U20
Pteridium aquilinum-Galium saxatile community

Synonymy
Pteridietum aquilinae auct. angl.

Constant species
Festuca ovina, *Galium saxatile*, *Potentilla erecta*, *Pteridium aquilinum*.

Physiognomy
Pteridium aquilinum is a characteristic member of a variety of vegetation types, being especially important as a constant in the field layers of a number of woodland, scrub and underscrub communities, often occurring there in abundance, and locally prominent also among some heaths and grasslands. In the *Pteridium-Galium saxatile* community, however, it is the sole dominant in the very familiar acidophilous bracken vegetation, occurring always here with a cover of more than 25%, and being overwhelmingly abundant in many stands, the fronds sometimes reaching 2 m or more in height and growing so thickly as to be virtually impenetrable by the middle of the season.

The annual crop of foliage begins to appear in spring, the fronds arising individually from the deep and far-creeping rhizomes and emerging, pale green and coiled like clenched fists, as Page (1982) so memorably puts it, through what is often a very thick mat of litter. Once up, the fronds expand fairly quickly, although it is usually mid-June in the south and at lower altitudes, and July on higher ground and to the north, before the canopy is fully developed. There is thus some opportunity for a vernal contribution from the associated flora before the leathery and dark green bracken foliage of mid-summer begins to cast its characteristic deep shade. With the first frosts of autumn, the fronds rapidly die, often snapping over mid-way and eventually subsiding into the slowly-decaying litter layer. The changing tints of the autumn bracken, through yellow-green to the striking rusty brown, provide much delight in their contribution to the landscape, and the colour of the dead fronds marks out stands of this vegetation right through the winter, should they by any chance have been missed before.

Within this general phenological pattern, there is much variation in the growth of *Pteridium* here, and in the structural contribution which it makes to particular stands of the community through the year and from one season to the next. Bracken is, in fact, a highly polymorphic and versatile plant (Page 1976, 1986) and the classic studies of Watt (1945, 1947*a*, *b*, 1956, 1969, 1971*a*, *b*, 1976) on *Pteridium-Galium* vegetation in Breckland have shown just how subtle fine differences in the growth and physiognomy of the fern can be here, with the suggestion of a cyclic pattern of development across bracken fronts, through pioneer, building and mature phases through to degenerate, and the possibility of complex competitive relationships with other potential dominants (see also Marrs & Hicks 1986).

On a general level, however, the structure and composition of the community are fairly simple and the major lines of floristic variation readily discerned. The common associates are few and their contribution to the cover varies inversely with the preponderance of the bracken. Only *Galium saxatile*, *Potentilla erecta* and *Festuca ovina* (occasionally *F. rubra*) attain constancy among the herbs and even these are often very sparse, limited to puny scattered individuals among the thick litter beneath the densest covers, *F. ovina* in particular being susceptible to shading and crowding out. Some other grasses also occur very often, *Agrostis capillaris* and *Anthoxanthum odoratum* chief among them, again frequently as small, widely-distributed tufts, though where there is any suggestion of a more continuous sward beneath a thinner cover of fronds, it is these species which commonly make up the bulk of the cover. *Deschampsia flexuosa* is also very frequent, tolerant of the deepest shade and sometimes quite abundant, but it has a narrower range of occurrence here, being more characteristic of heathy bracken stands in regions of more humid climate. *Agrostis curtisii* can be a notable component of such vegetation in the oceanic south-west of Britain, and like *D. flexuosa* can be especially abundant where *Pteridium* is recolonising after burning. More locally, *Holcus mollis* is prominent in such situa-

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tions and sometimes increases among bracken treated with herbicide (Sparke & Williams 1986, Lowday 1986). Other grasses found here include *Nardus stricta*, *Molinia caerulea*, *Danthonia decumbens*, *Agrostis canina* and *A. stolonifera*, each of which may show some local abundance and, on less impoverished soils, *Holcus lanatus* occurs occasionally. Some sedges, too, are found at low frequency, such as *Carex pilulifera* and *C. binervis*, with *C. arenaria* locally important where the *Pteridium-Galium* community occurs on dune sand. *Luzula multiflora* and *L. campestris* are occasional.

Apart from *G. saxatile* and *P. erecta*, the herbaceous dicotyledons of this vegetation are not very numerous or diverse and the striking vernal floras found in the more mesophytic *Pteridium-Rubus* community, where carpets of *Hyacinthoides non-scripta* can occur among the unfurling bracken fronds, are not characteristic here. Most commonly, there is just very occasional *Oxalis acetosella*, *Teucrium scorodonia* and *Rumex acetosella*, this last becoming especially conspicuous after clearance of bracken by burning or herbicide treatment. Then, especially in less heathy stands, there can be scattered plants of *Viola riviniana*, *Campanula rotundifolia*, *Veronica chamaedrys*, *V. officinalis*, *Rumex acetosa* and *Trifolium repens*, with coarse weedy species such as *Cirsium* spp., *Epilobium angustifolium* or even *Urtica dioica* becoming patchily abundant following disturbance or fire. The tall colourful racemes of *Digitalis purpurea* can also sometimes be seen emerging from the bracken canopy in summer.

For the most part, however, the associated herbs are small, forming a very low ground cover and, even where sub-shrubs occur in this vegetation, they often lack vigour and height. *Calluna vulgaris*, for example, can be locally abundant in bracken/heath mosaics and increase its cover in the community where the canopy of fronds thins out with ageing or after clearance, but from dense stands it is largely excluded by shade. *Vaccinium myrtillus* is more tolerant, sometimes persisting in reasonable abundance among thickly-growing bracken, though more often found as sparse sprigs poking up only a short distance through the litter. Other ericoids are rare, although *V. vitis-idaea* and *Erica cinerea* occur very occasionally. Quite often, too, the *Pteridium-Galium* community is found in close association with gorse heath or scrub, so bushes of *Ulex europaeus*, *U. gallii* or *U. minor* sometimes figure among the bracken canopy, but *Rubus fruticosus* agg., a constant companion in the *Pteridium-Rubus* community, is very rare here.

