs and underscrub. These latter components attain consistently high frequency here only in the *Dryopteris* sub-community, though lusher herbs can be found elsewhere where there is a measure of local protection. *Luzula sylvatica*, for example, can become very prominent in island stands (Tittensor & Steele 1971) and on precipitous slopes (Birse 1984) and, where the community extends over acid boulders, *Vaccinium myrtillus* may attain local abundance (as in some of the stands of McVean & Ratcliffe 1962 and Birks 1973). Sets of woodlands with different intensities of grazing, like those described from Loch Lomond (Tittensor & Steele 1971), may show a continuous gradation in the prominence of these grazing-sensitive elements in the vegetation, but, as a rule, they are not very obvious.

Third, since grazing generally keeps the field layer short, it encourages an abundance of bryophytes, especially those bulky pleurocarpous mosses which can grow amongst grass tillers and expand to fill any gaps developing in the cover. In very heavily grazed stands, as in those where there is much talus, bryophytes may account for the bulk of the ground cover.

Very often now, grazing in these woods is uncontrolled, representing the renewal of a treatment which has operated for many centuries and which has probably been the major factor in reducing the extent of the community (e.g. McVean & Ratcliffe 1962, McVean 1964*a*, Pearsall 1968, Pearsall & Pennington 1973). But there is also abundant evidence in many surviving stands of the past use of the *Quercus-Betula-Oxalis* woodland as coppice, perhaps managed in conjunction with controlled grazing, but carefully treated to yield a continual supply of underwood and timber. Some tracts have been used as hazel coppice, sometimes with oak standards (falling within the hazel-ash stand types 3C and 3D or hazel-rich birch-oak woods of Peterken 1981) but the most widespread crop was oak itself. In the north-west of Britain, this community, together with the more calcifugous *Quercus-Betula-Dicranum* woodland, has been the major source of oak for charcoal (particularly important for iron-smelting, especially from the sixteenth to the eighteenth centuries), tan-bark, pit-timber and constructional timber (e.g. Tittensor 1970*a*, *b*; Tittensor & Steele 1971, Pearsall & Pennington 1973, Linnard 1982). Birch and hazel also provided wood for cotton-bobbins in Lake District stands (Pearsall & Pennington 1973). For the most part, such treatments have become defunct but they have left a lasting legacy in the physiognomy and floristics of the woody component in many areas. Quite commonly, oak dominates as regularly-disposed old coppice stools and scattered through the woods there are often flat, circular platforms (pit-steads) where the charcoal heaps were constructed and, between them, interconnecting paths used repeatedly by the burners (e.g. Pigott & Huntley 1978, Barker 1985). In other cases, especially in stands towards the north-west of Scotland, the scarcity of oak is probably partly due to extensive extraction of the best timber over many generations. And, in eastern Scotland, too, repeated cutting of oak has led to a general run-down of many woods with an increasing prominence of birch.

There is evidence from some parts of the country that some oak coppices belonging to the *Quercus-Betula-Oxalis* woodland were planted to supplement the relatively small amount of woodland surviving from previous times. Planting in may explain the prominence of *Q. robur* or hybrid derivatives in eastern Scottish stands of the *Anemone* and *Stellaria-Hypericum* sub-communities (Jones 1959, Gardiner 1974). The causes of the floristic differences between these two kinds of *Quercus-Betula-Oxalis* woodland are uncertain, but it is possible that the *Stellaria-Hypericum* type includes younger or more modified stands. *Q. robur* elements are a little more prominent here, the slow-spreading *Anemone* is scarce and herbs such as *Veronica chamaedrys*, *V. officinalis*, *Hypericum pulchrum*, *Festuca rubra* and *Holcus lanatus* create the same effect as can be seen in the *Holcus* sub-community of the *Quercus-Pteridium-Rubus* woodland, often a planted replacement for southern 'bluebell woodland'. However, it is likely that, in time, hardwood plantations can acquire the essential features of the *Quercus-Betula-Oxalis* woodland, as seen in some of Watt's (1931) Scottish beechwoods which were established in the mid-nineteenth century.

Zonation and succession

Zonations within stands of the community and between the *Quercus-Betula-Oxalis* woodland and other vegetation types are most frequently related to edaphic differences and variation in grazing intensity. Often, the effects of these factors can be seen in isolation but, since lighter grazing and a tendency towards mull development can produce similar results in the field layer, it is sometimes difficult to disentangle their influence. Transitions from the *Blechnum* to the *Dryopteris* sub-community, for example, may result from either of these causes; and, in some cases, they may be operating together (e.g. Tittensor & Steele 1971).

Soil-related zonations here directly parallel the patterns found among analogous woodlands in the lowland south, with transitions to more calcicolous, more calcifugous and wetter woodlands occurring commonly. On more base-rich soils, the *Quercus-Betula-Oxalis* woodland typically gives way to the *Fraxinus-Sorbus-Mercurialis* woodland, provided the soils do not, at the same time, become very wet. Such zonations are frequent but local in the west and they often reflect a change in the character of the underlying rock, as where limy partings occur interbedded with shales in Silurian deposits in Wales, the Lake District and southern Scotland or in Carboniferous sequences in the Pennines, where andesite occurs within the Borrowdale Volcanics of the Lake District (Pearsall 1968, Pearsall & Pennington 1973), where Carboniferous Limestone replaces the intruded dolerite in Teesdale (Pigott 1956*a*, Graham 1971) and where Durness Limestone and Torridonian deposits are juxtaposed on Skye (Birks 1973). In such situations, there may be a fairly sharp switch from the *Blechnum* sub-community here to the Typical sub-community of the *Fraxinus-Sorbus-Mercurialis* woodland or, on less sharply contrasted soils and where grazing is less intense, from the *Dryopteris* sub-community to the *Crepis* sub-community of the *Fraxinus-Sorbus-Mercurialis* woodland.

