The effects of topography and rainfall on the distribution of Oceanic/Atlantic bryophytes in Wales – revised 2015

Sam Bosanquet

Evidence Report No 146

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Table of Contents

1. Crynodeb Gweithredol

Mae Cymru yn cynnal bryoffytau toreithiog iawn, gan gynnwys sawl rhywogaeth sy'n nodweddiadol o ardaloedd ym mhen pellaf gorllewin Ewrop lle ceir llawer o law. Dangosodd gwaith a wnaed yn y 1960au gydberthynas rhwng dosbarthiad y mwsoglau a'r llysiau'r afu 'Atlantig' hyn â sawl diwrnod o law a geir bob blwyddyn. Mae'r gydberthynas hon yn parhau i fod yn wir ar raddfa genedlaethol, ond mae ffactorau eraill yn berthnasol ar raddfa fwy lleol ac ni ellir ystyried glawiad fel yr unig elfen sydd wrth wraidd dosbarthiad ac amrywiaeth bryoffytau yng ngheunentydd Cymru.

Tynnir sylw at saith o fannau pwysig ar gyfer bryoffytau 'Atlantig' a leolir mewn mannau lle na cheir llawer o law. Mae'r rhan fwyaf o'r rhain i'w cael mewn coetiroedd ceunant i lawr yr afon o'r ucheldir glawog, lle mae cyfuniad o dopograffi a llif yr afon yn creu 'parthau niwl' a llecynnau o lif cyfnodol a reolir gan law i fyny'r afon yn hytrach nag yn uniongyrchol ar y cytrefi o fryoffytau 'Atlantig'. Dangosir cysylltiadau rhwng cyrsiau dŵr, rhaeadrau a bryoffytau y mae'n ofynnol iddynt gael lle llaith (hygrophilous) yn nosbarthiad craidd y rhywogaethau, fel *Aphanolejeunea microscopica*, *Drepanolejeunea hamatifolia* a *Harpalejeunea molleri*, ac ar ymylon eu dosbarthiad.

Ychydig o astudiaethau sydd wedi'u cynnal ar ffisioleg goddefiad dysychu bryoffytau 'Atlantig', er bod gwaith ymchwil yn y 1970au yn dangos amrywiad mewn goroesiad yn ystod sychder rhwng rhywogaethau, a hefyd rhwng tymhorau o fewn un rhywogaeth. Mae angen ymchwilio ymhellach i ecosystem ceunentydd er mwyn canfod pa newidiadau ecolegol sy'n arwain at ddigwyddiadau dysychu niweidiol, a pha mor wydn yw'r cynefin coetir 'Atlantig'.

2. Executive Summary

Wales supports a very rich bryophyte flora, including many species typical of the high-rainfall areas of westernmost Europe. Work in the 1960s showed a correlation between the distribution of these 'Atlantic' mosses and liverworts and the number of rain days each year. This correlation remains true at the national scale, but other factors play a role at a more local scale and rainfall cannot be considered the sole driver of bryophyte distribution and diversity in Welsh ravines.

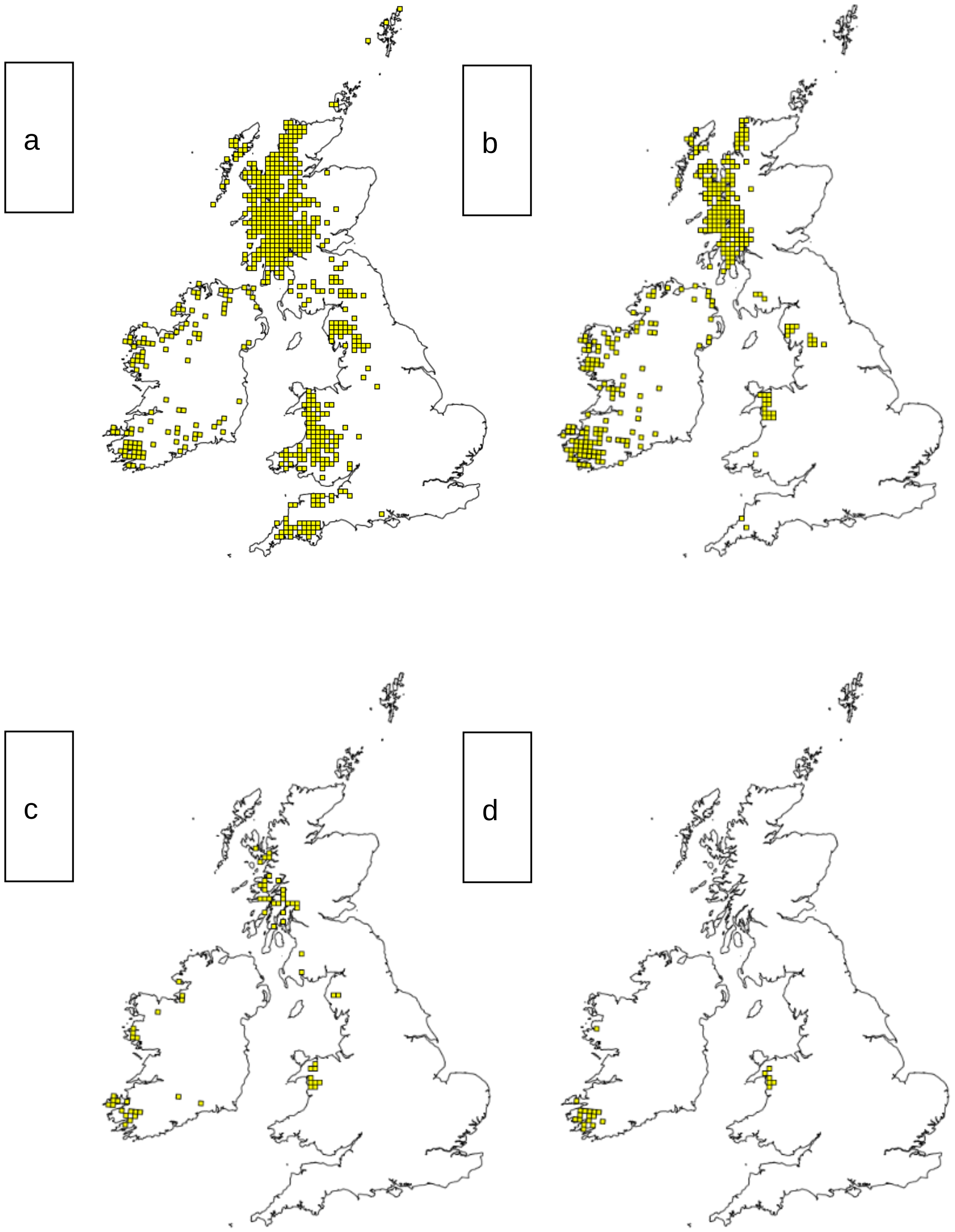
Seven hotspots for 'Atlantic' bryophytes that are located away from high-rainfall areas are highlighted. Most of these are in ravine woodlands downstream of a high-rainfall upland block, where a combination of topography and river flow provide 'mist zones' and areas of periodic inundation, governed by rainfall upstream rather than rainfall directly on the 'Atlantic' bryophyte colonies. Links between watercourses, waterfalls and humidity-demanding (hygrophilous) bryophytes are demonstrated both in the core of the range of species such as *Aphanolejeunea microscopica*, *Drepanolejeunea hamatifolia* and *Harpalejeunea molleri*, and at the edges of their range.

