

Vegetation and environmental variation in an Atlantic blanket bog in South-western Ireland

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Abstract A vegetation survey was carried out in a relatively intact Atlantic blanket bog in Southwest Ireland to study the vegetation patterns in relation to environmental variation, and to quantify the effect of artificial and natural borders on compositional variation. The data were analysed using canonical correspondence analysis. In terms of both vegetation and water chemistry, the study site can be categorized as typical of Atlantic blanket bogs in the maritime regions of North-western Europe. The distribution of plant species was explained mainly by depth of the water table. The distribution of bryophytes was secondarily explained by the pH of the bog water, while the distribution of vascular plants was secondarily explained by concentrations of ammonia. The vegetation distribution exhibited little variation between the central sector of the peatland and its disturbed edges (hill-grazing and restoration areas), but a substantial variation was observed between the area along a natural edge (stream) and the areas close

to the other peatland borders or centre. Similarly, the internal variation within each sector (centre, hill-grazing edge and restoration area edge) was small, but substantial vegetation variation was observed within the area located along the stream. The area along the stream was associated with relatively deep water table, shallow peat depth, high water colour, pH and NH_4^+ concentrations, and low Cl^- concentrations in the bog water. Our results suggest the existence of strong centre-natural margin gradients, as in raised bogs, and indicate that human or animal disturbance do not give rise to the marked transition zones that often characterize natural margins of mire systems. This indicates that even small areas and remnants of Atlantic blanket bogs are worthy of conservation and that their conservation value would benefit from the inclusion of sectors close to the natural peatland borders, which would increase the plant biodiversity of the conserved area.

Keyword CCA · Ecosystem margins · Ordination analysis · Peatland conservation · Plant communities · Water chemistry

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Introduction

Blanket bogs are peatlands that are so called because they blanket the landscape (Tansley 1965) on slopes with gradients up to 20–25° (Tallis 1998). Blanket bogs are complex mire systems, composed of a

mosaic of ecosystems with differing trophic status (bogs, flushes, percolation mires, etc.). The bog components consist of ombrotrophic areas, whose development is mostly independent of basin or topographical features where water can collect. Since the ombrotrophic areas typically dominate the blanket mire complex, these ecosystems are generally defined as bogs. Globally, blanket bogs are rare, accounting for ca. 3% of the world peatland area (Lindsay et al. 1988). The distribution of blanket bogs in northern latitudes is restricted to temperate maritime regions, as their development requires humid conditions with cool summers and mild winters (Lindsay et al. 1988). These ecosystems are important not only for their singular nature but also for their highly characteristic biodiversity and their role in regional carbon and water balances.

Blanket bogs are classified as Atlantic (lowland) or Montane, depending on whether they are located at elevations lower or higher than 200 m asl (Foss et al. 2001). In Europe, Atlantic blanket bogs are common only in Scotland and Ireland, where they constitute the major global concentration of this ecosystem (Douglas 1998). In the Republic of Ireland, they cover about 6% of the land area and contain ca. 19% of the nation's soil carbon stock (Tomlinson 2005). Although these ecosystems are worthy of conservation, only 21% of blanket bogs in the Republic of Ireland remain in relatively intact conditions (Foss et al. 2001) due to peat extraction, drainage and forest plantation. Current conservation strategies, therefore, need to be enhanced through a better understanding of these ecosystems (Douglas 1998).

The vegetation of Atlantic blanket bogs in Ireland is typically dominated by graminoids, mainly *Molinia caerulea* and *Schoenus nigricans*, while the bryophyte cover is low compared to raised bogs (Hammond 1981; Doyle 1990; Sheehy Skeffington and O'Connell 1998). The surface of blanket bogs generally forms a mosaic of vegetation communities organized in undulating microforms: hummocks, lawns and hollows (Lindsay 1995; Tallis 1998) that are supported by differences in water table (Belyea and Clymo 1998). The formation of a hummock-hollow pattern is triggered by different rates of peat accumulation (Tallis 1998), since different microforms exhibit dissimilar CO₂ and CH₄ flux dynamics (Laine et al. 2007a, b). The resulting carbon balance is, therefore, strongly connected with both vegetation

and environmental factors. Environmental factors are expected to be perturbed as a consequence of climate change. Therefore, a better understanding of the interaction between environmental factors with ecosystem functioning and vegetation patterns is essential if we are to predict the impact of climate change on these ecosystems.

In northern peatlands the vegetation pattern is controlled by three main factors: depth of the water table, chemical status and distance from the peatland margin (Malmer 1986). The relative importance of these various drivers depends on the regional characteristics of geology, hydrology and topography (Bubier 1995). The most direct approach to study the relationship between vegetation and environmental parameters is the ordination technique, which has been used in other peatland types (e.g., Glaser et al. 1990; Bubier 1995; Bubier et al. 1995; Hájková and Hájek 2004; Hájková et al. 2006), but never, to our knowledge, in Atlantic blanket bogs. Moreover, the effect of the ecosystem margins on the variation in the plant composition has not been quantified in Atlantic blanket bogs although it is known to form an important ecological gradient in peatland ecosystems (Wheeler and Proctor 2000; Økland et al. 2001).

Our objectives in this study were to quantify both (1) the link between vegetation patterns and environmental variation, and (2) the effect of artificial and natural borders on variation in vegetation composition in an Atlantic blanket bog.

Material and methods

Study site

The study was conducted in a 220 ha Atlantic blanket bog located at ca. 150 m above sea level near Glencar, County Kerry, in Southwest Ireland (Latitude: 51° 55' N, Longitude: 9° 55' W). In the study site, the average temperature for the warmest month of the year (August) during the 2003–2007 period was 15.1°C, and for the coldest (February) was 6.3°C. The average annual precipitation over the same period was 2,504 mm yr⁻¹, while the average number of rain days was 265 (see Sottocornola and Kiely 2005).

The vegetation survey was carried out in the relatively intact (Douglas et al. 1989) part of the bog, over an area of about 70 ha (Fig. 1). The study site is

limited by one natural border, a stream, on the west, and by artificial areas to the other directions. To the north, the study site is bordered by a road and to the east by a fence, which surrounds a peatland restoration area. This area (~30 ha) was drained and afforested about 30 years ago, and then in autumn 2003, the drainage ditches were blocked, the trees were cut and left on site. The southern limit of the study site is marked by a fence, beyond which occasional sheep grazing occurs. This area stretches for about 200 m on the blanket bog before meeting a slope covered by a few small patches of fertilized grassland on the side of a 300-m-high ridge. Hereafter this area is referred to as the “hill-grazing area”.