Quite often, however, changes in soil conditions are much more gradual or uneven than this, being related to quite slight differences in the calcareous character of a drift cover or bedrock or to diffuse flushing by base-rich waters. Then, particularly if the woodlands are grazed, the characteristic grasses of the *Quercus-Betula-Oxalis* woodland may continue some way into the *Fraxinus-Sorbus-Mercurialis* woodland and more calcicolous herbs like *Mercurialis perennis*, *Geum urbanum* and *Circaea lutetiana* make but a sporadic appearance at first. Over more complex topographies, as in ravines, there may be a very disorderly inter-digitation of the two communities over the surface of tumbled boulders, slumped masses of soil, rock faces and fragmentary patches of alluvium along the stream-side. Changes in the canopy, too, can be slight, especially in the far north-west, where *Q. petraea* and *Fraxinus* are scarce and where both these communities have a scrubby cover in which *B. pubescens* and *Sorbus* figure prominently. In such situations, a rise in the prominence of *Corylus* may mark the transition but, further south, it is *Fraxinus*, less commonly *Ulmus glabra* and *Acer pseudoplatanus*, that increase. Where the *Quercus-Betula-Oxalis* woodland gives way to the *Fraxinus-Sorbus-Mercurialis* type along streams, these can often be picked out from afar as very distinct streaks of brighter green, a feature well caught in Pearsall (1968). In the Lake District, where such situations are quite frequent, relic stools of *Tilia cordata*, sometimes of immense size, can be found growing on the ravine edge which marks the boundary between the two communities (Pigott & Huntley 1978). Here, too, treatment has sometimes sharpened up the distinction between the communities, the *Quercus-Betula-Oxalis* woodland of the interfluves having been used as oak coppice, the transitional zone and *Fraxinus-Sorbus-Mercurialis* woodland proper of the ravine slopes having been inaccessible (Pigott & Huntley 1978).

The fact that flushing is often the factor responsible for base-enrichment within sites where the *Quercus-Betula-Oxalis* woodland is represented, means that transitions of this kind often involve elements of the *Alnus-Fraxinus-Lysimachia* woodland disposed over the very wettest ground with local patches of plants such as *Lysimachia nemorum*, *Deschampsia cespitosa*, *Chrysosplenium oppositifolium* and large sedges such as *Carex remota*, *C. pendula* or *C. laevigata*. On gentler slopes, this community may form fairly well defined flushes within the *Quercus-Betula-Oxalis* woodland: these are very characteristic of Carboniferous and Silurian sequences where ground water emerges when it hits impervious shales. In analagous situations where less base-rich ground water emerges, the *Alnus-Fraxinus-Lysimachia* woodland is replaced by soligenous *Betula-Molinia* woodland.

Zonations to woodland of freely-drained, acidic soils with pronounced mor accumulation and/or podzolisation typically involve replacement by the *Quercus-Betula-Dicranum* woodland and they can be seen throughout the range of the community wherever the influence of pervious and acidic parent materials increases and leaching can have its full effect. Sometimes, this involves a switch in the nature of the bedrock, as in moving on to Torridonian sandstones or Lewisian gneiss in north-west Scotland (e.g. Birks 1973, Ratcliffe 1977), or to more acidic strata in the Devonian Old Red Sandstone in eastern Scotland and in Silurian sequences in the Lake District, southern Scotland and Wales, to sandstones and grits in the Pennine Carboniferous or to acidic igneous rocks in the Lake District. In other cases, it is related to the thinning of a cover of colluvium or drift over such deposits or to the lessening of a flushing effect.

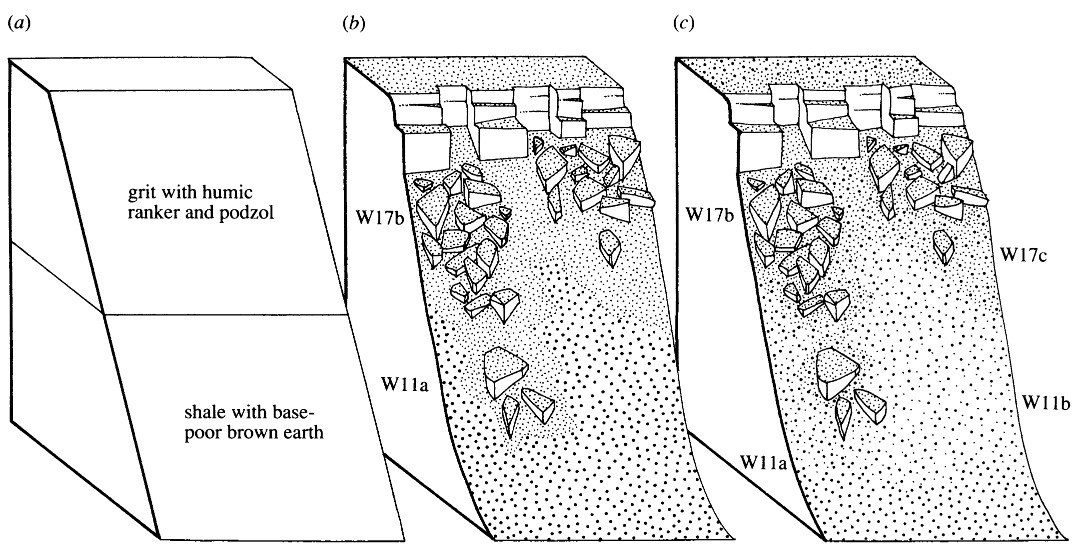
The floristic transitions involved here can already be seen to some extent within the *Quercus-Betula-Oxalis* woodland itself in the way in which the more strictly calcifugous element in the *Blechnum* sub-community rises to prominence as the soil cover thins to a humic cap over acidic boulders. But often the zonation continues over rankers and podzols to the *Isothecium-Diplophyllum* or Typical sub-communities of the *Quercus-Betula-Dicranum* woodland in the west (Figure 21). In eastern Scotland, there are analagous transitions from the *Anemone* and *Stellaria-Hypericum* sub-communities to the *Rhytidiadelphus* sub-community of the *Quercus-Betula-Dicranum* woodland. Locally, in this region, more calcifugous kinds of *Juniperus-Oxalis* woodland can replace the *Quercus-Betula-Dicranum* woodland in zonations of this kind and, in both east and west Scotland, the *Pinus-Hylocomium* woodland is locally associated with the *Quercus-Betula-Oxalis* woodland on more podzolised soils.