Non-vascular plants are not generally a prominent element in the vegetation but a number of bryophytes occur quite often and there is sometimes local enrichment and patchy abundance. Most common throughout are mosses such as *Pseudoscleropodium purum*, *Rhytidiadelphus squarrosus*, *Dicranum scoparium*, *Pleurozium schreberi*, *Hypnum cupressiforme s.l.* and *Hylocomium splendens*, which can survive in tufts and wefts among the litter. *Lophocolea bidentata s.l.* also occurs quite often and there is occasionally some *Polytrichum commune*, *P. formosum*, *Campylopus paradoxus* and *C. pyriformis* but, as a rule, smaller acrocarps are very few except where burning has provided patches of bare ground. It is in such situations, too, that lichens such as *Cladonia chlorophaea* and *C. squamosa* are most often found among *Pteridium-Galium* vegetation.

Sub-communities

***Anthoxanthum odoratum* sub-community.** Grasses make a much more consistent contribution to this kind of *Pteridium-Galium* vegetation, with *Anthoxanthum* and *Agrostis capillaris* joining *F. ovina* as constants, *Holcus lanatus* occurring occasionally with *D. flexuosa* somewhat less common and *Holcus mollis* decidedly local. Often the cover is sparse, visible just as an occasional touch of green before the fronds emerge, although in other stands, where the bracken canopy is thinner, various mixtures of these plants can compose a more extensive understorey, and there is every gradation from such vegetation to grassland with scattered or patchy *Pteridium*. *Carex pilulifera* and *Luzula campestris* occur quite frequently with occasional *C. binervis* and *L. multiflora*.

Along with very common *G. saxatile* and *P. erecta*, small dicotyledons tend to be more numerous and varied here, with frequent *Viola riviniana*, *Campanula rotundifolia* and occasional *Rumex acetosa*, *R. acetosella*, *Teucrium scorodonia*, *Veronica chamaedrys*, *V. officinalis*, *Trifolium repens*, *Lotus corniculatus*, *Galium verum*, *Achillea millefolium*, *Ranunculus repens*, *R. acris*, *Plantago lanceolata*, *Euphrasia officinalis* agg. and *Prunella vulgaris*. Very rarely there are sparse plants of *Hyacinthoides non-scripta*. *Cirsium vulgare* and *C. arvense* can become abundant in disturbed stands and *Epilobium angustifolium* is sometimes prominent after fires.

In contrast to the *Vaccinium-Dicranum* sub-community, ericoids are rarely found here and bryophytes tend to be sparse. *Pseudoscleropodium purum* and *Rhytidiadelphus squarrosus* are the commonest mosses, with *Hylocomium splendens*, *Dicranum scoparium*, *Hypnum cupressiforme* and *Pleurozium schreberi* occasional, *Lophocolea bidentata s.l.* quite frequent, but all usually of low cover.

***Vaccinium myrtillus-Dicranum scoparium* sub-community:** *F. ovina*, *A. capillaris* and, to a lesser extent, *Anthoxanthum*, can all remain frequent here, and *Deschampsia flexuosa* becomes more common than usual, and in some stands these give the kind of grassy appearance to the understorey associated with the last sub-community.

Nardus can be locally prominent too and, to the south-west, *A. curtisii*. Generally, though, the vegetation here has a heathy aspect, with *V. myrtillus* constant and sometimes abundant, *Calluna* quite frequent, though of patchy cover and in more open places. Apart from *G. saxatile* and *P. erecta*, however, dicotyledonous herbs are extremely sparse, with just very occasional *Oxalis acetosella*, *Rumex acetosella*, *Viola riviniana* and *Campanula rotundifolia*.

Bryophytes are quite numerous and occasionally abundant over the litter and bracken stools, with *Dicranum scoparium* and *Pleurozium schreberi* particularly diagnostic, *Hypnum cupressiforme*, *Pseudoscleropodium purum*, *Rhytidiadelphus squarrosus* and *Lophocolea bidentata s.l.* also frequent, *Campylopus paradoxus*, *Polytrichum commune*, *P. formosum*, *Isopterygium elegans*, *Ptilidium ciliare*, *Leucobryum glaucum*, *Lophozia ventricosa* and *Barbilophozia floerkii* occasional. Some lichens may be found here, too, with records for *Cladonia impexa*, *C. squamosa*, *C. chlorophaea*, *C. coccifera* and *Hypogymnia physodes*.

Species-poor sub-community. *Pteridium* is usually an overwhelming dominant here in dense bracken stands where the characteristic plants of the other sub-communities are reduced to very sparse and puny individuals, and even the constants are less frequent than usual. The commonest survivors of the heavy summer shade and thick litter are *G. saxatile* and *P. erecta* with occasional *F. ovina*, *A. capillaris*, *D. flexuosa*, *V. myrtillus*, *Dicranum scoparium*, *Polytrichum formosum* and *Campylopus pyriformis*.

Habitat

The *Pteridium-Galium* community is very widespread throughout Britain, occurring usually on deeper, well-aerated though often quite moist soils, base-poor to circumneutral, up to moderate altitudes in our mountains. It is most abundant on marginal land, and especially around the upland fringes of the west and north, where a combination of congenial climate, loamy colluvial soils and agricultural practice has enabled this vegetation to gain a tenacious hold. Over much of its range, it marks out formerly forested ground, though it now dominates whole valley sides and hill slopes, presenting a serious agricultural problem on poorer-quality but better-drained land and excluded from more fertile soils only by treatment history and continuing vigilance.

Pteridium is tolerant of a wide range of climatic and edaphic conditions (Watt 1976, Page 1976, 1982, 1986), though it does show some clear limits and preferences, and it is within these that the *Pteridium-Galium* community has its centre of distribution. In colder regions and with increasing altitude, for example, the major climatic limitation seems to be the sensitivity of the young fronds to late spring frosts as they emerge through the insulating blanket of litter (Watt 1969, 1976). Thus, although the fern is virtually ubiquitous throughout Britain, extending far into our mountains, vigorous growth at higher altitudes is exceptional: the extensive colonies characteristic of this vegetation rarely occur over 600 m and are mostly found below 450 m. Regional climate affects this general pattern with reduced altitudinal limits typical of, for example, the western Highlands with their increased lapse rates (Taylor 1986), and it is everywhere modified by relief, with slopes exposed to bitter winds and frost-hollows being very uncongenial for survival of the fern. At the opposite extreme of altitude, the community can thrive almost at sea-level, although salt-spray is damaging to *Pteridium* and limits its extension down exposed sea-cliff slopes here, as in the more mesophytic *Pteridium-Rubus* community (Malloch 1971).

