Biodiversity Climate change impacts repord card technical paper

8. Implications of climate change for UK bryophytes and lichens

Christopher Ellis

Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh, EH3

***5LR Email*: c.ellis@rbge.org.uk**

EXECUTIVE SUMMARY

This Technical Report:

1. Introduces the biology and conservation status of bryophytes and lichens, and our state of knowledge in their distribution (Section 1).

2. Matches species distributions in the British bryophyte and lichen flora to bioclimatic models applied to vascular plants, validating this comparison via cross-referencing against bioclimatic models specifically applied to case-study bryophytes and lichens (Section 2.1).

3. Compares the outcomes of predictive modelling to direct evidence for species range shifts (Section 2.2).

4. Examines climate impacts at a habitat scale, focussing on ecosystems in which bryophytes and lichens are important components of the vegetation (Section 3).

The key findings are as follows:

1. Bryophytes and lichens are poikilohydric organisms and are particularly sensitive to microclimatic variation, with local microhabitats providing a buffer which may weaken direct sensitivity to macroclimatic change.

2. Nevertheless, a number of species have range edges in their British distribution, which is predicted by their global biogeography and is strongly suggestive of macroclimatic sensitivity. In addition, certain bryophyte and lichen species are important to the ecosystem function of habitats which are climate dependent, e.g. blanket bogs.

3. There is emerging evidence for a direct bryophyte and lichen response to human-induced climate change with a number of species shifting their range northwards **(Medium Agreement, Limited Evidence)**; however, these shifts must be cautiously interpreted against changes in the pollution regime and land management.

4. Bryophytes and lichens, including rare and/or BAP species, are structurally and functionally important in several habitats which appear to be threatened by climate change, especially upland ecosystems such as late-lying snow beds and montane heath **(High Agreement, Medium Evidence)**.

5. For the globally important oceanic bryophyte and lichen flora, sensitivity to climate change remains unknown and represents a key area of uncertainty **(Low Agreement, Limited Evidence)**.

6. There are examples where the impact of climate change on bryophytes and lichens may be ameliorated by reducing additional pressures on habitats. There are also opportunities to proactively manage microhabitat heterogeneity to buffer against macroclimatic change, especially for epiphytic species.

7. Impacts on bryophytes and lichens may be directly attributed to climate change, may emerge as a consequence of a shift in habitat status, may be related to extreme events for habitats which are highly fragmented and vulnerable (e.g. storm surge impacts for coastal dune systems), or may occur as a consequence of changed land management during human adaptation to climate change.

1. Introduction

1.1 Understanding Bryophytes and Lichens

Bryophytes and lichens are evolutionarily unrelated and represent different Kingdoms (bryophytes: Plants; lichens: Fungi). 'Bryophyte' describes a group of beguilingly simple and often diminutive plants, including the mosses, liverworts and hornworts. Bryophytes are therefore autotrophic, and can produce sugars in their cells by photosynthesis. Lichens by contrast are heterotrophic fungi, and must assimilate a source of carbon from outside their cells (hyphae) to maintain respiration. Lichens are fungi which have evolved to grow self-contained structures (lichen thalli) within which the fungus maintains a population of photosynthetic algae and/or cyanobacteria, and from which it sequesters simple sugars. Despite these important differences, bryophytes and lichens share several ecological traits which make their joint assessment of climate impacts an efficient starting point. First, bryophytes and lichens have traditionally been grouped under the umbrella-term 'cryptogams', which indicates that the sexually-derived reproductive propagules involved in their dispersal are microscopic haploid spores (with one set of chromosomes), rather than seeds. A second important trait which unites the bryophytes and lichens is their 'poikilohydric' nature, i.e. they do not have active mechanisms to prevent desiccation.

Bryophytes and lichens lack a specialised system for water and nutrient transport, such as that found in 'vascular plants' or 'tracheophytes', including angiosperms (flowering plants) and gymnosperms (e.g. conifers). Instead, the water status of bryophytes and lichens is highly responsive to ambient environmental conditions, with the organism tending to be turgid and photosynthetically active when the daytime environment is wet, and in a state of desiccation when the environment is dry. Within these constraints, bryophyte and lichen species are differently adapted to a spectrum of moisture regimes (Dilks & Proctor, 1979; Davey & Rothery, 1997), with some species associated with constant wetness or humidity (e.g. the aquatic BAP lichen *Collema dichotomum*), while others demonstrate an extreme tolerance of prolonged desiccation (Proctor *et al.*, 2007; Kranner *et al.*, 2008) which is characteristic of poikilohydry.