As noted earlier, the effect of grazing on the ericoid sub-shrubs which help distinguish the field layers of these communities, can blur the boundaries. But grazing also mediates zonations of its own, most notably to different kinds of the *Festuca-Agrostis-Galium* grassland, which is composed of virtually the same species as the field-layer constants of the *Quercus-Betula-Oxalis* woodland and which, in wetter regions, can have a number of its characteristic bryophytes. Very often, on the lower slopes of the uplands, the *Festuca-Agrostis* grassland runs straight into unenclosed *Quercus-Betula-Oxalis* woodland, the only changes across the junction being the appearance of trees, an increase in the cover and variety of bryophytes with the greater shelter and a patchy dominance of *Hyacinthoides* or *Anemone* in the spring. In more inaccessible spots within such woodlands, there may be some patchy regeneration of the canopy but there is no doubt that such zonations often represent the near-final stages in the conversion of the woodland to the grassland and that the completion of the process is then attendant only on the final destruction of the trees, an event which has been only too frequent in the long history of upland grazing.

Continued grazing maintains the *Festuca-Agrostis-Galium* grassland as a plagioclimax and recolonisation is rarely seen but it can be observed in some extensive fenced reserves or where tracts of upland have been enclosed for commercial forestry or around lake and reservoir catchments. Around Thirlmere, in the Lake District, for example, recolonisation of open grassland has been speedy: *B. pubescens*, *Sorbus* and *Corylus* have established themselves in local profusion and young *Q. petraea* can be found growing up through the thickets (Pearsall & Pennington 1973). Such enclosures could also provide opportunities for studying uninterrupted primary invasion of bare talus, free of the disturbance which the roaming of sheep and walkers bring. We do not know what the natural precursors of the *Quercus-Betula-Oxalis* woodland in such situations might be. The most likely candidates would seem to be open communities of bryophytes and ferns such as *Thelypteris limbosperma* and *Blechnum spicant* and, where there is a more extensive soil cover, vegetation like that of the *Luzula sylvatica-Vaccinium myrtillus* community. Fragments of such vegetation can often be found in more rocky situations close to the *Quercus-Betula-Oxalis* woodland; and, on inaccessible ledges with seepage of fairly base-poor waters within tracts of *Festuca-Agrostis-Galium* grassland, they can reproduce fairly faithfully the field layer of ungrazed *Quercus-Betula-Oxalis* woodland without a cover of trees. They also extend the distribution of this kind of herbaceous vegetation above the present tree-line in the Scottish Highlands and were considered by McVean & Ratcliffe (1962) as a tree-less facies of the community.

Some of the characteristic herbs of the *Quercus-Betula-Oxalis* woodland can also be found under a cover of bracken in the *Pteridium aquilinum-Galium saxatile*

Figure 21. Patterns among oak-birch woodlands in relation to soils and treatment.
At a grit-shale junction (*a*), a common pattern on ungrazed slopes is for W17b Typical *Quercus-Betula-Dicranum* woodland to give way below to W11a *Dryopteris* sub-community of *Quercus-Betula-Oxalis* woodland (*b*). With grazing, there is often a gradual transition between these two, W17c *Anthoxanthum-Agrostis* sub-community of the former passing imperceptibly to W11b *Blechnum* sub-community of the latter (*c*).



https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press

community and stands of this vegetation type are commonly seen in close association with the woodland and *Festuca-Agrostis-Galium* grassland. A characteristic pattern is for *Pteridium* to be very dense and vigorous over the colluvium on the lower slopes adjacent to the wood, thinning out to a sparse cover in the grassland above. This is just the kind of distribution that bracken shows within stands of the *Quercus-Betula-Oxalis* woodland but there is no doubt that, with the destruction of the woodland cover and freedom from shade, it can increase greatly in abundance. Stands of the *Pteridium-Galium* community sometimes preserve elements of the richness of the woodland flora, with a vernal carpet of *Hyacinthoides* or *Anemone*, but very often they are poor in associates and the great extension of bracken over the deeper soils of the uplands is an unfortunate side effect of the widespread destruction of the community, and a change that is difficult and costly to reverse.