The other influential climatic factor is humidity. *Pteridium* can readily tolerate full daylight, though stands in the open show much higher evapotranspiration rates than under forest canopies (Pitman & Pitman 1986, Roberts 1986), and the most luxuriant growth here is made in cloudy environments with frequent rain (Page 1982), such as are typical of western and northern Britain. Again, local relief, such as shelter from prevailing desiccating winds, can be of great importance (Atkinson 1986), though the density of the bracken itself, once it is established in the *Pteridium-Galium* vegetation, can exert a strong influence on the microclimate in the stand (Smith 1986, Taylor 1986). Some of these effects are felt directly by the *Pteridium* and its associates through modification of the light and humidity environment among and beneath the fronds, while other influences work through the soil. It is also likely that climatic factors affect the establishment of bracken sporelings and the subsequent development of the gametophytes, but more needs to be known about this (Page 1986). Certainly, the spores, which are produced in vast quantities (Page 1979) and carried enormous distances (Page 1976), can be very important for establishment of new colonies.

One thing that is known about young bracken plants is that they are more base-tolerant than mature individuals, perhaps even base-demanding (Page 1976, 1982), and they readily appear in situations which could scarcely develop stands of full-grown *Pteridium*. Sometimes, as in the colonisation of burned ground from spores, such a characteristic could give bracken a head start in capitalising on the release of bases like potassium in the ash (Page 1976), and there are situations where the fern goes on to establish in vegetation on calcareous substrates, as on Carboniferous Limestone screes: it is possible in such cases that distinct genotypes are involved. Generally, however, adult plants favour more

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base-poor soils, although *Pteridium* could hardly be described as a strict calcifuge: even in this community, which includes most of the bracken-dominated vegetation on more acidic British soils, surface pH ranges quite widely, being mostly between 4 and 6. Impoverishment in major nutrients in soils of such acidity is no hindrance to the vigour of *Pteridium* either. The *Pteridium-Galium* community is very much a vegetation type of more infertile soils, although bracken can thrive on better ground: more mesotrophic soils which develop a cover of the fern tend to support the *Pteridium-Rubus* community, although on many profiles of intermediate quality through the upland fringes, the *Pteridium-Galium* vegetation is excluded not by inhospitable edaphic conditions, but by a history of good pastoral practice. Again, once established, bracken tends to affect the acidity and fertility environment by the production of huge amounts of litter which decompose very slowly to nutrient-poor and acidic mor (Frankland 1976, Page 1986).

Within the general edaphic limits, two features are of special importance for the vigour of bracken: a reasonable depth of soil and free movement of water and air through the profile. Adult plants seem to establish from spores in about three years (Conway 1949, Page 1976) and thereafter vegetative spread by the extension of the creeping rhizomes can be virtually indefinite. It is possible that, in this community, some clones are young but many may be very old, perhaps among the most venerable living things in the landscape (Oinonen 1967, Page 1986). Sometimes, stands may comprise single, very extensive individuals but it seems more likely that most larger tracts are made up of many intergrowing plants developed from separate invasions, cyclical rejuvenation or fragmentation and regrowth of the rhizome systems offering the prospect of perpetual renewal (Watt 1976, Page 1986). The need for some depth of soil is partly a simple matter of room to accommodate the bulky rhizome system, but if the available profile becomes shallow or choked with rhizomes, growth is checked by overwhelming demands on available nutrients and water and the plant may enter a degenerate phase (Watt 1969, 1971*a*, Taylor 1986). Also, roots and frond initials are brought closer to the surface, with the prospect of greater damage from drought or frost. A depth of 30 cm has been suggested as a crude minimum for really healthy growth although bracken will thrive in much shallower soils than this where rainfall is high.

Shortage of water is particularly limiting to vigour. *Pteridium* will continue to grow well in this vegetation in regions of dry climate, as in Breckland for example, where there are less than 600 mm annually with fewer than 120 wet days yr^{-1} (*Climatological Atlas* 1952, Ratcliffe 1968), but only where supplies of ground water are adequate. Rhizome reserves may provide a considerable buffer against shortage, but interception of rain by the canopy of fronds and the litter blanket, and evapotranspiration from unshaded bracken can run very high (Pitman & Pitman 1986, Smith 1986), so the impact of small rainfall events may be little, sub-surface run-off or deep reserves being very necessary to sustain growth. Certainly, throughout the upland fringes, the *Pteridium-Galium* community is most extensive and vigorous on colluvial soils through which passes downwash from the slopes above, though it is well able to thrive on even very permeable profiles because of the amount and constancy of the replenishing rainfall.

Stagnation, however, is strongly inimical to the vigour of bracken and drainage must always be free in the zone of rhizome growth (Poel 1961, Watt 1976). Impedence deep in the profile, where the parent materials are impervious or consolidated or where a pan has formed, does not necessarily prevent all growth, but they may curtail the available depth of soil to a critical extent, and if a fluctuating or permanent water-table reaches close to the surface, then *Pteridium* cannot survive. The sharp boundaries of the community where its spread is abruptly halted as the ground becomes waterlogged are very striking (see photographs in Jeffreys 1916, Tansley 1939), and it is often the case that the lower limit of this kind of vegetation down valley sides marks the shift from shedding to receiving drainage. Throughout the wetter north and west in particular, the general association of the *Pteridium-Galium* community with moderate to steep slopes cut into pervious bedrocks reflects this edaphic preference (Thompson *et al.* 1986, Atkinson 1986); and the situation is sometimes pointed up nicely on a regional scale by, for example, the preponderance of this vegetation on hills of Carboniferous sandstones and grits rather than over the more subdued scenery derived from shales. Profiles of loamy or uncompacted silty texture, largely stone-free, furnish the most congenial medium for growth, a further feature reflected in the association of the community with colluvium, although there is some evidence that bracken itself can improve oxygen diffusion rates in dense soils by the ramifying spread of its creeping rhizomes (Anderson 1961).

These edaphic requirements mean that, although bracken is a very widespread and familiar element of the British landscape, optimum growth is realised within a relatively circumscribed range of soil and topographic conditions, a fact nicely illustrated for Wales by Thompson *et al.* (1986). Thus the simple presence of the fern, and certainly the kind of dominance it exerts in the *Pteridium-Galium* community, are there largely associated with brown podzolic soils and base-poor brown earths, permeable though sometimes moist, fine-loamy or fine-silty profiles, developed over steeper ground, with some representation also on the ferric stagnopod-

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zols of plateau edges. It was possible for these workers to identify the major soil series involved and to map their combined distribution as a potential 'bracken province'. Distressingly, this accounted for some 20% of the land surface of Wales.