The physiology of desiccation tolerance in 'Atlantic' bryophytes remains relatively poorly studied, although research in the 1970s showed variation in survival of drought conditions between species and also between seasons within a single species. Further investigation of the ravine ecosystem is required to determine what ecological changes lead to damaging desiccation events, and how resilient the 'Atlantic' woodland habitat is.

3. Hyperoceanic, Oceanic and 'Atlantic' bryophytes

Wales supports an exceptionally rich lower plant flora, including a very high proportion of mosses and liverworts (collectively known as bryophytes) that show Hyperoceanic or Oceanic distributions in Europe (Hill & Preston, 1998). These species are restricted in Europe to the Atlantic coast, from the Azores and Canaries north to south-western Norway, extending only a few hundred kilometres east of the coast. Some are much rarer in the rest of Europe than in Britain and Ireland (Blockeel *et al.*, 2014), and *Radula voluta* is disjunct from the tropics, giving Wales a significant responsibility for their conservation in European and global terms. These species are a recognised part of the Annex 1 Habitat '<u>Old sessile oak woodlands with *Ilex* and *Blechnum* in the British Isles</u>' and are a critical component of Welsh woodland SACs: "A key feature of European importance is the rich Atlantic bryophyte communities that are often well-developed within this Annex I type" (www.jncc.defra.gov.uk description of the Annex 1 habitat). In addition, the Atlantic/Western assemblage of Ratcliffe (1968) was used in the *Guidelines for Selection of Biological SSSIs: non-vascular plants* (Hodgetts, 1992), and the oceanic categories of Hill & Preston (1998) help inform the revised Guidelines (Bosanquet *et al.*, in prep.). Atlantic/Western mosses and liverworts form the core of many notified bryophyte assemblage SSSI features.

The Hyperoceanic distribution pattern is illustrated for Britain and Ireland in Figures 1a to 1d. Only the north-west of the country is suitable for these species, and they become progressively rarer from *Plagiochila spinulosa* (Fig. 1a) to *Sematophyllum demissum* (Fig. 1d) because of increased ecological sensitivity. These maps present data at 10x10km resolution, as this is the standard way of exploring data at the national scale in both the UK and Ireland (e.g. Blockeel *et al.*, 2015). This does not mean that the species is present throughout each of the mapped 10x10km squares. Finer resolution reveals a very patchy distribution, for example *Drepanolejeunea hamatifolia* at 2x2km resolution (Fig. 2) is clearly much more restricted than Figure 1b might have suggested. These Hyperoceanic distributions also contrast with the distribution of less ecologically restricted mosses such as the wall-top *Tortula muralis* (Fig. 3).



Figures 1a to 1d: 10x10km distributions of the bryophytes *Plagiochila spinulosa* (1a), *Drepanolejeunea hamatifolia* (1b), *Radula voluta* (1c) and *Sematophyllum demissum* (1d) in Britain and Ireland (NBN).