Vegetation survey

The vegetation survey was carried out in August 2005 using a systematic sampling approach. A grid design was set up with an interval of 150 m and it included 42 grid points (Fig. 1). At each grid point, eight sample plots were radially placed at a random distance from 1 to 3 m. In total 336 sample plots

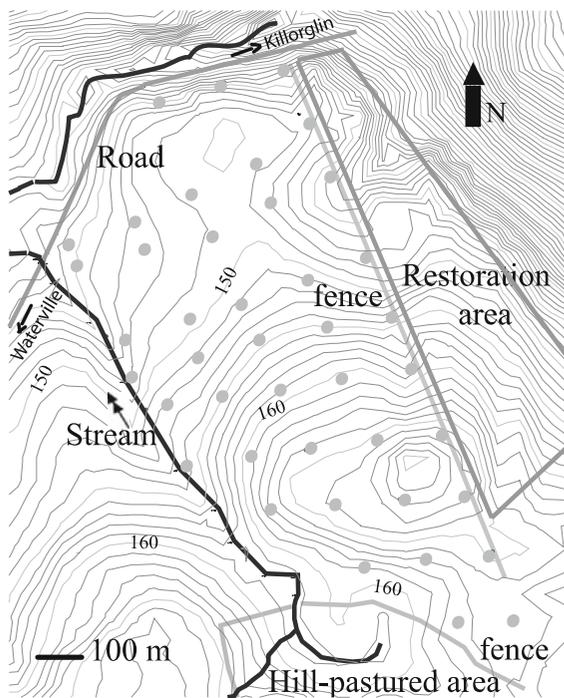


Fig. 1 Map of the study site, delimited by one natural (stream) and three artificial borders (road, peatland restoration area and hill-pastured area, the last two delimited by fences). The grey dots show the sampling grid points

were surveyed. The projection cover of each plant species inside 0.3×0.3 m quadrats was assessed to the nearest 1% for species with coverage less than 25% and to the nearest 5% for species with coverage greater than 25%. For very low plant occurrence, 0.01%, 0.1% and 0.5% covers were also assigned. Plant nomenclature followed Smith (1990) for Hepaticae, Hill et al. (2006) for other bryophytes and Stace (1997) for vascular plants.

Environmental measurements

At each sample plot, the peat depth was measured with a 2-m-long probe and the microform type was identified. Four types of microforms were identified based on their relative elevation: hummocks, high lawns, low lawns and hollows (see Laine et al. 2006). These correspond to hummocks, high ridges, low ridges and hollows used by Lindsay et al. (1988) and Lindsay (1995). To assess the highest and lowest water table, a bamboo stick covered with PVC insulating tape was inserted in the middle of each sample plot. The PVC tape becomes discoloured in reduced conditions and, therefore, gives an estimate of the fluctuation in water table (Belyea 1999). The bamboo sticks were inserted in August 2005 and collected on the 8th December 2005. One of the PVC tape brands did not react, confirming the risk of different responses to water table fluctuation by different PVC tapes (Booth et al. 2005). Moreover, while the mark of the lower water table was clear, the highest marks appeared vague. Only the estimates of the lowest water table from the clearly marked sticks were used in the analyses, while the unclear marks (22 out of 86) were replaced with the average of the reliable water level measurements in the same microform type.

Sampling wells were inserted into the peat to collect water samples for chemical analysis. At each grid point, one sampling well per each microform type, out of the eight sample plots, was installed. A maximum of four wells were installed at one grid point if all four microform types occurred. In total, 86 sampling wells were installed: 20 in hummocks, 42 in high lawns, 15 in low lawns and 9 in hollows. The water table was measured inside each sampling well on the 3rd of May 2006, during a period of very high precipitation (ca. 70 mm of rain over the previous three days), to get an estimate for the level of high water table.

Chemical analysis

Water samples for chemical analysis were collected in 150 ml polyethylene bottles using an electric water pump on a field visit between the 13th and 20th of December 2005. The first water obtained from the sampling wells was used to rinse the bottles and then discarded. Aeration of the samples was minimized by filling the bottles completely. The bottles were stored at 4°C and analysed within 24 h of collection. Conductivity and pH were measured in the field, directly inside the sampling wells, after the collection of the water samples. Conductivity was measured using a WTW LF 330 conductivity meter (Geotech Environmental Equipment, Inc., USA). Following this, pH was measured using a WTW pH 320 (Geotech Environmental Equipment, Inc., USA). A two-point calibration with 4.00 and 7.00 pH standards was used. Temperature corrections for conductivity and pH were automatically performed to a reference temperature of 25°C; conductivity was also corrected (K_{corr}) for proton concentrations using an equivalent conductivity of $349.6 \mu\text{S cm}^{-1}$ per $\text{meq H}^+ \text{ l}^{-1}$ (25°C) (Miller et al. 1988); thus K_{corr} indicates conductivity carried out by ions other than protons.

The water samples were analysed using a Lachat QuikChem IC+FIA 8000 (Lachat Instruments, Colorado, USA). Na^+ , Ca^{2+} , Cl^- , SO_4^{2-} were measured using a QuikChem Ion Chromatographer. NH_4^+ and total organic nitrogen (TON) were analysed using a QuikChem Flow Injection Analyser. Water colour, which is a proxy for dissolved organic carbon concentration, was measured at 455 nm using a spectrophotometer (UV-160A Shimadzu, Kyoto, Japan).

Data analyses

We applied canonical correspondence analysis (CCA) to study vegetation patterns in relation to environmental variation using the software CANOCO version 4.5 for Windows (Ter Braak and Šmilauer 2002). The species covers were transformed using a logarithmic transformation to reduce in the CCA the weight of the plants with a high cover.

Partial canonical correspondence analysis was used to detect the variability in the species composition that was best explained by the measured

environmental variables (Lepš and Šmilauer 2003). For this analysis, the effect of the sample plot location in the peatland was removed, by using the distances from the peatland borders as covariables. A manual forward selection was used to test the significance of the environmental variables in explaining the plant species distribution. A second partial CCA analysis was then performed on the same dataset, using only the significant environmental variables. This analysis did not apply a forward selection and the significance of the resulting CCA axes, which were linear combinations of the selected environmental variables, was evaluated with Monte Carlo permutation tests (Lepš and Šmilauer 2003). The analyses were performed on bryophytes and vascular plants together and then separately. Only the separate analyses are presented here, since separate analyses emphasized a different response of the two vegetation groups to the environmental parameters. Only the species, which occurred in at least five of the 336 surveyed plots, were included in these analyses.