There have been other permanent losses to coniferous forestry. The *Quercus-Betula-Oxalis* woodland will stand canopy replacement by *Fagus* (e.g. Watt 1931) and a moderate amount of coniferisation, but extensive planting of softwoods (except perhaps *Larix* spp.) greatly increases shade and speeds mor accumulation, thus accentuating the tendency to podzolisation in the wet climate, a process which is ameliorated by the natural cover of oak and birch.

Although the history of the loss of the *Quercus-Betula-Oxalis* woodland by these treatments has been long and complex, with local or temporary halts and reversals related to shifts in the balance of the upland economy, its decline has been progressive and very widespread. It seems to represent the climax type of oak-birch forest on less markedly leached soils in the north-west but now survives as fragments within its potential range, usually much affected by grazing and in landscapes devoted primarily to pastoral agriculture and commercial forestry. In one area, however, it is proportionately more prominent than might be expected and that is in east-central Scotland. Here, McVean & Ratcliffe (1962) proposed that pine-dominance was the more natural development in post-Glacial forests, a suggestion largely borne out by subsequent palynological studies (e.g. Birks 1970, Gunson 1975, O'Sullivan 1977). In fact, the tree cover of the original pine forest in this region seems to have been more diverse and intimately mixed than in surviving stands of the *Pinus-Hylocomium* woodland, such that both pine and birch probably occurred together over more acidic soils. With clearance, burning and grazing, birch has increased its relative prominence in this region, now holding sway in both the *Quercus-Betula-Dicranum* woodland on podzols and in the *Quercus-Betula-Oxalis* woodland on less strongly leached profiles in sites where *Pinus sylvestris* was once much better represented.

Distribution

The *Quercus-Betula-Oxalis* woodland is widely distributed through the upland fringes of Wales, north-west England and Scotland with a few stands in south-west England. To the west, the community is represented by the *Dryopteris* and *Blechnum* sub-communities, the former predominating in England, Wales and south-west Scotland, the latter present locally there but becoming much more prominent along the north-western seaboard of Scotland. Occasionally in southern Scotland but much more exclusively in north-east Scotland, these kinds of *Quercus-Betula-Oxalis* woodland are replaced by the *Anemone* and *Stellaria-Hypericum* sub-communities.

Affinities

The *Quercus-Betula-Oxalis* woodland as defined here unites some of the less heathy oak-dominated communities described in early studies (e.g. Crampton 1911, Tansley 1911, 1939) as falling within the general ambit of the *Quercetum petraeae*, and certain kinds of birch woodland characterised from higher altitudes and latitudes (e.g. Pigott 1956*a*, McVean & Ratcliffe 1962, Graham 1971, Birks 1973, Birse 1982, 1984). While recognising that, in more extreme habitats, the absence of oak may have some climatic basis, replacement by birch is often here a treatment-related phenomenon and, whichever tree is the dominant, the essential character of the field layer is preserved throughout (e.g. McVean 1964*a*, Tittensor & Steele 1971, Birks 1973). The diagnosis thus unites vegetation which has figured in some schemes under two different heads (e.g. Tansley 1939), or more, where weight has also been given to treatment-related prominence of *Corylus* or the presence of relic *Tilia* (e.g. Peterken 1981).

The distinctive features of the field layer here, though often much modified by grazing, help to place the *Quercus-Betula-Oxalis* woodland in a central position between communities of more calcareous soils on the one hand and more markedly leached soils on the other. Such a trio of woodland types has not generally been recognised in the north-west, though the need for the distinction is hinted at in McVean & Ratcliffe (1962) and given expression at sub-community level within associations described by Klötzli (1970) and Birse (1982, 1984). The difficulty has been that the most detailed studies have concentrated on areas where soil-related differences within the suite of woodlands tend to be masked by striking climatically-influenced similarities. In north-west Scotland, for example, all three communities occur under a scrubby cover in which *B. pubescens* predominates and have a very prominent bryophyte element in which many species are shared. In this region, the *Quercus-Betula-Oxalis* woodland as defined here includes only the central core of Klötzli's (1970) modifi-

https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press

cation of Braun-Blanquet & Tüxen's (1952) *Blechno-Quercetum*, and occupies a middle ground between the *Betuletum Oxalido-Vaccinietum* and *Betula*-herb nodum of McVean & Ratcliffe (1962) and the *Betula-Vaccinium* and *Corylus-Oxalis* Associations of Birks (1973), taking some of the less extreme samples from each. Likewise, it includes only the less calcifugous vegetation within Birse's (1984) version of the *Blechno-Quercetum*.

In eastern Scotland, the woodlands have been less extensively described but the prominence of such species as *Anemone nemorosa*, *Trientalis europaea* and *Rhytidiadelphus triquetrus* within communities of less- and more-leached soils led Birse (1982, 1984) to group together vegetation which is here divided between the *Quercus-Betula-Oxalis* and *Quercus-Betula-Dicranum* woodlands. The occurrence of *Trientalis* in these woodlands is not given as much diagnostic weight as in Birse (1982, 1984), so the *Quercus-Betula-Oxalis* woodland also subsumes most of his *Lonicero-Quercetum* which is virtually identical to less calcifugous stands of his *Trientali-Betuletum* apart from the absence of this Northern Montane plant.