The extent to which *Pteridium* has been able to exploit this potential, both there and on similar ground widespread through the rest of Britain, is already very impressive and still increasing (Taylor 1986). Essentially, the success of the fern is a function of its own innate abilities to capitalise on the kinds of physical conditions described above, under the influence of particular types of land-use history (Page 1976, 1986). Originally, *Pteridium* seems to have been a plant of forests and their margins, and probably not so aggressive or invasive there as it is in the open today, but woodland clearance, by felling and burning, and the subsequent expansion of pasture and cultivated ground, appear to have provoked a very quick response (Godwin 1975, Rymer 1976, Huntley & Birks 1983). The opening of the canopy, beginning with the sporadic and shifting clearances of the Mesolithic and Neolithic, are marked by pronounced local increases in the amount of bracken spores in the pollen record (Smith 1970, Turner 1970, Bolwell 1982, Pinder 1985, Taylor 1985, 1986), and such activity has continued, with periodic reversals, throughout the whole of recorded history in Britain.

Particularly important for the entrenched position which *Pteridium* has in our landscape today, was probably the sustained deforestation and establishment of upland grazings, increasingly for sheep, over the last few centuries (Rymer 1976, Page 1976). On a more local scale, especially provocative treatments are those associated with less intensive agriculture on land of marginal quality: the creation of smallholdings vulnerable to shifts in farm economics, for example, with fluctuations in grazing intensity, abandonment of cleared or arable land from time to time, and the absence of sustained programmes of liming or fertilising (Taylor 1986). Very often, as on the *ffridd* land around the upland fringes of Wales, such patterns of activity have unfortunately been concentrated on the very ground likely to sustain the most vigorous growth of bracken (Thompson *et al.* 1986), and such sites can then serve as centres from which invasion of less congenial situations can occur (Salisbury 1964). In such economies, too, the general decline in cutting bracken for bedding has removed one check on its spread (Hughes & Aitchison 1986).

Much of the original impetus to bracken expansion from its locus in forest vegetation must have come from the sudden release from shading by natural woody competitors, but there are particular features of the biology of *Pteridium* which enable it to respond well, often aggressively, to the treatments it receives in the open, and to consolidate its hold in the *Pteridium-Galium* community. First, it is unpalatable, having a variety of chemicals to protect the fronds against the predation of herbivores (Cooper-Driver 1976, 1985, Cooper-Driver *et al.* 1977). Grazing by sheep and other stock is not unknown (Garrett-Jones 1958), but bracken is rarely taken as a preferred food (Page 1986), indeed it can be fatally poisonous, sometimes causing significant stock losses (Hannam 1986, Evans 1986), and the determined attempt to sustain high grazing intensities on ever-decreasing bracken-free areas of upland pasture has probably been an important factor in a spiral of degradation in which the *Pteridium-Galium* community has become even more firmly established (Page 1986, Barber 1986). It is perhaps possible that, where there is a sparse cover of fronds, predation helps hold the bracken in check (Lee *et al.* 1986) but trampling is likely to be more important than grazing itself in such situations: this is very damaging to the emerging fronds which generally do not survive on pathways with heavy hoof or foot traffic.

The second important adaptation is to fire. Burning of standing material and litter can be damaging where it increases exposure of the frond initials and expanding foliage to frost, but generally bracken is well able to take advantage of fire. For one thing, rhizome growth is quickly resumed even after severe burning and a new crop of fronds readily produced before most potentially competing plants have got away (Page 1976, Fletcher & Kirkwood 1979). Furthermore, spores are able to achieve a more widespread and rapid initial colonisation on burned ground: indeed, they may have a specific requirement for prior fire-damage for optimal invasion. And, because of their early demand for bases, the sporelings thrive on the ash-enriched ground before showing their switch in pH tolerance as the beneficial minerals are leached away (Page 1982, 1986).

Once bracken is established, the dense summer shade of the frond canopy and the smothering effect of the persistent litter layer (Frankland 1976) give the fern a very strong competitive advantage against survivors from the preceding vegetation or any other potential invaders. Moreover, *Pteridium* produces a variety of allelopathic compounds which are released from both the standing fronds and, during the autumn and winter months, the decaying herbage (Gliessman 1976, Gliessman & Muller 1978). The associated flora of the *Pteridium-Galium* community thus comprises the relatively small number of plants able to tolerate the formidable ability of bracken to make the environment its own. The general character of the assemblage is calcifuge and shade-tolerant, with some opportunity for herbs to benefit from the vernal insolation, and an advantage to those species able to grow through or over the thick litter. With increasing dominance of the fern, there is a floristic convergence to a progressively more impover-

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ished flora, such as is seen here in the Species-poor sub-community. In somewhat more open stands, which may be earlier stages in invasion or phases of bracken degeneration with a resurgence in associated plants (Watt 1976), the species complement is a more accurate reflection of prevailing soil, climate and treatment conditions. The *Anthoxanthum* sub-community, for example, with its richer and more mesophytic herbaceous flora, is characteristic of less base-poor, less humic and less impoverished profiles, where the surface pH quite often approaches 6. The context and immediate progenitors of such vegetation are generally pastures, with which there is every gradation of spatial and temporal continuity. The *Vaccinium-Dicranum* sub-community, on the other hand, with its heathier assemblage, is often located among and developed from sub-shrub vegetation, where burning as much as grazing is the usual treatment, and the soils are typically more base-poor, with pH generally from 4 to 5, more humic and more infertile. Each of the sub-communities subsumes quite a range of floristic and structural variation, some of it phytogeographical, as with the local importance of *Agrostis curtisii* among stands in the south-west, and further sampling may well suggest finer divisions among this kind of vegetation (e.g. Lee *et al.* 1986).

However, any floristic interest that the *Pteridium-Galium* community presents is likely to be far outweighed by concern over the 'bracken problem'. This kind of vegetation is not entirely without its virtues: it adds much-appreciated colour to the autumn landscape, can shelter populations of small mammals and some invertebrates, and can improve the texture and stability of some soils (Brown 1986). But against these must be balanced the loss of valuable agricultural and amenity land, the reduction in diversity of the natural vegetation and associated fauna, the encouragement of sheep tick and the production of powerful poisons including some carcinogens (Smith & Taylor 1986). The scale of the problem is also vast. Recent calculations and estimates (Hendre 1958, Taylor 1978, 1986, Bunce *et al.* 1980) put the total area under bracken in Great Britain at about 6361 km^2 or 2.8% of the land surface, about the size of Lincolnshire. In this scheme, some of this would be included in the *Pteridium-Rubus* community, but the majority certainly in the west and north of the country, is *Pteridium-Galium* vegetation. In these regions, the area is proportionally that much greater, with perhaps as much as 6% of the land under bracken. And encroachment still continues apace, with rates of between 1 and 3% increase annually commonly recorded. As Taylor (1986) so startlingly put it, for every two hectares of farming land lost to forestry or urban development, between one half and one hectare is being lost to bracken spread at the present time.