The relationships of the most common species to the main environmental gradients were further investigated using generalized additive models (GAM) with Poisson distribution (Ter Braak and Šmilauer 2002). The models were run over 68 sample plots for each species and were selected based on their complexity using an Akaike Information Criterion with a maximum of three degrees of freedom. Only species with significant responses were considered and their resulting response curves were used to support the interpretation of the ordination analyses on the species distribution.

To investigate the effect of artificial and natural borders on the vegetation, we performed a CCA using only the distances from the peatland borders as explanatory variables. To identify the environmental variation related to the different peatland sectors, the peat depth, water table and water chemistry variables were included as passive supplementary variables into the CCA. The water chemistry values and missing water table measurements were extended to the same microform types in each grid point. The CCA, with biplot scaling, was applied to the whole sample plot dataset including all observed plant species. The significance of the CCA axes was assessed with a Monte Carlo permutation test.

Results

General features of the vegetation

During the vegetation survey, 32 vascular plants and 39 bryophyte species were identified; of the latter, 16 species were Hepaticae, 11 were *Sphagnum* species and 12 were Bryopsida (Table 1). On average the bryophytes covered 25% of the peatland area. *Racomitrium lanuginosum*, *Sphagnum rubellum*, *Pleurozia purpurea*, *S. papillosum* and *S. tenellum* were the most abundant and together with *Mylia anomala* and *Kurzia pauciflora*, the most frequent species observed in the sample plots. The average vascular plant cover was about 30%. *Molinia caerulea*, *Calluna vulgaris*, *Erica tetralix* and *Narthecium ossifragum* were the most abundant species and, together with *Eriophorum angustifolium*, were also the most frequent vascular plants. The plant occurrence followed a clear trend, with the percentage cover of both bryophytes and vascular species significantly decreasing along the water table gradient, from hummocks to hollows. The only exceptions were the bryophytes in the hollows, which were more abundant than in the low lawns (Fig. 2).

Nine percent of the surveyed sample plots were identified as hummocks. These highest microforms were typically only a few tens of centimetres above the water table. Hummocks were relatively round in shape, with a diameter ranging between 50 and 100 cm. The bryophyte cover on hummocks was about 71%, mainly composed of *S. rubellum* or *R. lanuginosum*. Hummocks were covered by herbaceous plants (19%), principally *M. caerulea*, and by ericaceous shrubs (*C. vulgaris* and *E. tetralix*).

The flat areas at intermediate water table (i.e., lawns) were divided into high and low lawns, because the vegetation in low lawns was both shorter and less dense by comparison with high lawn vegetation (Laine et al. 2006). High lawns were by far the most common microform, covering 77% of the bog area. The dominant vascular plant in high lawns was *M. caerulea*. High covers were observed also for *C. vulgaris* and *E. tetralix*, while *R. lanuginosum* was the most abundant bryophyte.

Low lawns were much less frequent than high lawns, occurring only in 9% of the sample plots. Among the vascular plants, *Rhynchospora alba* occurred very frequently, while *S. auriculatum*,

R. lanuginosum and *Campylopus atrovirens* had the highest bryophyte coverage.

The wettest microforms, hollows, were submerged by standing water for most of the year. Hollows were oblong in shape, ranging between 50 and 300 cm in length and were stretched parallel to the contour lines on slopes. Only 3% of the sample plots belonged to this microform type. Two forms of hollows occurred: hollows with a mud bottom and hollows with a full moss cover. In both cases, the plant communities were very sparse and variable, with bryophytes and vascular plants both having a mean cover of about 15%. The most abundant and frequent moss species was *S. auriculatum*, while *Menyanthes trifoliata* and *Utricularia minor* had the highest vascular plant covers.

Soil water chemistry and water table

Water chemistry showed little variation between microforms across the blanket bog (Table 2). The pH ranged between 4.28 and 5.14, with hummocks and high lawns having a significantly lower pH than hollows. The corrected conductivity varied little between microforms, averaging at 46.7 $\mu\text{S cm}^{-1}$. Na^+ , Ca^{2+} , NH_4^+ and TON were only slightly higher in the drier than in the wetter microforms. A similar pattern occurred for SO_4^{2-} , with concentrations ranging between 0.64 and 3.81 mg l^{-1} , with significantly higher concentrations in high lawns than in low lawns and hollows. Cl^- concentrations and water colour did not show a clear trend between the different microforms.

The water table ranged between 27 cm above and 22 cm below the soil surface for the highest and between 0 and 40 cm below the surface for the lowest level (Table 2). The high water table significantly differed among all microforms, while the lowest water table was significantly different only between the highest and lowest microforms. The shallowest peat depth was 55 cm. For 65% of the measured points the peat depth was over 200 cm.

Plant community composition in relation to environmental variation

The first CCA explained the bryophyte distribution and showed that high water table and pH were the only measured environmental variables significantly

Table 1 Mean percentage cover (and frequency) of the plant species in the Glencar Atlantic blanket bog (All) and in the four different identified microforms. HU = hummocks; HL = high lawns; LL = low lawns; HO = hollows. r = percentage cover <0.5; + = percentage cover ≥0.5% and <1%