Although Scottish stands of the *Quercus-Betula-Oxalis* woodland in both the east and west closely approach in their floristics the composition of more heathy woodlands dominated by *B. pubescens*, *Juniperus* and *Pinus*, the affinities of the community as a whole lie not with the Vaccinio-Picetea but with the Quercetea robori-petraeae, and the alliance Quercion robori-petraeae. This includes West European deciduous woodlands and their modified derivatives on acidic to only moderately base-rich soils, characterised by the prominence of oak and birch (and often in mainland Europe, beech) and the presence of such herbs as *Lathyrus montanus*, *Hypericum pulchrum*, *Teucrium scorodonia*, *Melampyrum pratense* and Hieracia of the Sabauda and Umbellata sections. The field layers are often grassy, with *Holcus mollis* and *Deschampsia flexuosa* well represented, frequently have some *Lonicera* and *Pteridium* and varying amounts of *Vaccinium myrtillus* and *Calluna*. The *Quercus-Betula-Oxalis* woodland is thus the British equivalent of such associations as the Quercetum medioeuropaeum. Br.-Bl. 1932 or the *Querceto-Betuletum* Tx. 1937 or their subsequent modifications described from France (Issler 1926, Malcuit 1929, Dethioux 1955), Switzerland (Braun-Blanquet 1932), Germany (Tüxen 1937, 1955, Oberdorfer 1957, Hartmann & Jahn 1967), the Netherlands (Westhoff & den Held 1969) and Belgium (LeBrun *et al.* 1955). The distinctive feature of these woodlands in north-west Europe, as in their counterparts in the Carpinion, is the vernal dominance of *Hyacinthoides* and those *Quercus-Betula-Oxalis* woodlands where this is combined with an abundance of bryophytes present a unique spectacle.

Floristic table W11

	a	b	c	d	11
Betula pubescens	III (1–9)	IV (1–9)	III (1–9)	II (1–7)	III (1–9)
Quercus petraea	V (5–10)	II (2–9)	I (4–8)	II (2–9)	II (2–10)
Betula pendula	I (1–10)	I (6)	III (1–8)	III (1–7)	II (1–10)
Quercus robur	I (1–6)	I (2–5)	I (7–9)	II (1–8)	I (1–9)
Betula hybrids	I (6–7)	I (6)	I (7)	I (2)	I (2–7)
Larix spp.	I (1–5)		I (1)	I (5–7)	I (1–7)
Fagus sylvatica	I (1–5)		I (1–10)	I (1–10)	I (1–10)
Fraxinus excelsior	II (1–7)	I (3–6)			I (1–7)
Sorbus aucuparia	II (1–3)	IV (1–7)	I (1)	I (5)	II (1–7)
Quercus hybrids	I (6)	I (2–4)	III (5–10)	II (3–9)	I (2–10)
Corylus avellana	III (1–7)	II (1–7)	II (1–5)	II (1–8)	II (1–8)
Betula pubescens sapling	II (1–6)	I (4–5)	I (1–7)		I (1–7)
Crataegus monogyna	II (1–3)	I (1–2)		I (1–4)	I (1–4)
Juniperus communis communis	I (1–2)		I (1)	I (6)	I (1–6)
Betula pendula sapling	I (1–2)		I (2–4)		I (1–4)
Quercus robur sapling		I (1)	I (3)		I (1–3)
Anthoxanthum odoratum	IV (1–7)	V (3–8)	V (1–8)	V (2–7)	V (1–8)
Oxalis acetosella	IV (1–9)	V (2–7)	IV (1–8)	V (1–7)	V (1–9)
Agrostis capillaris	IV (1–9)	IV (1–6)	IV (1–9)	V (1–7)	IV (1–9)
Deschampsia flexuosa	IV (1–7)	IV (2–8)	V (1–8)	III (1–6)	IV (1–8)
Holcus mollis	III (1–8)	III (1–7)	IV (1–8)	V (1–7)	IV (1–8)
Rhytidiadelphus squarrosus	III (1–5)	IV (1–4)	III (1–5)	V (1–8)	IV (1–8)
Pteridium aquilinum	III (1–9)	IV (1–5)	IV (1–9)	IV (1–8)	IV (1–9)
Galium saxatile	III (1–6)	IV (1–4)	V (1–5)	IV (1–6)	IV (1–6)
Pseudoscleropodium purum	II (1–5)	III (1–6)	IV (1–8)	V (1–7)	IV (1–8)
Viola riviniana	II (1–4)	IV (1–4)	V (1–6)	V (1–5)	IV (1–6)
Thuidium tamariscinum	II (1–9)	V (2–7)	V (1–8)	IV (1–8)	IV (1–9)
Potentilla erecta	I (2–5)	V (2–7)	IV (1–6)	III (1–4)	IV (1–7)
Hylocomium splendens	I (4)	IV (1–7)	V (1–8)	IV (1–6)	IV (1–8)
Rubus fruticosus agg.	III (1–8)	I (1)	I (1–2)		I (1–8)
Dryopteris dilatata	III (1–9)	I (1)	I (1–5)		I (1–9)
Dryopteris borreri	II (1–6)	I (1–3)	I (1–4)	I (1–4)	I (1–6)