Traditional control measures have been of a mechanical kind with bracken-cutting having the additional advantage of yielding a crop. Harvesting for winter bedding was the usual kind of treatment but, although this still continues locally (Hughes & Aitchison 1986), it can hardly be significant now as a check to the spread of the fern, and for really effective control repeated cuts in a few successive seasons, timed so as to effect maximum damage on the food reserves of the rhizomes, are necessary (Williams & Foley 1976, Lowday 1983). Other, now defunct, uses of bracken have included extraction of potash for glass and soap manufacture and burning as a fuel in brick-making, baking and brewing (Rymer 1976) and, with increasing pressure on non-renewable energy sources, Lawson *et al.* (1986) have suggested that harvesting the fern as an energy crop would be feasible on biological, environmental and technological grounds and almost financially viable.

Apart from frequent cutting, other forms of mechnical treatment such as crushing are still used in bracken control and are eligible for government support (Johnson 1986), but attention has increasingly shifted to chemical spraying, particularly, since the 1970s, with asulam, a foliage-applied compound, translocated by the phloem and inhibiting the development of frond initials and rhizome apices. The activity of these in the overall metabolic economy of the bracken at the time of spraying is of critical importance to the success of the treatment (Kirkwood & Archibald 1986), but other considerations include the size of the dose and the method of application (Robinson 1986, Soper 1986). Aerial spraying has been much improved (Davies 1986), although a continuing source of anxiety about less precise targeting is that asulam is also toxic to many other ferns of greater conservation interest than *Pteridium* (Page 1982). Even with adequate dosage and delivery, asulam often holds out the prospect of simply checking rather than eradicating bracken, and it is clear that careful attention needs to be given to the prior assessment of the status of *Pteridium* in a particular landscape, and to aftercare (Robinson 1986, Soper 1986, Horsnail 1986), and that herbicides of any kind should be regarded as just one of a battery of control methods which need to be applied flexibly and with imagination. Other chemicals may prove more successful in the end (Oswald *et al.* 1986) and there is the eventual prospect of some kind of biological control (Lawton *et al.* 1986, Lawton 1986), but Page (1986) has given a timely warning about being deceived into thinking of bracken as a simple and uniform organism which, once the correct treatment has been found, will yield universally to its application.

Zonation and succesion

The *Pteridium-Galium* community is a very common and often extensive element in zonations and mosaics with a variety of woodlands, grasslands and heaths. The character of these associated vegetation types reflects the considerable differences in regional and local climate across the wide range of country where this kind of bracken stand has become established, and their disposition frequently reflects variations in treatments subsequent to forest clearance on a range of more free-draining base-poor soils. The *Pteridium-Galium* community is a particularly successful replacement for woodlands on such ground and the regeneration of good quality pasture or heath presents a major problem. Much bracken-infested land has been planted up for commercial coniferous forestry, but control by the encouragement of natural woodland regeneration has been little tried.

Zonations to forest vegetation are widespread throughout the range of the *Pteridium-Galium* community and often show a continuous gradation in floristics and structure between the bracken stands characteristic of margins and clearings and the closed stretches of woodland. Indeed, in many cases, the differences between the *Pteridium-Galium* vegetation and the field layers of the adjacent woodland are qualitative ones, evident mainly in the thinning of the bracken and the increased abundance of the ground cover of herbs and bryophytes as shade deepens beneath the canopy of trees. This is particularly striking in the west and north of the country, where the associated woodlands are usually of the *Quercus-Betula-Oxalis* or *Querus-Betula-Dicranum* types, the climax forest communities of more acidic but free-draining mineral soils such as brown earths and podzolised profiles. Bracken can be locally abundant beneath the canopies of oak and birch most typical of these woodlands, with the constants and preferentials of the *Anthoxanthum* sub-community continuing to be important in the field layer of grazed forests of these kinds on more mesotrophic soils, the species of the *Vaccinium-Dicranum* sub-community figuring prominently in ungrazed woodlands on rockier and less fertile ground (e.g. Tittensor & Steele 1971). Particularly around the eastern Highlands, the *Pteridium-Galium* vegetation can also be found in association with *Juniperus-Oxalis* and *Pinus-Hylocomium* woodlands and, again, there is a close similarity between it and the drier and less mesophytic field layers of these communities.

Where tracts of woodland are unenclosed, as is usually the case through the upland fringes, the cover of trees around their margins often thins out gradually, though this is generally a reflection of decline in moribund forest fragments, rather than of expansion of young woody growth on to the surrounding bracken-infested land. There are places, however, where a thickening zone of saplings, usually birch or *Sorbus aucuparia*, marks the transition from *Pteridium-Galium* vegetation to newly-developing woodland. And, where the community occurs on stretches of base-poor soils in lowland Britain, it is very commonly found in mosaics with young scrubby woodland, and also with overgrown heath, as on commons where traditional management has fallen into disuse (Tansley 1939, Wooldridge & Goldring 1953, Tubbs 1986, Webb 1986). In this part of the country, with its drier, warmer climate, it is the *Quercus-Betula-Deschampsia* woodland that is the most usual forest type found in association with the *Pteridium-Galium* community, once more often grading continuously to it. More mesotrophic brown soils, where the *Quercus-Pteridium-Rubus* woodland is the climax, frequently develop bracken infestation, but the vegetation is typically of the *Pteridium-Rubus* type. This generally has a more mesophytic flora, but it comes close to the *Pteridium-Galium* community in its *Teucrium* sub-community and, in the south-east, the two kinds of bracken stand can occur together where there are shifts from less to more fertile soils related to the disposition of different bedrocks or drift or to local eutrophication as on disturbed heaths. Mosaics with *Ulex-Rubus* scrub, in which bracken is a frequent and locally prominent associate, are also very common in the latter situations, as around abandoned settlements.