	Code	All	(336)	HU	(31)	HL	(259)	LL	(29)	HO	(10)
Hepaticae											
<i>Kurzia pauciflora</i> (Dicks.) Grolle	<i>Kur pau</i>	r	(250)	r	(20)	r	(203)	r	(19)	r	(1)
<i>Calypogeia sphagnicola</i> (H. Arn. & J. Perss.) Warnst. & Loeske	<i>Cal sph</i>	r	(19)	.		r	(19)	.		.	
<i>Cephalozia</i> cfr. <i>bicuspidata</i> (L.) Dum.*	<i>Cep.zia</i>	r	(31)	r	(2)	r	(27)	r	(2)	.	
<i>Cephalozia</i> cfr. <i>connivens</i> (Dicks.) Lindb.*											
<i>Nowellia curvifolia</i> (Dicks.) Mitt.	<i>Now cur</i>	r	(5)	+	(2)	r	(3)	.		.	
<i>Cladopodiella fluitans</i> (Nees) Buch	<i>Clad flu</i>	r	(34)	r	(2)	r	(22)	r	(6)	r	(2)
<i>Cephaloziella</i> sp. (Spruce) Schiffn.	<i>Cep.lla</i>	r	(187)	r	(18)	r	(153)	r	(8)	r	(3)
<i>Odontoschisma sphagni</i> (Dicks.) Dum.	<i>Odo sph</i>	r	(204)	r	(19)	r	(173)	r	(6)	r	(1)
<i>Mylia anomala</i> (Hook.) S.F. Gray	<i>Myl ano</i>	r	(302)	1	(31)	r	(247)	r	(16)	r	(1)
<i>Diplophyllum albicans</i> (L.) Dum.	<i>Dip alb</i>	r	(52)	r	(3)	r	(46)	r	(1)	.	
<i>Scapania nemorea</i> (L.) Grolle	<i>Sca nem</i>	r	(1)	.		r	(1)	.		.	
<i>Scapania gracilis</i> Lindb.	<i>Sca gra</i>	r	(2)	.		r	(2)	.		.	
<i>Lophocolea bidentata</i> (L.) Dum.	<i>Lop bid</i>	r	(2)	.		r	(2)	.		.	
<i>Pleurozia purpurea</i> Lindb.	<i>Ple pur</i>	3	(242)	+	(12)	3	(202)	1	(22)	r	(1)
<i>Aneura pinguis</i> (L.) Dum.	<i>Ane pin</i>	r	(18)	r	(2)	r	(13)	r	(1)	.	
<i>Riccardia latifrons</i> (Lindb.) Lindb.	<i>Ric lat</i>	r	(25)	.		r	(21)	r	(2)	.	
Sphagnopsida											
<i>Sphagnum austiini</i> Sull.	<i>Sph aus</i>	r	(2)	2	(1)	r	(1)	.		.	
<i>Sphagnum magellanicum</i> Brid.	<i>Sph mag</i>	r	(6)	r	(1)	r	(4)	.		.	
<i>Sphagnum palustre</i> L.	<i>Sph pal</i>	r	(3)	.		r	(3)	.		.	
<i>Sphagnum papillosum</i> Lindb.	<i>Sph pap</i>	2	(178)	4	(18)	2	(142)	1	(13)	.	
<i>Sphagnum compactum</i> Ehrh. ex Hoffm	<i>Sph com</i>	r	(3)	.		r	(3)	.		.	
<i>Sphagnum cuspidatum</i> Ehrh. ex Hoffm.	<i>Sph cus</i>	r	(30)	.		r	(18)	r	(6)	1	(3)
<i>Sphagnum pulchrum</i> (Lindb. ex Braithw.) Warnst.	<i>Sph pul</i>	r	(4)	.		r	(4)	.		.	
<i>Sphagnum tenellum</i> (Brid.) Pers. ex Brid.	<i>Sph ten</i>	2	(237)	2	(16)	2	(200)	1	(18)	.	
<i>Sphagnum auriculatum</i> Schimp.	<i>Sph aur</i>	+	(51)	.		r	(24)	4	(16)	13	(8)
<i>Sphagnum rubellum</i> Wilson	<i>Sph rub</i>	7	(217)	41	(29)	4	(181)	r	(5)	.	
<i>Sphagnum subnitens</i> Russ.ow & Warnst.	<i>Sph sub</i>	r	(37)	2	(2)	r	(32)	r	(1)	.	
Bryopsida											
<i>Racomitrium lanuginosum</i> (Hedw.) Brid.	<i>Rac lan</i>	10	(263)	14	(21)	11	(213)	2	(23)	r	(1)
<i>Campylopus atrovirens</i> (De Not.)	<i>Cam atr</i>	+	(105)	r	(5)	+	(83)	2	(15)	r	(1)
<i>Leucobryum glaucum</i> (Hedw.) Ångstr.	<i>Leu gla</i>	r	(9)	.		r	(9)	.		.	
<i>Breutelia chrysocoma</i> (Hedw.) Lindb.	<i>Bre chr</i>	r	(11)	r	(3)	r	(8)	.		.	
<i>Campyliadelphus elodes</i> (Lindb.) Kanda	<i>Cam elo</i>	r	(1)	.		r	(1)	.		.	
<i>Calliergon cordifolium</i> (Hedw.) Kindb.	<i>Cal cor</i>	r	(1)	
<i>Thuidium tamariscinum</i> (Hedw.) Br. Eur.	<i>Thu tam</i>	r	(3)	.		r	(3)	.		.	
<i>Pseudoscleropodium purum</i> (Hedw.) M. Fleisch	<i>Pse pur</i>	r	(2)	.		r	(2)	.		.	
<i>Brachythecium rutabulum</i> (Hedw.) Schimp.	<i>Bra rut</i>	r	(2)	.		r	(2)	.		.	
<i>Hypnum jutlandicum</i> (Holmen & Warncke)	<i>Hyp jut</i>	+	(113)	3	(26)	r	(84)	r	(1)	.	
<i>Pleurozium schreberi</i> (Willd. ex Brid.) Mitt.	<i>Ple sch</i>	r	(1)	.		r	(1)	.		.	
<i>Rhytidiadelphus squarrosus</i> (Hedw.) Warnst.	<i>Rhy squ</i>	r	(12)	.		r	(12)	.		.	