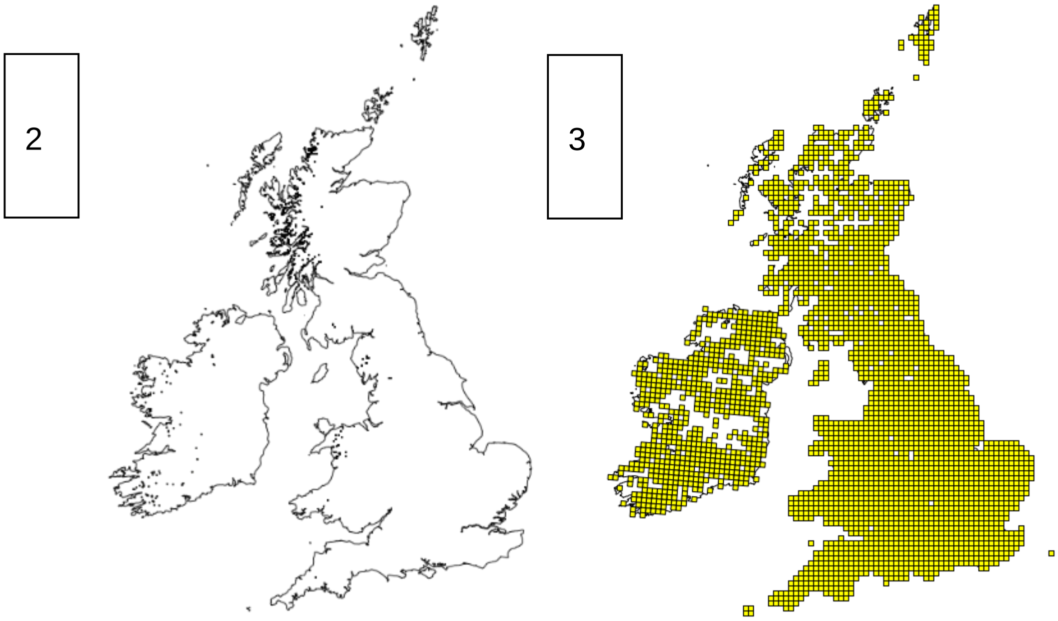


Figure 2: 2x2km distribution of *Drepanolejeunea hamatifolia*; Figure 3: 10x10km distribution of *Tortula muralis*.

Although the distribution of these Hyperoceanic species varies they are united by a requirement for high humidity provided by periodic submergence, regular splash or spray, or a more generally humid environment (Averis, 2011). In its most visible form, the generally humid environment may be apparent as a 'mist zone' around a cascade or waterfall.

4. 'Atlantic' bryophytes and rain days

Derek Ratcliffe (1968) recognised a close correlation between the average number of rain days in a year and the richness of the Atlantic[1] bryophyte flora. This correlation is clearly visible at the scale of the British Isles, with the greatest diversity of 'Atlantic' bryophytes in north Wales, western Scotland and south-west Ireland.

[1] The biogeographic term 'Atlantic' covers the Atlantic coast of Europe whereas the biogeographic terms 'Oceanic' and 'Hyperoceanic' cover the high rainfall coasts of all continents, in particular the Pacific coast of north America. In UK and European terms, the 'Atlantic' bryophytes of Ratcliffe (1968) are largely synonymous with the 'Hyperoceanic' bryophytes of Hill & Preston (1998).

This published information has led to a widespread view that humidity levels at key sites are generated by the number of days of rainfall and the topography and tree cover, and that the rivers contribute only a very small amount of the humidity.

Topography clearly plays a major role, both in holding humidity and reducing exposure to the wind. This is illustrated by the Western Isles, which experience a very high number of rain days per year (Fig. 2), but have a relatively poor oceanic bryophyte flora compared with the Inner Hebrides and the western Scottish mainland, probably because of the paucity of ravines due to the local geology. Land use history and continuous tree cover are also demonstrably key factors (Edwards, 1986), although some unwooded sites in areas of high rainfall support a rich assemblage of oceanic species – for example Rhaeadr Ogwen in Snowdonia and many sites in south-west Ireland, where ravines, boulders and waterfalls combine to provide suitable conditions.

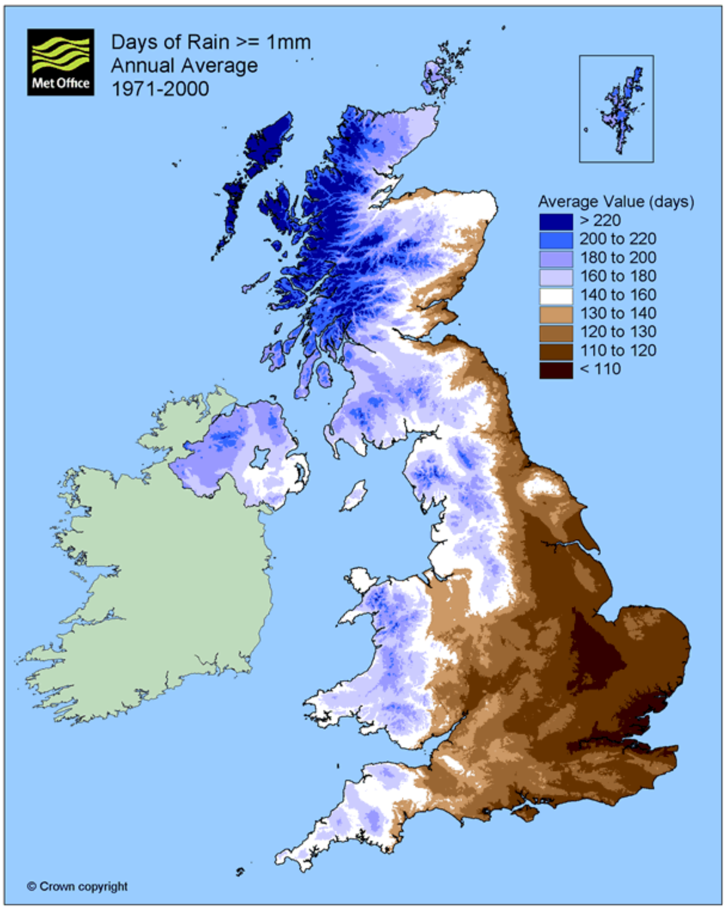


Figure 3: Mean annual number of days with >1 mm of rain in the UK (© The Met Office).