Floristic table W11 *(cont.)*

	a	b	c	d	11
Digitalis purpurea	II (1–7)		I (1–7)	I (1)	I (1–7)
Dryopteris filix-mas	II (1–5)	I (3)	I (1)	I (4)	I (1–5)
Deschampsia cespitosa	II (1–3)	I (1–5)	I (1–6)	I (1–4)	I (1–6)
Pleurozium schreberi	II (1–5)	IV (2–6)	III (1–7)		III (1–7)
Dicranum majus	II (1–5)	V (1–6)	III (1–4)		III (1–6)
Hyacinthoides non-scripta	III (1–10)	IV (2–5)	I (1–4)	II (1–2)	III (1–10)
Polytrichum formosum	III (1–5)	IV (1–4)	I (1–5)	I (1–3)	II (1–5)
Blechnum spicant	I (1–5)	V (1–7)	II (1–8)	I (1–2)	II (1–8)
Hypnum cupressiforme	III (1–4)	III (1–5)	I (1–4)	I (1–3)	II (1–5)
Primula vulgaris	II (2–3)	III (1–4)	I (1–3)	II (1–3)	II (1–4)
Isothecium myosuroides	II (2–4)	III (1–6)	I (1–2)	I (1–3)	II (1–6)
Rhytidiadelphus loreus	I (1–7)	III (1–5)	I (1–5)	I (2)	I (1–7)
Thelypteris limbosperma	I (1–5)	III (2–5)	I (1–5)	I (4)	I (1–5)
Athyrium filix-femina	I (1–2)	II (1–3)	I (1)	I (2)	I (1–3)
Plagiothecium denticulatum	I (1–3)	II (1–3)	I (1–3)	I (1–5)	I (1–5)
Corylus avellana seedling	I (1–3)	II (1)			I (1–3)
Diplophyllum albicans	I (2–4)	II (1–3)			I (1–4)
Hylocomium brevirostre		II (1–5)	I (4)		I (1–5)
Sphagnum quinquefarium		I (1–4)			I (1–4)
Plagiochila spinulosa		I (1–2)			I (1–2)
Rhytidiadelphus triquetrus	I (1–3)	II (2–6)	IV (1–9)	IV (3–6)	III (1–9)
Luzula pilosa	II (1–4)	II (2–3)	IV (1–4)	I (1–3)	III (1–4)
Anemone nemorosa	I (1–4)	II (1–4)	IV (1–7)	II (1–7)	II (1–7)
Trientalis europaea		I (2)	III (1–5)	I (1–4)	I (1–5)
Lathyrus montanus		I (1–3)	II (1–4)	I (1–4)	I (1–4)
Melampyrum pratense	I (3–9)	I (4–5)	II (1–8)	I (5)	I (1–9)
Rubus idaeus	I (1–2)	I (2)	II (1–3)	I (1)	I (1–3)
Plagiomnium affine			I (2–5)		I (2–5)
Vaccinium vitis-idaea			I (1–3)		I (1–3)
Convallaria majalis			I (6)		I (6)
Pyrola minor			I (1)		I (1)
Brachypodium sylvaticum			I (1)		I (1)

https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press

Veronica chamaedrys	I (1)	II (1–3)	III (1–5)	V (1–3)	III (1–5)
Lophocolea bidentata s.l.	III (1–5)	I (1–3)	II (1–5)	IV (1–5)	III (1–5)
Plagiomnium undulatum	I (1–5)	I (2–3)	I (1–3)	IV (1–3)	II (1–5)
Hypericum pulchrum		II (1–3)	II (1)	III (1–2)	II (1–3)
Veronica officinalis		II (1–4)	II (1–4)	III (1–2)	II (1–4)
Stellaria holostea	II (2–6)	I (3–4)	I (1–6)	III (1–3)	I (1–6)
Luzula multiflora	I (1–2)	I (1)	I (1–3)	III (1)	I (1–3)
Ajuga reptans	I (1–2)		II (1–4)	III (1–4)	I (1–4)
Festuca rubra		I (4)	I (1–2)	III (2–5)	I (1–5)
Cerastium fontanum			I (1–2)	III (1)	I (1–2)
Holcus lanatus	I (4–7)	I (3–4)	I (1–5)	II (1–4)	I (1–7)
Rumex acetosa	I (1–2)		I (1–2)	II (1–2)	I (1–2)
Fraxinus excelsior seedling		I (1)	I (1–3)	II (1)	I (1–3)
Angelica sylvestris		I (1)	I (1)	II (1–3)	I (1–3)

Lonicera periclymenum	III (1–6)	II (1–4)	II (1–6)	II (1–6)	II (1–6)
Teucrium scorodonia	III (1–7)	II (1–4)	II (1–6)	II (1–7)	II (1–7)
Agrostis canina montana	II (1–7)	III (2–5)	III (1–7)	I (2–3)	III (1–7)
Dicranum scoparium	II (1–3)	II (2–4)	II (1–4)	II (1–2)	II (1–4)
Mnium hornum	III (1–4)	III (1–6)	I (1–3)	II (1–3)	II (1–6)
Conopodium majus	I (1–3)	II (1–4)	II (1–4)	II (1–3)	II (1–4)
Eurhynchium praelongum	III (1–5)	I (1–2)	I (1–2)	III (1–4)	II (1–5)
Plagiochila asplenoides	I (1–3)	II (1–3)	I (1)	II (1–4)	I (1–4)
Vaccinium myrtillus	I (1–5)	II (1–4)	II (1–9)	I (1)	I (1–9)
Plagiothecium undulatum	II (1–4)	II (1–3)	I (1–4)		I (1–4)
Atrichum undulatum	II (1–3)		I (1)	II (1–3)	I (1–3)
Poa pratensis		I (1)	II (1–4)	II (2–5)	I (1–5)
Succisa pratensis		II (3–6)	II (1–5)	I (1)	I (1–6)
Festuca ovina		II (1–5)	II (1–6)	I (1–4)	I (1–6)
Luzula sylvatica	I (1–9)	I (1–4)	I (1–9)	I (1)	I (1–9)
Betula pubescens seedling	I (1–3)	I (1)	I (1–2)	I (1–2)	I (1–3)
Poa trivialis	I (1–2)	I (1)	I (1–3)	I (2–5)	I (1–5)
Lysimachia nemorum	I (1–3)	I (1–3)	I (1–4)	I (1–2)	I (1–4)
Eurhynchium striatum	I (1)	I (2)	I (1–2)	I (2–4)	I (1–4)
Polytrichum commune	I (1)	I (1)	I (1–2)		I (1–2)
Quercus hybrids seedling	I (2)		I (1–3)	I (1)	I (1–3)
Crataegus monogyna seedling	I (1–3)		I (1)	I (1)	I (1–3)
Carex pilulifera	I (1–2)		I (1–2)	I (1)	I (1–2)