Table 1 continued

	Code	All	(336)	HU	(31)	HL	(259)	LL	(29)	HO	(10)
Gymnospermae											
<i>Pinus sylvestris</i> L.	<i>Pin syl</i>	r	(2)	r	(1)	r	(1)
Angiospermae											
<i>Caltha palustris</i> L.	<i>Cal pal</i>	r	(3)	.	.	r	(3)
<i>Myrica gale</i> L.	<i>Myr gal</i>	r	(7)	.	.	r	(7)
<i>Rumex acetosa</i> L.	<i>Rum ace</i>	r	(2)	.	.	r	(2)
<i>Drosera rotundifolia</i> L.	<i>Dro rot</i>	r	(167)	r	(16)	r	(127)	r	(15)	r	(2)
<i>Drosera anglica</i> Huds.	<i>Dro ang</i>	r	(18)	.	.	r	(9)	r	(6)	r	(2)
<i>Drosera intermedia</i> Hayne	<i>Dro int</i>	r	(32)	r	(1)	r	(14)	+	(12)	r	(2)
<i>Calluna vulgaris</i> (L.) Hull	<i>Cal vul</i>	6	(249)	14	(26)	6	(201)	+	(15)	r	(1)
<i>Erica tetralix</i> L.	<i>Eri tet</i>	4	(297)	5	(28)	5	(239)	2	(22)	r	(2)
<i>Potentilla erecta</i> (L.) Raeusch.	<i>Pot ere</i>	+	(40)	r	(4)	+	(35)	r	(1)	.	.
<i>Polygala serpyllifolia</i> Hosé	<i>Pol ser</i>	r	(91)	r	(10)	r	(79)	r	(2)	.	.
<i>Angelica sylvestris</i> L.	<i>Ang syl</i>	r	(1)	.	.	r	(1)
<i>Menyanthes trifoliata</i> L.	<i>Men tri</i>	r	(17)	r	(2)	r	(8)	r	(2)	6	(4)
<i>Pedicularis sylvatica</i> L.	<i>Ped syl</i>	r	(31)	r	(3)	r	(27)	r	(1)	.	.
<i>Pinguicula lusitanica</i> L.	<i>Pin lus</i>	r	(8)	.	.	r	(7)	r	(1)	.	.
<i>Pinguicula grandiflora</i> Lam.	<i>Pin gra</i>	r	(4)	.	.	r	(4)
<i>Utricularia minor</i> L.	<i>Utr min</i>	r	(2)	3	(2)
<i>Hieracium</i> sp. L.	<i>Hierac</i>	r	(3)	.	.	r	(3)
<i>Juncus acutiflorus</i> Ehrh. ex Hoffm.	<i>Jun acu</i>	r	(7)	.	.	r	(7)
<i>Juncus effusus</i> L.	<i>Jun eff</i>	r	(3)	.	.	r	(3)
<i>Eriophorum angustifolium</i> Honck.	<i>Eri ang</i>	2	(267)	2	(23)	2	(206)	2	(27)	2	(7)
<i>Eriophorum vaginatum</i> L.	<i>Eri vag</i>	r	(82)	r	(7)	+	(74)	r	(1)	.	.
<i>Trichophorum cespitosum</i> (L.) Hartm.	<i>Tri cae</i>	+	(119)	r	(9)	+	(104)	r	(5)	.	.
<i>Schoenus nigricans</i> L.	<i>Sch nig</i>	1	(112)	1	(7)	2	(87)	1	(11)	r	(2)
<i>Rhynchospora alba</i> (L.) Vahl	<i>Ryn alb</i>	2	(158)	r	(9)	2	(110)	6	(28)	+	(5)
<i>Rhynchospora fusca</i> (L.) W.T. Aiton fil.	<i>Rhy fus</i>	r	(2)	r	(1)
<i>Carex panicea</i> L.	<i>Car pan</i>	r	(17)	.	.	r	(16)	r	(1)	.	.
<i>Carex limosa</i> L.	<i>Car lim</i>	r	(40)	r	(2)	r	(25)	r	(3)	+	(6)
<i>Holcus lanatus</i> L.	<i>Hol lan</i>	r	(1)	.	.	r	(1)
<i>Agrostis stolonifera</i> L.	<i>Agr sto</i>	r	(3)	.	.	r	(3)
<i>Molinia caerulea</i> (L.) Moench	<i>Mol cae</i>	13	(325)	15	(31)	14	(258)	4	(26)	r	(4)
<i>Narthecium ossifragum</i> (L.) Huds.	<i>Nar oss</i>	3	(254)	2	(22)	3	(194)	2	(27)	2	(4)
Lichens	<i>Lichens</i>	r	(95)	r	(9)	r	(83)	r	(2)	.	.

**Cephalozia* species were not distinguished on the field but only in the laboratory; it was, therefore, not possible to assign the cover

correlated with the bryophyte distribution (Fig. 3). Axis 1 (expressing the strongest variation) was mainly composed of a moisture gradient. *S. auriculatum*, *Cladopodiella fluitans*, *S. cuspidatum* and *Campylopus atrovirens* were grouped together at the wettest end of the water table, whereas *Hypnum jutlandicum*,

S. rubellum and *M. anomala* occurred in the driest areas. The GAM analysis suggested that, even with wider tolerance to moisture conditions, also *R. lanuginosum* and *S. papillosum* had their highest occurrence in the driest areas of the peatland (Fig. 4a). The CCA axis 2 was mostly composed of a pH

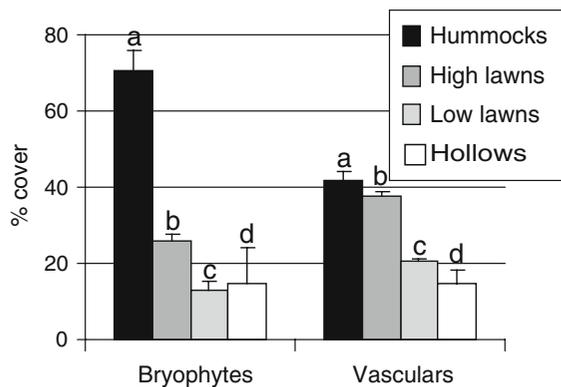


Fig. 2 Mean percentage cover and standard error of bryophytes and vascular plants in the different microform types. Bars with different letters indicate that plant groups are statistically different ($P < 0.05$, Mann–Whitney test following a Kruskal–Wallis test) between microform types

gradient. *Cephalozia* spp. and *K. pauciflora* had their optimum at lower pH than the other bryophytes, while *Diplophyllum albicans* and *S. subnitens* were located in less acidic areas (Fig. 3). Despite a wider habitat range, the GAM analysis suggested that also *S. auriculatum* peaked in areas with higher pH, while *S. tenellum* had its optimum in areas with lower pH (Fig. 4c).

The second CCA explained the vascular plant distribution and indicated that their distribution was significantly correlated to high and low water tables and NH_4^+ concentrations, among the measured

environmental parameters (Fig. 5). Axis 1 was primarily a combination of high and low water tables and suggested that *M. trifoliata*, *Drosera intermedia*, *D. anglica* and *Carex limosa* were located in the wettest, whereas *Potentilla erecta* and *Pedicularis sylvatica* were in the driest areas of the bog, together with *M. caerulea*, as suggested by the GAM diagram (Fig. 4b). The CCA axis 2 was mostly composed of a NH_4^+ concentration gradient. *Potentilla erecta* was centred at the highest NH_4^+ concentrations (Fig. 5). The GAM analysis indicated that *M. caerulea* also has an inclination for high ammonia, while *M. trifoliata* and *N. ossifragum* for low NH_4^+ concentrations (Fig. 4d).