The view that water flows play a minor role in ravine systems appears to result from merging Ratcliffe's correlation between high rainfall areas and Atlantic bryophyte diversity – which clearly holds true at a national level – and evidence of the presence of a rich Oceanic bryophyte flora in at least one site with depleted water levels: Ceunant Llenyrch NNR. Close examination of the distributions in Wales of (a) sites with rich Oceanic assemblages and (b) mean annual rain days shows many exceptions to the rule that rain days govern species richness (see Rain Days in Wales below), with sites outside the highest rainfall areas being characterised by both steep ravine sections and abundant cascades and/or waterfalls. Rainfall is a critical driver of ravine systems – hence Ratcliffe's correlation – but that is in part because it maintains sufficient flows in rivers both to have created ravines in the past and to create spray zones in the present. There is insufficient historic data to prove that Ceunant Llenyrch was unaffected by the construction of the Llyn Trawsfynydd dam and abstraction of water since the 1920s: it supports a remnant, albeit a relatively rich remnant, of the richest, most topographically suitable, north-facing ravine in Wales, and the current populations of notable bryophytes are not necessarily equal to their past (unknown) size.

The southernmost UK populations of desiccation-intolerant liverworts such as *Aphanolejeunea microscopica*, *Plagiochila exigua* and *Radula aquilegia* are within the zone made humid by a waterfall (but not where there is direct splashing), as are the southernmost Welsh colonies of *Harpalejeunea molleri*. The sites at which these species grow have been subject to intensive bryophyte survey in the last 15 years and the restriction of these liverworts to the waterfalls' environs is beyond doubt (see Waterfall case studies, below). The situation in north Wales is less clear, and it is likely that the wetter climate allows some species that are restricted to waterfall areas in the south to exploit rocks further from spray, albeit still in close proximity to rocky water courses. However, there are several species, such as *Hageniella micans*, *Sematophyllum demissum* and *Radula voluta*, that are not found at all in south Wales, and these often require humidity derived from a waterfall, for example by the Afon Gamlan, where the cascades of Rhaeadr Ddu produce a humid zone that extends some distance from the falls themselves (see Waterfall case studies, below).

5. Rain Days in Wales

The broad-brush map of the mean number of rain days per year, as observed between 1971 and 2000 (Fig. 3) shows that some parts of north Wales rival western Scotland, but that the number of rain days in Wales is generally considerably lower than in the heart of the 'Celtic Rainforest' zone (Plantlife, 2010) and more akin to Galloway and the English Lake District. When sites with rich Oceanic bryophyte assemblages are plotted on a map of rain days (Fig. 4), the concentration of extremely rich sites in north Wales is clearly visible. However, the majority of sites sit within the 180-200 rain days per year band, and very few are subject to higher levels of direct precipitation, although most do lie downstream of very high rainfall areas (>200 rain days per year).

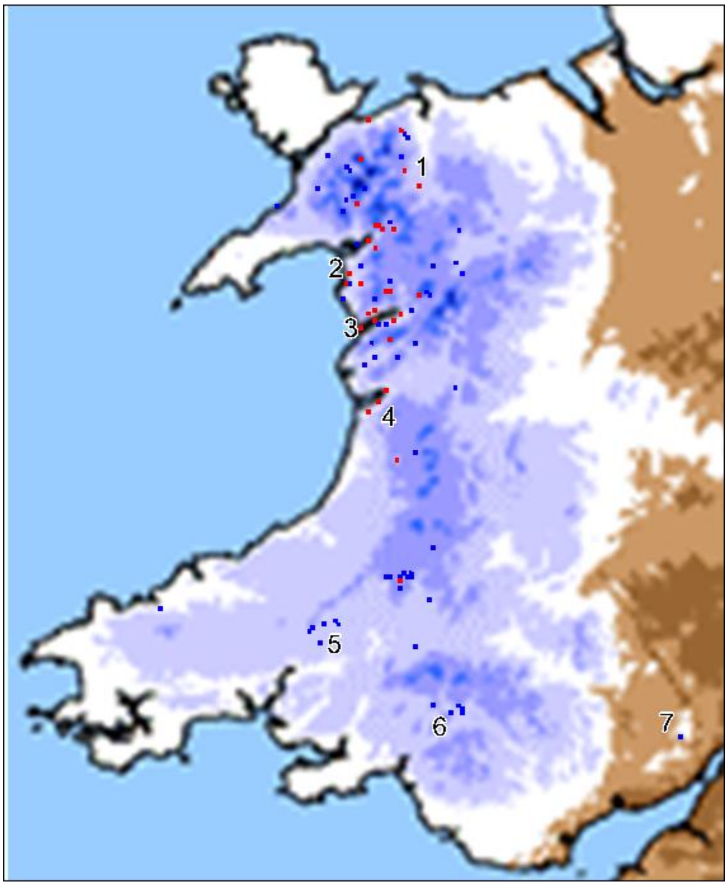


Figure 4: recorded assemblages of Hyperoceanic and Oceanic bryophytes in Wales related to rain days. Red dots are sites that score 40 points or more using the Weighted Ravine Markers Score of Bosanquet (2015) and blue dots are sites that score 20-39 points using the scoring system. Numbers relate to some high-scoring sites that sit outside the areas of highest rainfall. For key to rain

days see Figure 1; values are 200-220 dark blue; 180-200; 160-180; 140-160; 130-140; 120-130 dark brown. The numbers 1-7 in this map refer to sites/areas described below.