The apparent simplicity of bryophyte and lichen water relations belies a delicate equilibrium between their anatomical and physiological traits, and small-scale environmental variation. This equilibrium has been shown to control the species' realised niche for a range of contrasting systems:

1. For a macrolichen species (*Teloschistes lacunosus*) in a desert system (Almeria, Spain), spatial distribution was related to a brief period of dawn photosynthetic activity, following the condensation of dew in the pre-dawn (reactivating the thallus), but before thallus drying in the late-dawn. The duration of this critical period for carbon-gain was controlled by small-scale topography, which explained the local occurrence and abundance of the species (del Prado & Sancho, 2007).

2. The realised niche position of ten moss species partitioned among forest microhabitats (Oahu, Hawaii) was explained by their contrasting anatomical and physiological traits, including a trade-off between adaptation to promote photosynthesis in microhabitats with high irradiance, and a complimentary requirement for desiccation tolerance (Waite & Sack, 2010).

Anatomical and physiological differences thus explain species-specific responses to microsite moisture regime for bryophytes (Alpert & Oechel, 1985) and lichens (Beckett, 1995; Souza-Egipsy *et al.*, 2000), presenting a major challenge in understanding the sensitivity of these organisms to global macroclimatic change; species may respond to variability at a microhabitat scale (possibly in the order of millimetres or centimetres), weakening the direct relevance of coarse-grained climate information as an explanatory factor when predicting climate impacts.

Nevertheless, for certain species it is possible to identify regional trends in their British distributions that are strongly suggestive of macroclimatic sensitivity, and which are supported by species' varying biogeographies globally. Additionally, it has been observed that the spectrum of microhabitats occupied by a species may shift along climatic gradients (Poelt, 1987; Scheidegger, 1991), with increased specificity towards 'buffering' microhabitats in sub-optimal climatic regimes. This report considers evidence for the sensitivity of bryophytes and lichens to spatial and temporal macroclimatic variation (including human-induced climate change), in addition to an accompanying suite of non-climatic drivers which also control distribution and abundance.

1.2 Conservation Importance

Bryophytes and lichens are among the UK's most important contribution to international and especially European biodiversity. There are > 1000 bryophyte species in Britain, which represents c. 65 % of European bryophyte diversity; for lichens there are c. 1900 species in Britain, representing c. 47 % of European lichen diversity. This is compared to c. 15 % of European diversity for flowering plants (angiosperms). The conservation importance of bryophytes and lichens was reflected in the 2007 review of UK BAP priority species. For a total BAP list of 1150 species, lichens and bryophytes made the third and fourth largest contributions among the different taxonomic groups considered (138 & 111 spp., respectively), following vascular plants (212 spp.) and moths (152 spp.).

1.2.1 Knowledge Gaps

It should be acknowledged that an exhaustive analysis of climate change impacts for bryophytes and lichens is weakened by an incomplete knowledge of species distributions. New species continue to be discovered within Britain, as well as at a regional and site-scale. These discoveries are generated through basic inventory work, which continues to be extremely important, and through the application of increasingly sophisticated tools for species discrimination.

Molecular analysis has revolutionised our knowledge of bryophyte and lichen diversity, especially the recognition of 'cryptic' species which could not previously be discerned using traditional morphological characters. This has led to an improved understanding of species with surprising disjunctions, e.g. the discrimination of the montane liverworts *Anastrophyllum joergensenii* and *A. alpinum*, the former known only from Scotland, Norway and the Sino-Himalaya (Long *et al.*, 2006), and rarity, e.g. the identification of the liverwort *Herbertus borealis* known only from a single site in Scotland (Bell *et al.*, 2012). These recent discoveries highlight the global relevance of Britain's bryophyte and lichen flora, including montane species which are potentially vulnerable to climate change. The wider application of molecular techniques, including the DNA barcoding of bryophytes and lichens (Kelly *et al.*, 2011), will increase the future quality of distributional and monitoring data for difficult-to-identify and under-recorded species.

2. Biogeographic Patterns and Exposure to Climate Change

Biogeographic patterns for bryophytes (Hill & Preston, 1998; Bates & Preston, 2011; Preston *et al.*, 2011) and lichens (Coppins, 1976; Ellis *et al.*, 2007b) have been relatively well explored for Britain, with evidence for spatial distributions that are related to climatic variation and suggestive therefore of a potential sensitivity to human-induced climate change under UKCP09 scenarios (Jenkins *et al.*, 2010).