The CCA focusing on the effect of peatland borders indicated a rather homogeneous distribution of different plant communities across the bog. Most of the plots overlapped in the centre of the ordination diagram, suggesting that there is little variation among communities regarding their distance from the peatland margins (Fig. 6a). The only communities clearly departing from the others were the high lawns close to the stream, and the low lawns and hollows close to the road. The high lawns close to the stream were displayed at some distance from the other high lawns, stretched along axis 1, suggesting that the area close to the stream is covered solely by high lawns, which have a substantial internal variation and are different from high lawns in other sectors of the bog (Fig. 6a). The area along the stream appears to be

Table 2 Mean values (standard deviations in parenthesis) of soil water chemical variables and water tables in the different vegetation communities

	Weighted average of all microforms	Hummocks ($n = 20$)	High lawns ($n = 42$)	Low lawns ($n = 15$)	Hollows ($n = 9$)
pH	4.53 (0.13)	4.54 ^a (0.14)	4.51 ^a (0.12)	4.59 ^{ab} (0.15)	4.75 ^b (0.25)
K_{corr} ($\mu\text{S cm}^{-1}$)	46.7 (5.3)	46.0 ^a (4.5)	46.8 ^a (5.3)	46.5 ^a (6.4)	46.5 ^a (4.8)
Na^+ (mg l^{-1})	6.70 (1.20)	6.38 ^a (0.92)	6.78 ^a (1.35)	6.33 ^a (0.45)	6.31 ^a (0.52)
Ca^+ (mg l^{-1})	0.76 (0.43)	0.93 ^a (0.56)	0.74 ^a (0.41)	0.76 ^a (0.49)	0.66 ^a (0.37)
Cl^- (mg l^{-1})	8.89 (1.20)	8.64 ^a (1.25)	8.94 ^a (1.22)	8.81 ^a (1.21)	8.69 ^a (0.69)
SO_4^{2-} (mg l^{-1})	1.93 (0.50)	1.86 ^{ab} (0.47)	2.00 ^a (0.50)	1.60 ^b (0.54)	1.48 ^b (0.49)
NH_4^+ (mg N l^{-1})	0.042 (0.047)	0.039 ^a (0.033)	0.044 ^a (0.053)	0.027 ^a (0.017)	0.023 ^a (0.012)
TON (mg N l^{-1})	0.019 (0.060)	0.011 ^a (0.022)	0.022 ^a (0.072)	0.005 ^a (0.005)	0.006 ^a (0.006)
Colour (Hazen)	109 (68)	83 ^a (45)	113 ^a (72)	88 ^a (49)	123 ^a (76)
WThigh (cm)	-3.6 (4.2)	-10.7 ^a (6.1)	-4.0 ^b (4.1)	1.1 ^c (1.1)	11.9 ^d (7.8)
WTlow (cm)	-18.7 (6.9)	-22.9 ^a (7.0)	-20.2 ^a (7.0)	-6.5 ^b (5.4)	-3.2 ^b (7.0)

The mean values followed by a different letter within a row were significantly different at $P < 0.05$ based on ANOVA and Tukey test (for SO_4^{2-} and WTlow) or Kruskal–Wallis and Mann–Whitney tests (for pH and WThigh, when Levene's test was significant)

WThigh = high water table; WTlow = low water table

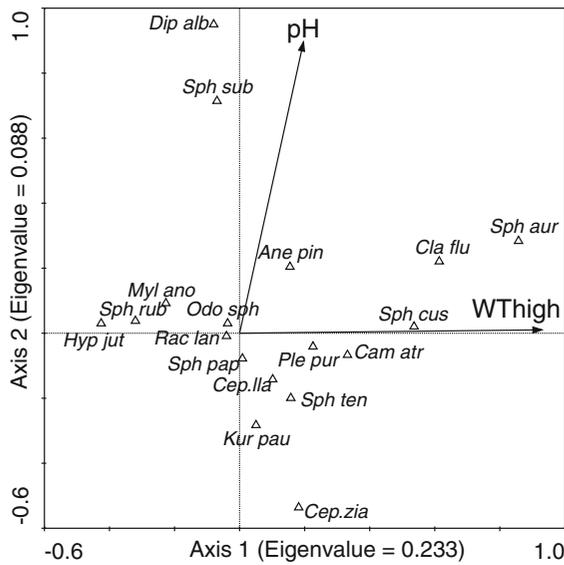


Fig. 3 Partial CCA ordination showing the distribution of bryophyte species in relation to high water level (WThigh) and pH. The proximities of the peatland borders were standardized by using the distances to the peatland borders as covariables. See Table 1 for the complete species names. Axis 1 ($P = 0.002$) explained 10.3% of the species data and axis 2 ($P = 0.004$) 3.1%. The inter set correlations of WThigh with axis 1 was 0.73. The inter set correlations of pH with axis 2 was 0.52

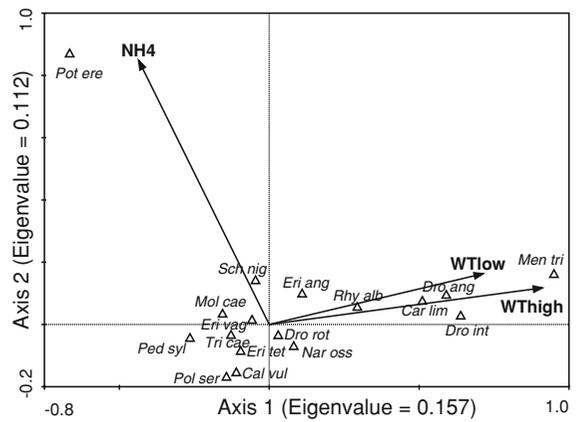


Fig. 5 Partial CCA ordination showing the distribution of vascular species in relation to high (WThigh) and low water tables (WTlow) and NH_4^+ concentration (NH_4). The proximities of the peatland borders were standardized by using the distances to the peatland borders as covariables. See Table 1 for the complete species names. Axis 1 ($P = 0.002$) explained 8.9% of the species data and axis 2 ($P = 0.004$) 3.1%. The inter set correlations of WThigh and WTlow with axis 1 were 0.71 and 0.57, respectively. The inter set correlations of NH_4 with axis 2 was 0.47