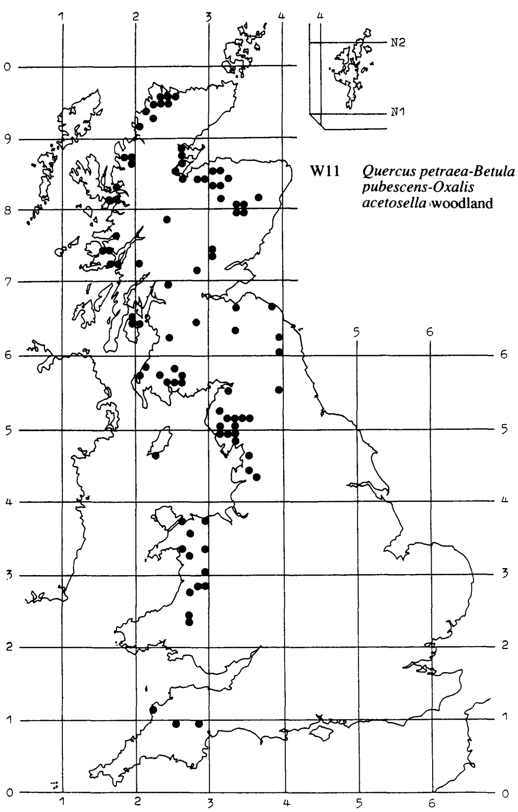
https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press