To provide a preliminary assessment of possible climate impact, species' British distributions for bryophytes generally (Hill & Preston, 1998; Bates & Preston, 2011), liverworts specifically (Preston *et al.*, 2011) and lichen epiphytes (Coppins, 1976), were matched to vascular plant groups (Berry *et al.*, 2002; see also Berry *et al*., 2007a,b) for which the loss or gain of bioclimatic space has been robustly assessed in the British Isles (Table 1). While bioclimatic envelope models have been widely used to give an indication of potential exposure of vascular plant species to climate change, bryophytes and lichens have not been subject to the same level of predictive bioclimatic research. The comparison of analogous distributional patterns is a feasible short-cut however, because similar distributional trends among vascular plants and co-occurring bryophyte and lichen species are expected to yield a broadly comparable assessment for the gain or loss of bioclimatic space in spatial regression models. However, this mode of assessment is limited in several respects: (i) it does not account for important functional differences between vascular plants and poikilohydric bryophytes and lichens, which may differentiate their actual climatic response (Proctor, 2011), (ii) it deals only with a theoretical exposure to climate change, and treats climate as a factor isolated from other ecological drivers, and (iii) it requires support from experimental studies, though this is not feasible for more than a relatively small set of species and habitats. Accepting these caveats, cross-referencing with bioclimatic assessments specifically applied to bryophytes (Anderson & Ohlemüller, 2011) and lichens (Ellis *et al.*, 2007b) helps to validate the approach (Table 1), while matches made against British distributions for bryophytes are supported through a comparison against their global biogeography (Hill & Preston, 1998; Bates & Preston, 2011 Preston *et al.*, 2011).

2.1 Exposure to Climate Change

The comparison yielded four key observations; these are exemplified for a sub-section of British bryophytes (25 % of species) for which a convincing match could be made between their British distributions and the case-study vascular plants which have been subject to bioclimatic modelling (Fig. 1).

2.1.1 Widespread Species

Vascular plant species which are widespread and for which the entire British climate is thought to lie within their tolerance of macroclimatic conditions did not appear sensitive to climate change scenarios (Berry *et al.*, 2002). Certain lichen species also have a wide British distribution (Coppins, 1976), though have not been assessed in a bioclimatic framework. Only c. 4 % of British bryophytes (10 % of liverworts) appear to fall within this group, and analysis of these species within a broader biogeographic setting appears to confirm that the British climate is nested within their global occurrence across major biomes, i.e. for circumpolar Boreal and Temperate elements (Hill & Preston, 1998; Bates & Preston, 2011; Preston *et al.*, 2011). These species are likely to be robust to climate change under UKCP09 scenarios.

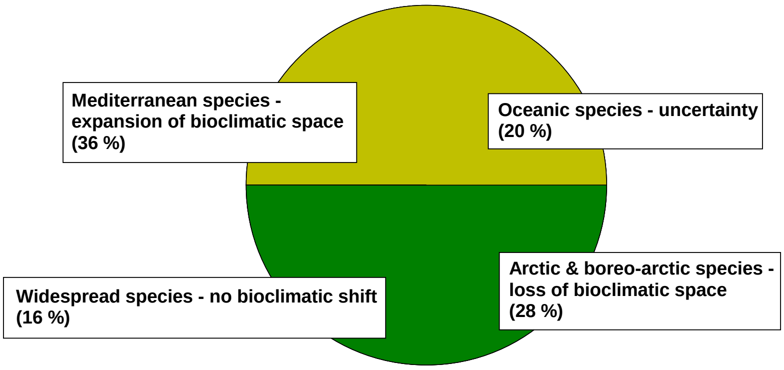

Figure 1. Proportion of British bryophytes in different bioclimatic response groups, based on species for which a match could be made with the distribution of British vascular plants subject to bioclimatic modelling.

However, the vascular plant analysis revealed important exceptions in which widely distributed species lost suitable bioclimatic space. This included wetland plants, such as *Eriophorum vaginatum* and *Valeriana dioica*, for which changed habitat conditions (regional soil drying) may result in a loss of suitable habitat (Berry *et al.*, 2002). This emphasises the importance of coupling species distributional shifts with habitat information also (see Section 3, below).

2.1.2 Northern and Montane Species

Vascular plant species with a northern distribution including a defined southern range limit in Britain may be exposed to a loss of suitable climate space (Berry *et al.*, 2002), though it is possible that for bryophytes and lichens a direct climatic effect may be less important than changing edaphic factors and species interactions (Crabtree & Ellis, 2010). This broad distributional group was partitioned for lichens into a separate northern-montane element (tending to include higher-altitude terricolous and saxicolous species) and a northern-boreal element (including epiphytes), which were each independently projected to lose suitable bioclimatic space in Britain (Ellis *et al.*, 2007b). The recognition of a distinct montane lichen flora matched with the distribution of arctic-montane bryophytes (Hill & Preston, 1998; Bates & Preston, 2011), accounting for c. 7 % of bryophyte species, and including liverworts (c. 19 % of species) with arctic and boreo-arctic affinities (Preston *et al.*, 2011). These bryophyte groups are also expected to be vulnerable to climate change impacts.