Sites that score highly using the Weighted Ravine Markers Score of Bosanquet (2011) and that sit relatively far from areas of high rainfall include:

1. Afon Llugwy and Fairy Glen: two sites east of the main high rainfall area where waterfalls and cascades provide suitable conditions for diverse oceanic bryophyte assemblages with Weighted Ravine Markers Scores of >50.
2. Coed Aberartro. Sits to the west of the high rainfall area of Rhinogau, and has an average of 160–180 rain days per year. This is one of only two sites for *Hageniella micans* in Wales, and its score of 68 points places it in the top 3 sites in Wales.
3. Sites around the Mawddach Estuary, including Arthog Hall Woods, Afon Cwm Mynach and Bontddu, all of which have an average of <180 rain days per year but support very rich oceanic bryophyte assemblages associated with cascades on rivers that drain high-rainfall mountains.
4. Coed Cwm Einion, Coed Cwm Clettwr and Coed Cwm Clettwr. These sites each score >40 points, although they lack the most humidity-demanding species. These steep-sided valleys with frequent cascades and waterfalls have an average of 160–180 rain days per year.
5. Brechfa Forest. Home to outlying colonies of *Drepanolejeunea hamatifolia* and *Plagiochila exigua*, as well as a suite of valleys that score between 20 and 35 points. This area has an average of 160–180 rain days per year, although the hills to the north have 180–200.
6. ‘The Waterfalls’ area around Pontneddfechan and Ystradfellte supports Britain’s southernmost known populations of *Aphanolejeunea microscopica* and *Plagiochila exigua*, associated with substantial waterfall mist zones in valleys with less than 180 rain days per year, although they receive water from the higher rainfall Brecon Beacons.
7. Cleddon Shoots. Wales’ south-easternmost rocky stream scores 22 points and holds *Trichomanes speciosum* gametophyte as well as *Jubula hutchinsiae*, *Lophocolea fragrans* and *Solenostoma paroicum*. The rocky

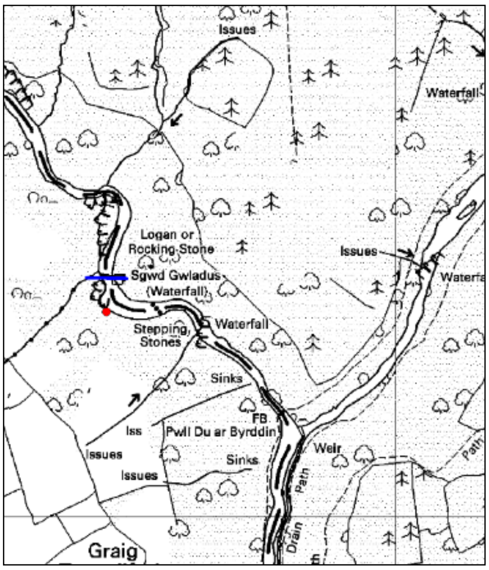
cascade is the key feature making this site suitable for Oceanic bryophytes, as it has an average of 140–160 rain days per year.

6. Waterfall case studies

Oceanic bryophytes grow in greatest abundance at sites such as Rhaeadr Ddu on the Afon Gamlan at Ganllwyd, where a number of environmental factors combine to provide humid conditions that rarely drop below optimal levels for the most sensitive species. Elsewhere, suitable conditions can be extremely localised, with humidity from a single waterfall making conditions suitable on just one rock face. The most notable species are seldom found in the waterfall splash zone itself, but prefer boulders or rock faces set slightly back from any spray but where humidity levels are constantly high (Averis, 2011). Examples of three species with their southernmost Welsh and only county sites opposite or adjacent to a waterfall are: *Aphanolejeunea microscopica* at its only site in Glamorgan, where it grows on an oak trunk opposite Sgwd Gwladus (Fig. 5); *Sphenolobopsis pearsonii* at its only site in Glamorgan, where it is found on a rock face adjacent to Sgwd yr Eira (Fig. 6); *Harpalejeunea molleri* at its only site in Carmarthenshire, where it is scattered amongst *Plagiochila exigua* on a rock face above a waterfall in the Cothi Gorge (Fig. 7). Meanwhile, the second most southerly Welsh colony of *H. molleri* is next to a waterfall on the Afon Doethie south of Ty'n-y-cornel (Fig. 8). On all maps in Figs. 5–8 the species is shown as a red dot and the waterfall as a blue line. In all cases these are the only localities at which these species have been found in the vicinity, despite south Wales being one of the most intensively recorded areas for bryophytes in the UK (Blockeel *et al.*, 2014).

Similar patterns are visible in many of Wales' richer ravines, revealed by the very accurate "Grid-mapping" technique used by Dr Des Callaghan. Desiccation-sensitive Hyperoceanic liverworts such as *Drepanolejeunea hamatifolia* and *Harpalejeunea molleri* are restricted to the vicinity of rocky cascades (Figs. 9-11). Grid-mapping has also helped elucidate the link between watercourses and the rare moss *Sematophyllum demissum* (Callaghan, 2015c), although in that case the action of high flows to limit the extent of colonisation of boulders by commoner species is considered to be a significant factor in the species' distribution along with desiccation intolerance. A number of other hyperoceanic bryophytes are also poor competitors and periodic scouring to remove competitive common mosses is likely to combine with stable humidity levels to provide suitable ecological conditions for their growth.

In contrast to these watercourse-linked distributions, other uncommon species with different ecological requirements show no such link to the river – for example the liverwort *Jamesoniella autumnalis*, which grows on rotting logs and birch trunks (Fig. 12).