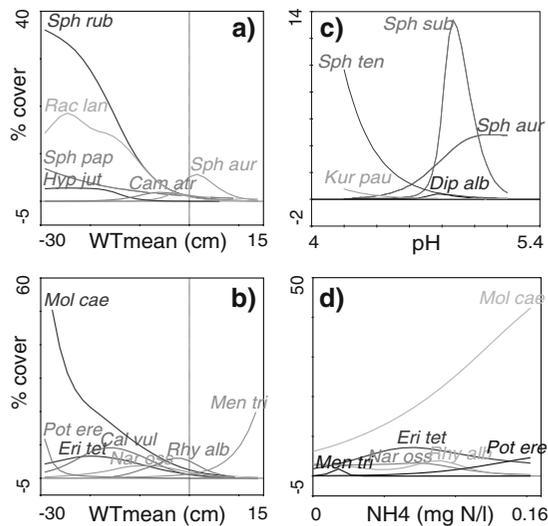


Fig. 4 Response of plant species to **a, b** mean water table (WTmean), **c** pH and **d** NH_4^+ concentration (NH_4). General Additive Models with Poisson distribution were used to estimate the response of the most common species. Only species having a significant ($P < 0.05$) response to the environmental variables are shown. See Table 1 for species complete names

correlated with lower water table, shallower peat depth, higher water colour and lower concentrations of Cl^- than other peatland sectors, while also pH and NH_4^+ concentration appear to be at the highest range (Fig. 6b). The vascular flora along the stream was composed of *M. caerulea*, *P. erecta* and *Myrica gale*, together with plant species usually found in marshes and wet meadows, such as *Caltha palustris*, *Juncus acutiflorus*, *J. effusus* and *Agrostis stolonifera* (Fig. 6c). The bryophyte vegetation was characterized by a rich flora uncommon in other parts of the bog, consisting of *D. albicans*, *S. palustre* and *Rhytidadelphus squarrosus* (Fig. 6c). Similar to the high lawns close to the stream, the hollows and low lawns show large internal variation. The wetter areas appear to bring diversity to otherwise rather homogeneous high lawn vegetation (Fig. 6).

Discussion

General nature of the bog

The plant communities observed in this study closely resemble those previously described for Atlantic blanket bogs in Western Ireland (Boatman 1961;

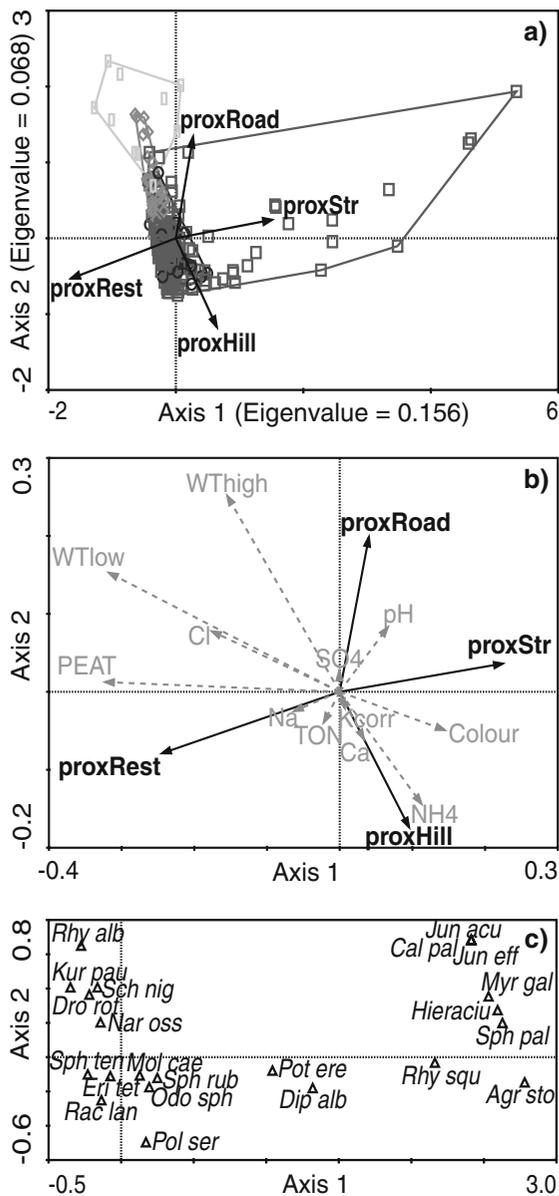


Fig. 6 CCA ordination showing the distribution of **a** different microforms, **b** environmental variables and **c** plant species in relation to distance from peatland borders. Only species with at least 5% of the variability explained by the CCA axes are shown. Axis 1 ($P = 0.002$) explained 3.0% of the samples data and axis 2 ($P = 0.002$) explained 1.4%. The inter set correlations of proxRest and proxStr with axis 1 were -0.35 and 0.32 , respectively. The inter set correlations of proxRoad and proxHill with axis 2 were 0.42 and -0.37 , respectively. proxRest = proximity to the restoration area border; proxStr = proximity to the stream; proxRoad = proximity to the road; proxHill = proximity to the hill-grazing area. Microforms are indicated with different signs: \circ for hummocks, \square for high lawns, \diamond for low lawns, \square for hollows. WThigh = high water table; WTlow = low water table; PEAT = peat depth. See Table 1 for species complete names

typical of hollow vegetation such as *Sphagnum auriculatum* (Lindsay et al. 1988; Lindsay 1995), the water level of these transitional areas stayed below the soil surface for most of the time in Glencar. Based on their dryness we included them into the low lawn group (Laine et al. 2006). Compared to Glencar, a lower occurrence of *Molinia caerulea*, higher cover of dwarf shrubs and no *Schoenus nigricans* were reported for a Montane blanket bog in South-western Scotland (Silver Flow, Boatman 1983). This represents the typical difference in the general vegetation appearance between Montane and Atlantic blanket bogs (Foss et al. 2001). Hummocks and lawns in the Glencar Atlantic blanket bog are likely to belong to the phytosociological association of the *Pleurozia purpureae*–*Ericetum tetralicis*, described for deep-peat ombrotrophic blanket bogs, due to the presence of the characteristic species *S. nigricans*, *Pleurozia purpurea* and *Campylopus atrovirens* (Doyle 1990). The hollows occurring in the study site are likely to belong to the *Sphagno tenelli*–*Rhynchosporium albae* syntaxon, thus one of the two hollow vegetation associations typical of Atlantic blanket bogs, due to the presence of the characteristic species *Rhynchospora fusca* and *Sphagnum cuspidatum* (Doyle 1990). The vegetation close to the stream resembles the *Myrica gale* dominated vegetation described along drainage channels in Atlantic blanket bogs (Doyle 1990). Our results are in good agreement with Doyle (1990), who suggested that this vegetation colonizes shallow peat areas near streams and drains, where water movement occurs in seepage and occasional inundation causes additional nutrient input.