Very often, heaths and grasslands form part of the vegetation patterns in which the *Pteridium-Galium* community is found, and indeed these usually predominate as associates of bracken stands in the largely deforested landscape of Britain, the proportions of the vegetation types largely reflecting differences in soils and treatments on the once-wooded ground, with some effects, too, from variations in local climate. Regional climate and contrasts in land-use history from one part of the country to another are also important because, although the *Pteridium-Galium* community occurs in almost every area of Britain with great uniformity in its floristics, associated grasslands and heaths show great variety in their composition in moving from east to west, south to north and with increasing altitude or exposure to maritime influence. The patterns in which this kind of bracken vegetation occurs are thus multitudinous and can only be outlined here.

Beginning in the warm Continental part of the country, like Breckland, where Watt (1936) carried out his studies on pattern and process in bracken vegetation, the *Pteridium-Galium* community is an important element in mosaics with *Festuca-Agrostis-Rumex* grassland and *Calluna-Festuca* heath on the more acidic sandy soils, with *Carex arenaria* and *Carex-Cladonia* vegetation figuring on loose, wind-blown material. Here, the *Pteridium-Galium* stands are usually of the *Anthoxanthum* sub-community, though a mesophytic element is poorly developed and the major continuity is provided by plants such as *Festuca ovina*, *Agrostis capillaris*, *Galium saxatile*, *Luzula campestris*, *Rumex acetosella* and certain of the bryophytes.

With the shift into the south-east, very similar patchworks of vegetation occur widely on the commons and heaths around London and in the Home Counties. The

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Festuca-Agrostis-Rumex grassland retains its representation here on more open ground with summer-parched soils, but the dry heath is often of the *Calluna-Ulex minor* type (Harrison 1970). This continues to be important among the sub-shrub vegetation of drier acidic soils through central southern England where, in areas like the New Forest and remnants of the Dorset heaths, it occurs widely with *Pteridium-Galium* stands of all kinds. Increasingly here, though, with the higher rainfall, the calcifuge swards are of the *Festuca-Agrostis-Galium* type or, where *Agrostis curtisii* has got a hold on somewhat moister humic soils, of the *Agrostis* type, with greater floristic continuity with the bracken vegetation. West of Poole, both these communities remain common among bracken stands in south-west England, but the *Calluna-Ulex gallii* heath replaces the *Calluna-U. minor* type (Ivimey-Cook *et al.* 1975) in the mosaics, remaining important with *Pteridium-Galium* vegetation at lower altitudes right round the coast of Wales (Rodwell 1974) and into the north Midlands. In these regions, too, and northwards around the Scottish coast, bracken stands of this kind can be found in association with *Calluna-Scilla* heath on the more sheltered sections of sea cliffs of base-poor rocks and drift (Malloch 1971, South Gower Coast Report 1981).

Through the north Midlands, the fringes of the southern Pennines and across into the North York Moors, the *Pteridium-Galium* community is found with *Calluna-Deschampsia* heath and *Deschampsia* grassland (Elgee 1914, Fidler *et al.* 1970, Daniels 1983). Here, however, down through Wales and into the fringes of the moorlands of south-west England, can be seen the major shift in the kind of landscape patterns in which *Pteridium-Galium* vegetation occurs, from lowland commons to upland hill slopes. Stands of the community are here often much more extensive and frequently occupy a distinct physiographic zone, between the improved and more intensive grazing of the valley floors and the unenclosed pasture, heaths and mires of the hill slopes above. Downslope, then, there is often a sudden cut-off to the bracken where assiduous management keeps Cynosurion or more mesophytic Nardo-Galion swards within the limits of enclosure free of the fern. Above, the zonations are more gradual, the bracken thinning as the soils become more shallow and rocky or where the surrounding grasslands or heaths have not yet been invaded. The most widespread calcifuge sward in these patterns is the *Festuca-Agrostis-Galium* grassland, the major plagioclimax pasture of free-draining base-poor soils throughout the north and west, but *Nardus-Galium* grassland also becomes very important where there is some impedence on the slopes around, and, as with the *Pteridium-Galium* community, the spread of this vegetation is a strong indication of poor pastoral treatment. Accompanying these swards, there is very often some *Calluna-Vaccinium* heath or, in more oceanic areas, *Calluna-Erica* heath with *Vaccinium-Deschampsia* heath at higher altitudes. Species such as *F. ovina*, *A. capillaris*, *Anthoxanthum*, *Nardus*, *G. saxatile*, *P. erecta*, *V. myrtillus*, *Calluna* and the pleurocarpous mosses are a more or less constant feature of much of this vegetation, with differences in the abundance of bracken, the grasses and sub-shrubs providing most of the contrasts. Patterns of this kind, often covering huge areas, are a very familiar feature of most parts of upland Britain (Eddy *et al.* 1969, Ward *et al.* 1972*a*,*b*, Meek 1976, Evans *et al.* 1977, Hill & Evans 1978).

Here, too, *Pteridium-Galium* vegetation is frequently found closely juxtaposed with mire communities of various kinds. Even in the south-east, bracken stands of this type can occur on the more free-draining ground around *Ericetum* wet heath and *Narthecio-Sphagnetum* valley bog, but these communities are local. To the north and west, soligenous mires become very common below flushes and in water-tracks gathering run-off from the slopes, and frequently form an abrupt interruption running down through stretches of *Pteridium-Galium* vegetation (Ward *et al.* 1972*a*,*b*, Lee *et al.* 1986, Brown & Wathern 1986). Typically, this vegetation is of the *Carex-Sphagnum* type, though often rush-dominated, and marking out ground which is far too wet for bracken to survive. More gradual transitions can be seen where *Juncus-Galium* rush-pasture is interposed between the mire and surrounding grasslands and bracken.

Elsewhere in the north and west, *Pteridium-Galium* vegetation runs up gentle, free-draining slopes towards stretches of wet heath and blanket bog on ombrogenous peats of benches and plateaus. Again, boundaries are clearly marked here if the peats are wet and actively growing: indeed, there is often a zone of wet heath interposed between the bracken and the mire vegetation. But where the bog surface has dried out, naturally or as a result of drainage, *Pteridium* can encroach on to the peats occurring among mosaics of *Scirpus-Erica* heath and *Scirpus-Eriophorum* or *Calluna-Eriophorum* blanket mire, with tracts of *Molinia-Potentilla* mire running down over slopes that remain moist but free-draining.