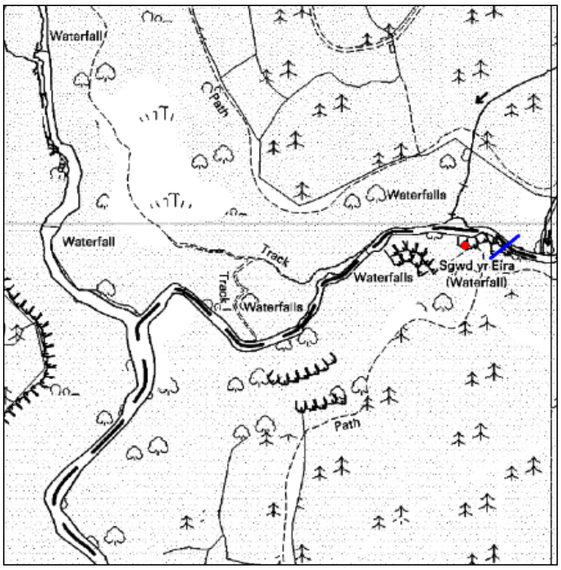
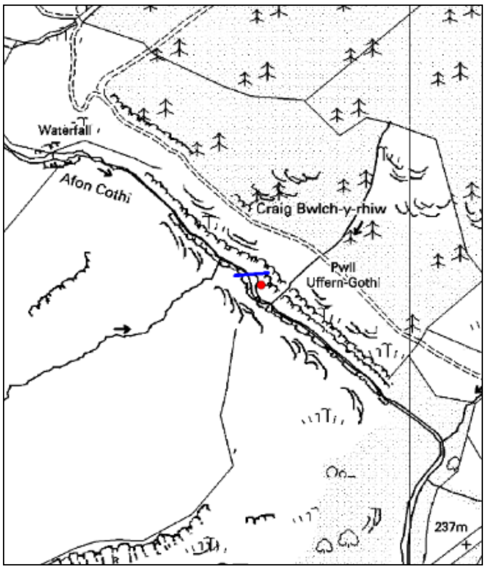


Figure 5: *Aphanolejeunea* in Glamorgan Figure 6: *Sphenolobopsis pearsonii* in Glamorgan



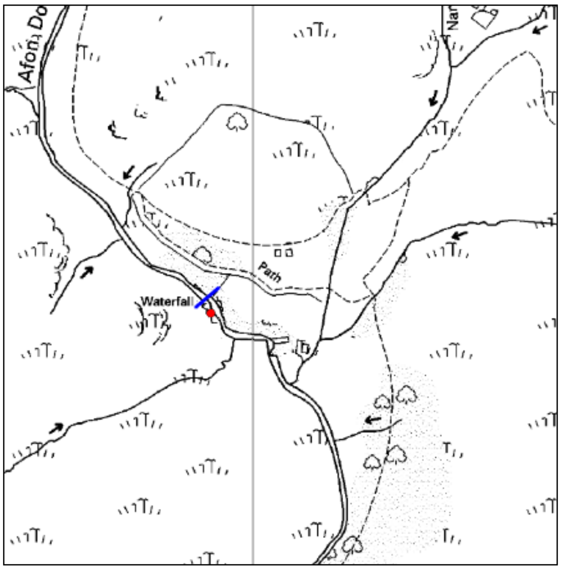


Figure 7: *Harpalejeunea molleri* in Carms. Figure 8: *Harpalejeunea molleri* in Ceredigion.

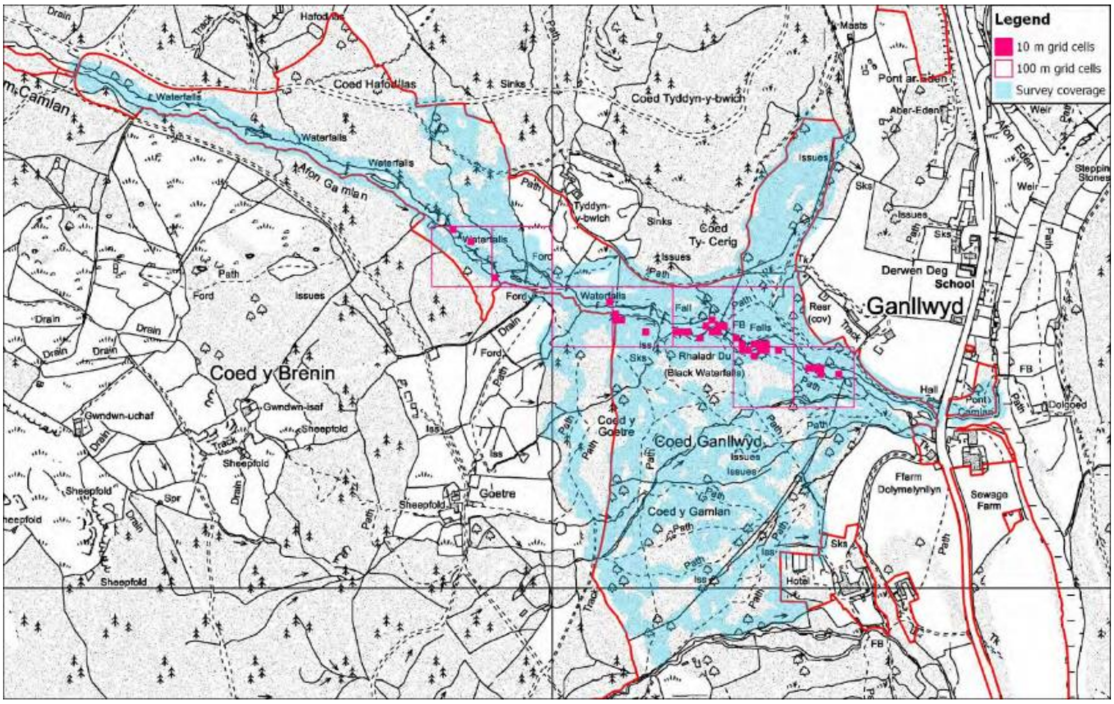


Figure 9 (from Callaghan, 2015b): the distribution of *Drepanolejeunea hamatifolia* in Coed Ganllwyd.