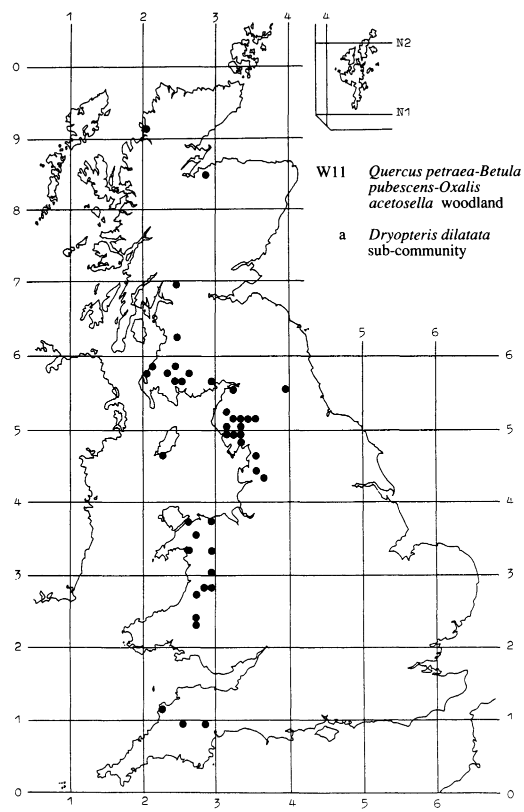
Floristic table W11 *(cont.)*

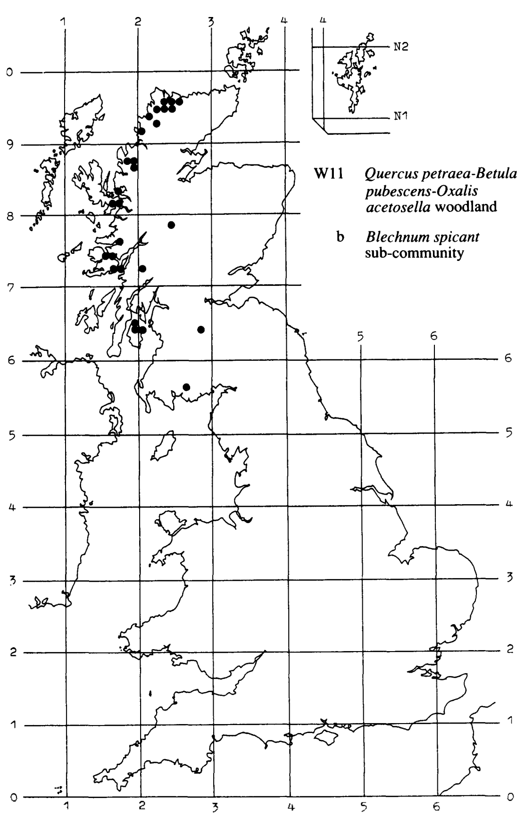
	a	b	c	d	11
Ilex aquifolium seedling	I (1–3)		I (1–2)	I (1)	I (1–3)
Galium aparine	I (2)		I (1)	I (2)	I (1–2)
Cirriphyllum piliferum	I (1)		I (1–3)	I (1–3)	I (1–3)
Geranium robertianum	I (2–3)		I (2)	I (2)	I (2–3)
Ranunculus repens	I (1)		I (2)	I (1)	I (1–2)
Betula hybrids seedling		I (2)	I (1–2)	I (2)	I (1–2)
Rubus saxatilis		I (1)	I (2–6)	I (1)	I (1–6)
Prunella vulgaris		I (1–2)	I (1)	I (1–3)	I (1–3)
Campanula rotundifolia		I (1)	I (1–2)	I (1–2)	I (1–2)
Luzula campestris		I (1–3)	I (1–2)	I (1–3)	I (1–3)
Ranunculus acris		I (1–2)	I (1)	I (5)	I (1–5)
Quercus robur seedling		I (3)	I (1)		I (1–3)
Calluna vulgaris		I (1–2)	I (1–4)		I (1–4)
Erica cinerea		I (1–3)	I (1–2)		I (1–3)
Polytrichum longisetum			I (1–5)	I (1)	I (1–5)
Cytisus scoparius			I (1)	I (1)	I (1)
Number of samples	40	18	61	20	139
Number of species/sample	27 (11–65)	34 (25–52)	29 (19–42)	31 (20–35)	29 (11–65)
Tree height (m)	20 (5–35)	10 (8–15)	15 (8–22)	15 (6–22)	16 (5–35)
Tree cover (%)	80 (30–95)	56 (10–100)	59 (10–80)	46 (5–75)	63 (5–100)
Shrub height (m)	3 (1–8)	5 (4–6)	4 (1–9)	4 (4–5)	4 (1–9)
Shrub cover (%)	23 (0–95)	10 (8–15)	1 (0–40)	12 (0–80)	10 (0–95)
Herb height (cm)	37 (10–100)	27 (15–47)	49 (13–120)	49 (10–137)	43 (10–137)
Herb cover (%)	82 (10–100)	72 (50–100)	77 (45–100)	81 (55–95)	78 (10–100)
Ground height (mm)	24 (10–40)	45 (30–80)	40	20 (10–30)	25 (10–40)
Ground cover (%)	13 (2–70)	63 (10–85)	47 (1–90)	44 (4–85)	39 (1–90)
Altitude (m)	132 (15–280)	131 (40–458)	156 (30–314)	124 (50–366)	141 (15–458)
Slope (°)	19 (0–45)	31 (5–70)	14 (0–50)	16 (0–37)	18 (0–70)

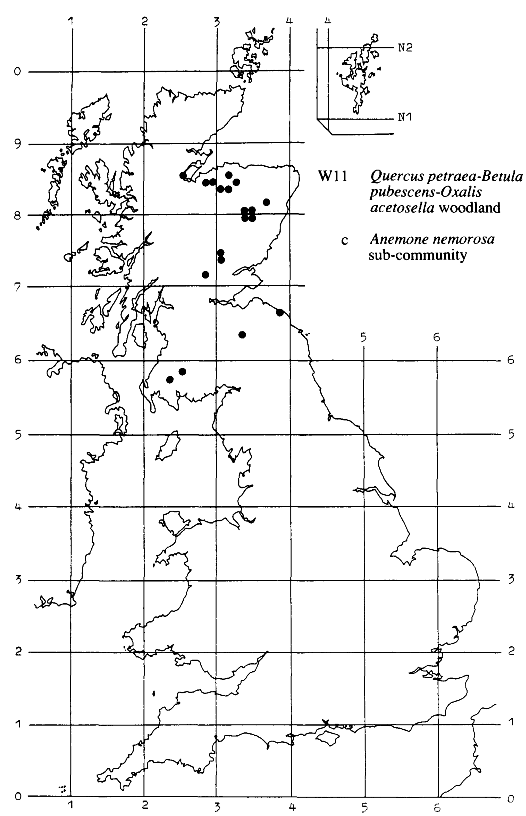
a *Dryopteris dilatata* sub-community
b *Blechnum spicant* sub-community
c *Anemone nemorasa* sub-community
d *Stellaria holostea-Hypericum pulchrum* sub-community
11 *Quercus petraea-Betula pubescens-Oxalis acetosella* woodland (total)

https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press

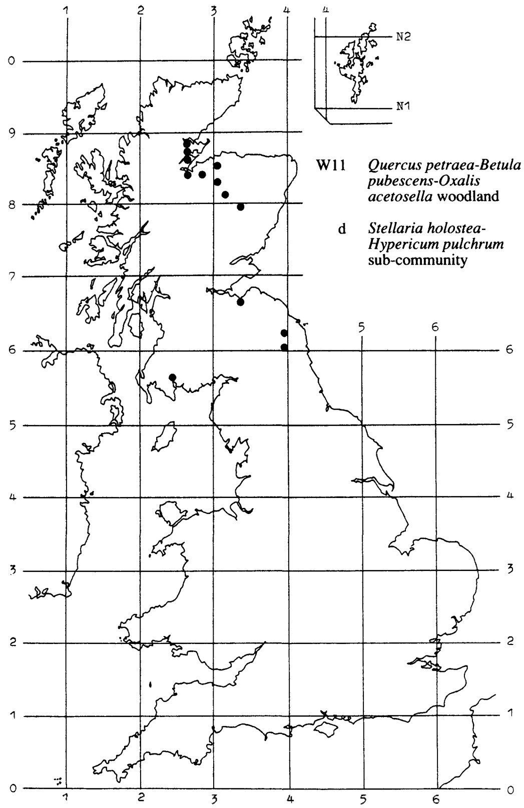








https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press



https://doi.org/10.1017/9780521235587.016 Published online by Cambridge University Press