To maintain and exert itself in all these very varied contexts, bracken must obviously be a resourceful plant. It is clearly a replacement for forest vegetation in most situations, but beyond this we know very little more about its competitive and seral relationships with the vegetation it invades than those features described by Watt from the rather unusual climatic conditions of Breckland. Watt's (1945, 1947*a*,*b*) account of cyclical change in bracken populations may not be universally applicable (Lee *et al.* 1986), although Marrs & Hicks (1986) have recently confirmed extensive natural degeneration of dense bracken to grass-heath, the *Festuca-Agrostis-Rumex* grassland of this scheme, at

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Lakenheath Warren. At the same time, however, they showed that the phasic interdigitation of *Pteridium-Galium* vegetation with *Calluna-Festuca* heath, bracken and heather advancing and retreating over the ground in an overall state of balance (Watt 1955), had broken down with succession proceeding towards bracken-dominance. The reasons for this change, though, are not clear and may relate more to alterations in grazing, with reductions in both rabbit and sheep populations since the time of Watt's work.

The prospect of waiting for natural and perhaps only temporary declines in bracken populations is a dismal one for those concerned with the urgent need to maintain the quality of pastures and heaths, and considerable attention has been given to the possibilities of reconstituting swards and sub-shrub vegetation after artificial clearance of *Pteridium*. Indeed, the necessity of adequate aftercare for treated land is a vital part of judicious control (Robinson 1986, Soper 1986, Horsnail 1986), and rarely does the death of the fern reveal the kind of lush grazing that some seem to think lies beneath their bracken. Immediate developments depend on the kind of herbicide treatment and on the plants initially present in the bracken understorey or with seed sources near at hand, recolonisation sometimes being strongly related to vegetative survivors (Sparke 1982, Sparke & Williams 1986), in other cases to soil seed stores or nearby seed-parents (Lowday 1986). Asulam is more specific for bracken than is, for example, glyphosate, although even with the former, early stages in revegetation may be dominated by plants like *Digitalis*, *Cirsium* spp., *Urtica* or *Rumex acetosella*, able to take rapid advantage of newly-cleared ground, and wherever particular elements of the understorey are important to conserve it is necessary to resort to a laborious method of directed application such as a rope-wick technique (Lowman 1985). Subsequent developments in swards are partly dependent on the extent of bracken regrowth and partly on the style of grazing: where *Pteridium* does not reassert itself continuance of the same pattern of grazing has been shown to favour predominance of grasses over dicotyledons, although shifts in their proportions, such as the demise of *Agrostis* spp. with glyphosate spraying, or the local abundance of *Holcus mollis*, can persist long (Sparke & Williams 1986). Surface treatments, such as the raking off, burning or incorporation of the bracken litter, may also have an effect, because some species are unable to grow over a thick blanket of decaying fronds, while others are stimulated to germinate by disturbance of stored seed (Cadbury 1976, Sparke 1982, Sparke & Williams 1986). More vigorous aftercare, with burning of litter, application of lime and phosphate and re-seeding, can result in the establishment of a good quality artificial sward (Sparke & Williams 1986).

Removal of litter after spraying has also been shown to be beneficial for the re-establishment of *Calluna* on bracken-infested lowland heaths, although in experiments in Breckland, invasion of *Betula pendula* from buried seed and nearby trees was rapid too, and seen as a possible threat to the regeneration of sub-shrub vegetation (Lowday 1986).

The possibilities of controlling bracken itself by stimulating renewed succession to forest have not escaped notice. Indeed, the *Pteridium-Galium* community frequently occupies soils which remain above average in their potential for tree growth, planting not usually necessitating ploughing or draining, although of course it is often necessary to hold back the shading or swamping fronds by cutting or herbicide treatment until the saplings are tall and robust enough to grow clear (Helliwell 1986). Many stands of this kind of vegetation thus persist within and around tracts of commercial forests, invariably coniferous, through the upland fringes, grading into the field layers wherever the shade is not too dense. Natural regeneration among bracken may also be more likely than at first sight (Watt 1976). It was one of the surprises of the study of Marrs & Hicks (1986) that, at Lakenheath, *Pinus sylvestris* had invaded and grown to maturity since 1946 not only among sparse *Pteridium-Galium* vegetation, but also where the cover was dense, the major limit on pine spread apparently being seed dispersal. Such results will perhaps help us regain a view of bracken as originally a pioneer plant, seral to forest, and they hold out one hope of natural control (Page 1986).

Distribution

The *Pteridium-Galium* community is virtually ubiquitous on suitable soils at low to moderate altitudes throughout the British Isles.

Affinities

The distinctive character of this kind of bracken vegetation has long been remarked upon (White 1788) and a less mesophytic *Pteridietum* figures among accounts of British plant communities from the earliest days (Tansley 1911), although systematic accounts are scarce. The associated floras retain a strong affinity with the vegetation invaded by the bracken and generally have a Nardo-Galion character, although the community could scarcely be located in this alliance. With its submontane nature, the vegetation does not belong with the tall-herb and fern communities of higher altitudes placed in the Adenostyletea, and it is equally ill at home among the pioneer fern communities of acidic rocky habitats grouped in the Thlaspietea rotundifoliae. A much better solution is to regard it as part of the Quercetea robori-petraeae, lacking any shrubs or trees, but effectively a replacement for forest, often anthropo-

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genically derived. Birse (1984) used the Pteridio-Rubetalia order (Doing 1962) to contain his bracken-rich gorse scrub (here included in the *Ulex-Rubus* community) and this would provide a suitable locus for the *Pteridium-Galium* stands. With their less oceanic climate, Continental phytosociologists are largely spared the dubious pleasure of having to live with or classify this kind of vegetation.