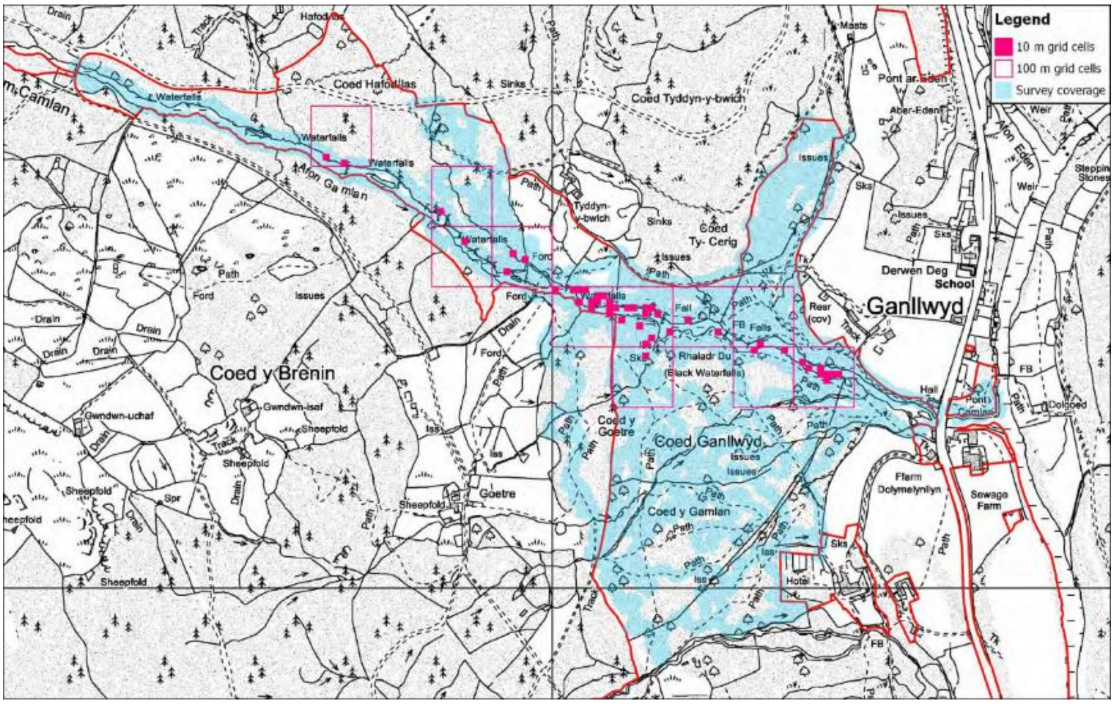


Figure 10 (from Callaghan, 2015b): the distribution of *Harpalejeunea molleri* in Coed Ganllwyd.

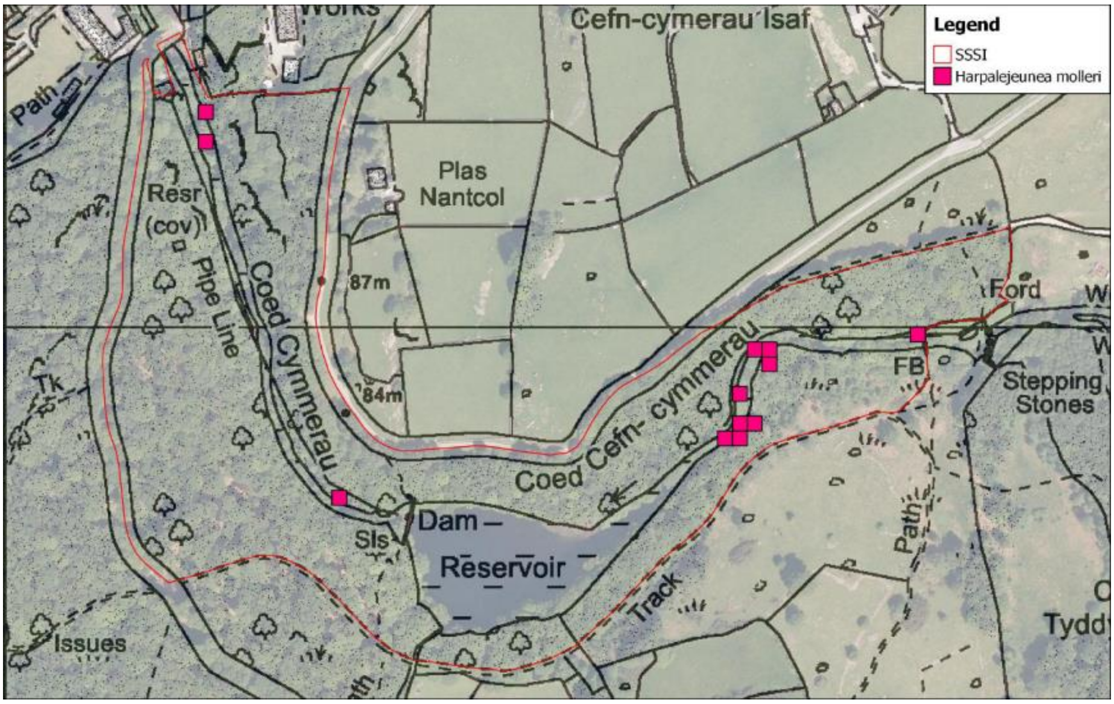


Figure 11 (from Callaghan, 2015a): the distribution of *Harpalejeunea molleri* in Coed Aber Artro.