Differences in water sampling procedures can complicate the comparison of water chemistry

Doyle 1982; Doyle 1990). Compared to blanket bogs in Scotland, Glencar shows similarities with the “low relief ‘western’” vegetation described by Lindsay et al. (1988) for a peatland complex in Sutherland, north Scotland. Both bogs are largely dominated by lawns with occasional hummocks and hollows and some quaking areas. Moreover, both bogs contain surfaces of bare peat that can be seen as transitions between the terrestrial and aquatic phase (Lindsay et al. 1988), although in Glencar those are very sparse and scattered. Despite the occurrence of some species

between different peatlands (Tahvanainen and Tuomala 2003). Even with this limitation, the comparison of the chemical analyses suggests that the water chemistry in Glencar is similar to other Atlantic blanket bogs, even if with slightly lower ion concentrations (Proctor 1992; Shotyck 1997). The chemical status of our study site is strongly influenced by the proximity of the sea. The falling of sea spray increases the sea-origin ion concentration in the bog water (Sparling 1967a; Proctor 1992), which in turn enhances the corrected conductivity and pH (Sparling 1967a). The concentration of ions of marine origin (Na^+ and Cl^-), pH and K_{corr} were indeed higher in Glencar, with similar values as in other Atlantic blanket bogs (Sparling 1967a, b; Boatman and Armstrong 1968; Sheehy Skeffington and O'Connell 1998), than in peatlands located at higher distance from the sea, as Montane blanket bogs (Adamson et al. 2001; Proctor 2006), boreal poor fens and bogs (Vitt and Chee 1990; Vitt et al. 1995; Wind-Mulder et al. 1996; Tahvanainen et al. 2002). In contrast, the land origin ion Ca^{2+} had similar concentrations as in Montane blanket bogs (Adamson et al. 2001; Proctor 2006), but typically lower than in peatlands more remote from the sea, as boreal poor fens and bogs (Vitt and Chee 1990; Vitt et al. 1995; Tahvanainen et al. 2002). The concentration of NH_4^+ and SO_4^{2-} in ombrotrophic peatland waters increases in regions influenced by human activities (Proctor 1992; Adamson et al. 2001); SO_4^{2-} also slightly increases close to the sea due to marine inputs (Proctor 1992). Since Glencar lies in a region distant from industrial activities, sulphate was generally lower than in a Montane blanket bog in northern England (Adamson et al. 2001) and in a number of Canadian boreal bogs (Wind-Mulder et al. 1996), but higher than in a boreal fen complex in North-east Finland (Tahvanainen et al. 2002). NH_4^+ had slightly lower concentrations than in a Montane blanket bog (Adamson et al. 2001) and in a Finnish boreal base poor-rich fen complex (Tahvanainen et al. 2002), but generally higher than in a number of boreal fens in Western Canada (Vitt and Chee 1990). Similar to the vegetation composition, the water chemistry suggests the general ombrotrophic character of the site. The difference of chemical status between microforms was small as previously observed in a *Sphagnum*-dominated peatland in the Alps (Bragazza and Gerdel 2002).

Variation in vegetation in relation to environment

The bryophyte cover in the study site decreases sharply from 71% in hummocks to about 25% in high lawns and less in the wetter microforms (Fig. 2). The bryophyte cover in the Glencar blanket bog is very low compared to other ombrotrophic bogs (e.g., Glaser et al. 1990) due to the paucity of hummocks and the scarcity of mosses in lawns. *Sphagnum* species in the study site are generally restricted to either the driest (*S. rubellum*) or to the wettest (*S. auriculatum* and *S. cuspidatum*) microforms (Table 1). Vascular plants have a higher occurrence in high lawns and hummocks (Fig. 2). Yet, even if with different coverage, most vascular species (e.g., *Eriophorum angustifolium*, *Narthecium ossifragum*, *Molinia caerulea*, *Erica tetralix* and *S. nigricans* (Table 1)) do not appear to be as restricted to certain microforms as bryophytes.

Many studies suggest that the vegetation distribution in peatlands is mostly controlled by water table, chemical status and distance from the peatland margins (e.g., Malmer 1986; Glaser et al. 1990; Bubier 1995; Bubier et al. 1995). In our study water table appeared to best explain the distribution of the plant species (Figs. 3, 4a, 4b and 5). The separate analyses for bryophytes and vascular species, which revealed a different primary control after water table (pH gradient for bryophyte and NH_4^+ concentration for vascular plant distributions, Figs. 3, 4c, 4d and 5) agree with some previous studies (Vitt and Chee 1990; Bubier 1995; Bragazza and Gerdel 2002). Working on vegetation distribution between different boreal fen types in Western Canada (Vitt and Chee 1990) and in two *Sphagnum*-dominated peatlands in the Italian Alps (Bragazza and Gerdel 2002), these authors observed that the distribution of bryophytes followed a gradient relating to pH and mineral content, while a gradient of NH_4^+ concentration and other nutrients was more important for the distribution of vascular plants.

The role of the bog margins

There was little variation in the vegetation between the central part of the bog and its artificial edges (hill-grazing and restoration areas), but a substantial variation related to the distance from its natural edge (stream) (Fig. 6a). The distance from the natural

margins is recognized to be one of the drivers of northern peatland vegetation patterns (e.g., Malmer 1986), but acknowledged as being unclear and caused by different and varying local effects (Wheeler and Proctor 2000; Økland et al. 2001). The area near the stream in the Glencar Atlantic blanket bog appears well defined: high vegetation biodiversity was accompanied with relatively dry conditions, shallow peat depth, low Cl^- but high water colour, pH and NH_4^+ compared to other areas in the bog (Fig. 6b). On the contrary, little differentiation of vegetation close to disturbed areas indicated that the disturbance on the blanket bog is restricted to its close vicinity.

Conclusively, the work indicated that while natural margins to Atlantic blanket bogs provide clear gradients in microform and associated vegetation patterns, margins with areas that have undergone artificial disturbance do not show such marked changes. This is not to say that such disturbance has had no impact on the adjacent bog system, but the transition zones are not as marked as in the case of natural boundaries. Consequently there is a strong argument for the maintenance of even small surviving areas of relatively intact blanket bogs for conservation purposes, because they do not appear to become dominated by transitional vegetation.

Climate change is expected in peatlands to cause a decrease in summer water table and consequent decrease in pH and modification of the nutrient cycle. Since the distribution of bryophytes and vascular plants is explained by such environmental factors, climate change in Atlantic blanket bogs will likely affect the distribution of both vegetation groups. However, as bryophytes have a narrower niche than vascular plants, it is probable that climate change will have a higher impact on the bryophyte than on the vascular plant composition.

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