Floristic table U20

	a	b	c	20
Pteridium aquilinum	V (4–10)	V (4–10)	V (4–10)	V (4–10)
Galium saxatile	V (1–8)	V (1–4)	IV (1–5)	V (1–8)
Potentilla erecta	V (1–5)	IV (1–4)	III (1–4)	IV (1–5)
Festuca ovina	IV (1–8)	IV (1–7)	II (1–8)	IV (1–8)
Agrostis capillaris	V (1–8)	III (1–4)	II (1–4)	III (1–8)
Anthoxanthum odoratum	V (1–6)	III (1–6)	I (1–3)	III (1–6)
Holcus lanatus	III (1–5)	I (1–4)	I (1–3)	II (1–5)
Viola riviniana	III (1–6)	I (1–3)		II (1–6)
Campanula rotundifolia	III (1–4)	I (1–3)		II (1–4)
Carex pilulifera	II (1–4)	I (1–4)	I (1–4)	II (1–4)
Hylocomium splendens	II (1–6)	I (1–5)	I (1)	II (1–6)
Luzula campestris	II (1–4)	I (1–4)	I (1)	II (1–4)
Rumex acetosa	II (1–4)	I (1)	I (1)	I (1–4)
Holcus mollis	II (1–5)	I (1)		I (1–5)
Veronica chamaedrys	II (1–3)			I (1–3)
Trifolium repens	II (1–3)			I (1–3)
Veronica officinalis	I (1–3)			I (1–3)
Lotus corniculatus	I (1–3)			I (1–3)
Achillea millefolium	I (1–3)			I (1–3)
Cirsium vulgare	I (1–3)			I (1–3)
Ranunculus repens	I (1–3)			I (1–3)
Ranunculus acris	I (1–4)			I (1–4)
Cirsium arvense	I (1–3)			I (1–3)
Galium verum	I (1–3)			I (1–3)
Poa pratensis	I (1–4)			I (1–4)
Conopodium majus	I (1–3)			I (1–3)
Euphrasia officinalis agg.	I (1–3)			I (1–3)
Plantago lanceolata	I (1–4)			I (1–4)
Prunella vulgaris	I (1–3)			I (1–3)
Hyacinthoides non-scripta	I (1–5)			I (1–5)
Dicranum scoparium	II (1–3)	V (1–6)	II (1–6)	III (1–6)
Pleurozium schreberi	II (1–4)	IV (1–6)	I (1)	III (1–6)
Deschampsia flexuosa	II (1–6)	III (1–6)	II (1–6)	II (1–6)
Hypnum cupressiforme	II (1–3)	III (1–6)	I (1–4)	II (1–6)
Vaccinium myrtillus	I (1–6)	IV (1–4)	II (1–4)	III (1–6)
Calluna vulgaris	I (1–6)	III (1–8)	I (1–3)	II (1–8)
Nardus stricta	I (1–3)	II (1–4)		I (1–4)
Campylopus paradoxus	I (1–3)	II (1–3)		I (1–3)
Polytrichum commune	I (1–3)	II (1–4)		I (1–4)
Lophozia ventricosa		I (1–3)		I (1–3)
Isopterygium elegans		I (1–3)		I (1–3)

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Ptilidium ciliare		I (1–3)		I (1–3)
Barbilophozia floerkii		I (1–3)		I (1–3)
Agrostis curtisii		I (1–8)		I (1–8)
Leucobryum glaucum		I (1–4)		I (1–4)
Cladonia impexa		I (1–3)		I (1–3)
Hypogymnia physodes		I (1–3)		I (1–3)
Cladonia chlorophaea		I (1–3)		I (1–3)
Cladonia squamosa		I (1–3)		I (1–3)
Cladonia coccifera		I (1–3)		I (1–3)
Polytrichum formosum	I (1–3)	I (4–10)	II (1–3)	I (1–10)
Campylopus pyriformis	I (1)	I (1)	II (1–3)	I (1–3)
Pseudoscleropodium purum	III (1–5)	III (1–4)	I (2)	III (1–5)
Rhytidiadelphus squarrosus	III (1–6)	III (1–6)		III (1–6)
Lophocolea bidentata s.l.	II (1–4)	II (1–3)	I (1–3)	II (1–4)
Rumex acetosella	I (1–3)	I (1–3)	I (1–4)	I (1–4)
Oxalis acetosella	I (1–6)	I (1–4)	I (1–3)	I (1–6)
Danthonia decumbens	I (1–4)	I (1–3)	I (1)	I (1–4)
Molinia caerulea	I (1–4)	I (1–4)	I (1–6)	I (1–6)
Luzula multiflora	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Teucrium scorodonia	I (1–4)	I (1)	I (1–4)	I (1–4)
Agrostis stolonifera	I (1–4)	I (1–4)	I (1)	I (1–4)
Rhytidiadelphus loreus	I (1–4)	I (1–4)		I (1–4)
Carex binervis	I (1–4)	I (1)		I (1–4)
Agrostis canina	I (1–6)	I (1–3)		I (1–6)
Thelypteris limbosperma	I (1–6)	I (1)		I (1–6)
Thuidium tamariscinum	I (1–8)	I (1–4)		I (1–8)
Erica cinerea	I (1–6)	I (1–4)		I (1–6)
Plagiothecium undulatum	I (1–3)	I (1–3)		I (1–3)
Digitalis purpurea	I (1–4)		I (1–4)	I (1–4)
Number of samples	66	55	15	136
Number of species/sample	19 (5–65)	16 (6–43)	12 (6–23)	17 (5–65)
Vegetation height (cm)	42 (6–120)	57 (6–120)	60 (7–110)	49 (6–120)
Vegetation cover (%)	92 (50–100)	97 (80–100)	96 (80–100)	94 (50–100)
Altitude (m)	245 (45–450)	338 (30–488)	216 (46–440)	282 (30–488)
Slope (°)	9 (0–50)	9 (0–60)	19 (0–50)	10 (0–60)

a *Anthoxanthum odoratum* sub-community
b *Vaccinium myrtillus-Dicranum scoparium* sub-community
c Species-poor sub-community
20 *Pteridium aquilinum-Galium saxatile* community (total)

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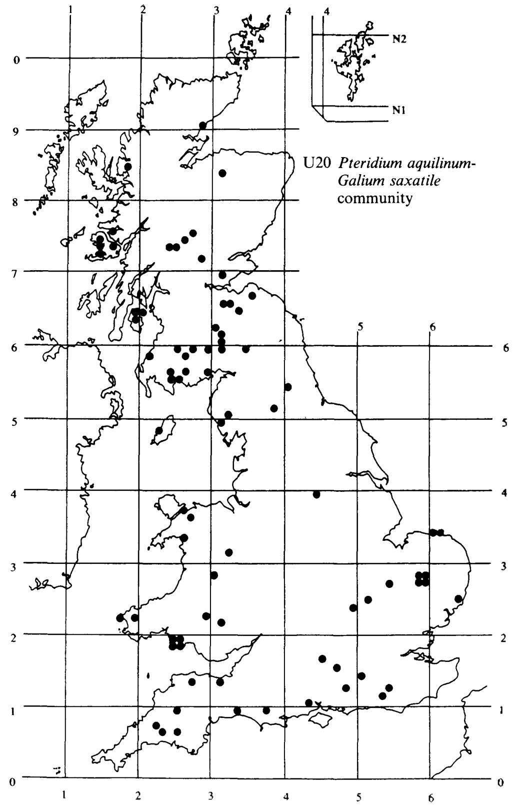
U20 *Pteridium aquilinum-Galium saxatile* community
N2
N1