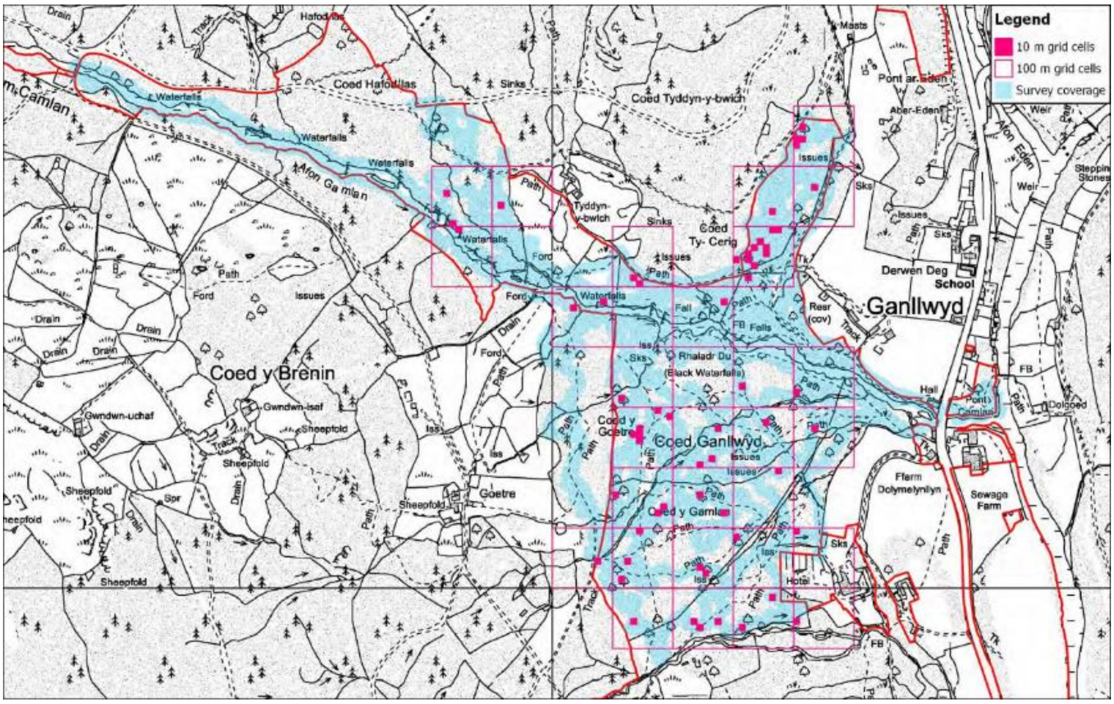


Figure 12 (from Callaghan, 2015b): the distribution of *Jamesoniella autumnalis* in Coed Ganllwyd.

Photographs of colonies of some of the Hyperoceanic bryophytes that mark the richest Welsh examples of ‘Atlantic’ woodland help to reinforce the link between cascades/waterfalls and these desiccation-sensitive species (Figs. 13–16).


Figures 13 (left) & 14 (right): the only localities for the Hyperoceanic liverwort *Plagiochila exigua* on two sites in north Wales – Ceunant Dulyn and Coed Garth Gell – both on the sheltered, downstream sides of boulders in cascade mist zones.


Figures 15 (left) & 16 (right): the only locality for *Harpalejeunea molleri* in Carmarthenshire, adjacent to a waterfall in the Cothi Gorge, and the location of a colony of *Harpalejeunea* on a boulder choke by a cascade in Cwm Gelli-Iago.

7. Desiccation intolerance and a need for humidity

Ecological studies by Derek Ratcliffe (1968) indicate that the primary factors that cause ‘Atlantic’ bryophytes to be restricted to the western edge of Europe are an intolerance of desiccation and a sensitivity to frost. A series of physiological studies into desiccation tolerance by Michael Proctor (e.g. Dilks & Proctor, 1976) showed that there is enormous variation in desiccation tolerance by British bryophytes, and that some species can survive with almost no atmospheric water for many months whereas others are killed almost immediately when dried. Bryophytes take in water from their surroundings, rather than from the ground, and in dry conditions they shut off their physiological processes in order to survive. Humid conditions, where there is an abundance of available water in the atmosphere, suit many desiccation-intolerant species, and the term humidity-demanding has often been used in place of desiccation-intolerant. Most of the uncommon liverworts and mosses that are restricted to the ravines of north-western Britain are specifically humidity-demanding because they require atmospheric water (high relative humidity and/or rainfall) rather than inundation from a water body, such as a river.

A rainfall episode will allow a bryophyte to become wetted and physiologically active, but even in the high rainfall areas of north Wales that would leave most species inactive for the rain-free majority of the year. In reality, a combination of rocky topography, northerly aspects and ravine depth mean that bryophytes remain covered by a thin film of water for some time even when it is not raining. Within a mist zone generated by a waterfall or cascade they can remain hydrated and physiologically active for much of the year.

Dilks & Proctor (1976) collected six species of bryophyte with varying desiccation tolerance throughout one year and tested their ability to withstand drought. They showed that the most sensitive species they tested, *Plagiochila spinulosa* (one of the most desiccation tolerant and least geographically restricted of Britain’s Hyperoceanic liverworts, see Fig. 1a), was killed by fewer than 30 days of drought (32% humidity) when collected in winter but survived 100 days of drought when collected in summer. Humidity levels in ravine systems seldom drop as low as 32%, but the study demonstrates that the relationship between humidity and species survival is not a simple one. *P. spinulosa* effectively aestivates, remaining largely inactive in summer when low flow levels happen routinely, and does most of its growth in winter. Reducing flow levels in winter to mirror, say, moderate summer flows could have a much more significant impact on *P. spinulosa* and ecologically similar species than might be expected.

8. Conclusions

Despite calls in 2011 for ecological investigations into the humidity profiles of ravine systems to determine exactly what role is played by different factors in governing humidity levels and thus the extent of potentially suitable habitat for desiccation intolerant species, no research has yet taken place. It is clear from observations that several factors are involved in determining Oceanic bryophyte richness, including rainfall, water flows, rock type and topography (including ravine depth, rockiness and height of waterfalls). Past assumptions that water flows are not a critical determiner of bryophyte richness can be countered by numerous examples where the most desiccation intolerant species are restricted to areas around waterfalls. Without accurate information on variation in a ravine's humidity profile at different flow rates throughout the year it is not possible to be confident that reduced flows will not reduce humidity levels and thus impact on the bryophyte flora. Sites need to be assessed on a case by case basis where sensitive species are present, so as to determine the roles of each factor in determining the distribution of the bryophyte flora.

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