2.1.3 Southern Species

An increase of suitable bioclimatic space was projected for species with southern and low elevational distributions, for both vascular plants and lichens (Berry *et al.*, 2002; Ellis *et al.*, 2007b). The distribution of these species matched broadly with that of British bryophytes with Mediterranean affinities (c. 9 % of species), including c. 10 % of the liverwort flora which occur mostly in England and Wales with a temperate, southern-temperate and Mediterranean-Atlantic distribution (Preston *et al.*, 2011). Borrowing data from bioclimatic projections examining the response of bryophytes in England and Wales (Anderson & Ohlemüller, 2011), and focussing on nine species with Mediterranean affinities (c. 21 % of the species modelled), the results suggested a mean northwards shift in range of c. 102 km, and an elevational shift upwards of c. 40 m, through to the 2051-2080 period (HADCM3 A2 scenario).

2.1.4 Oceanic Species

Bioclimatic models for oceanic species were not attempted for vascular plants, and for lichens demonstrated a loss of bioclimatic space for a ‘northern oceanic group’ and mixed results (no change, or an increase of suitable bioclimatic space) for a ‘southern oceanic’ group (Ellis *et al.*, 2007b). The distributions for oceanic lichens matched with the eastern-limit for hyper-oceanic elements in the British bryophyte flora (c. 5 % of species), including c. 14 % species in the liverwort flora, suggesting an equivocal response for these species also.

The results of bioclimatic modelling for oceanic lichen species need to be treated with special caution, as different bioclimatic models for oceanic lichens have demonstrated a loss (Ellis *et al.*, 2007b) or an increase in bioclimatic suitability (Ellis & Coppins, 2007), or mixed results for contrasting species (Ellis *et al.*, 2009), under equivalent climate change scenarios. There is significant uncertainty in trends for future precipitation – implicit in the UKCP09 probabilistic output (Jenkins *et al.*, 2010) – while contrasting species responses among different bioclimatic models might be explained by seasonal shifts inherent in climate change scenarios (Jenkins *et al.*, 2010) – decreasing summer precipitation, increasing winter precipitation, and temperature increases across seasons – which may importantly control the distribution of oceanic species:

1. While the distribution of oceanic species is most obviously associated with frequent precipitation (distributions skewed towards the high-rainfall west coast of Britain), the phytogeography of oceanic lichen species includes southern-temperate and sub-tropical elements (Ellis *et al.*, 2009), similar to associated liverworts which have a hyper-oceanic *and* southern-temperate distribution (Preston *et al.*, 2011). The individual species response will therefore be

governed partly by temperature, with increased warmth possibly favouring oceanic species, though such species may also be vulnerable to longer periods of summer dryness.

2. The oceanic lichen epiphyte flora includes an abundance of 'cyanolichens' (lichen fungi with N-fixing cyanobacterial partner). These species require liquid water for the reactivation of cyanobacterial photosynthesis (Lange *et al.*, 1986; Lange *et al.*, 1993), benefitting from frequent wetting cycles and increased rates of N-fixation with consistently warmer temperatures (MacFarlane & Kershaw, 1977; Antoine, 2004). Again, while these species may respond positively to an increase in warmth and wetness, they may be vulnerable to longer periods of summer dryness which can inhibit N-fixing activity (Kershaw & Dzikowski, 1977).

3. Bryophytes (Rincon & Grime, 1989) and lichens (Fisher & Procter, 1978; Muir *et al.*, 1997) demonstrate seasonal growth patterns in response to monthly variation in temperature and precipitation, and in order to resolve the interacting effects of changed temperature and precipitation regimes (points 1. and 2., above), annual averages may be less important than accounting for changed seasonal trends, which includes the possibility for non-analogue climates when investigating intra-annual variability.

2.2 Direct Evidence for Climate Related Distributional Change

As a complement to bioclimatic modelling, there is only limited observed evidence for the direct response of bryophytes and lichens to climate change in Britain. This is partly because of the sensitivity of these organisms to a range of alternative factors controlling their British distributions, in particular air-pollution including the effect of SO_2 levels (Gilbert, 1968, 1970; Hawksworth & Rose, 1970). Statistical partitioning has indicated that pollution (not climate) remains the most important driver explaining the composition and richness of lichen epiphytes across Britain (Ellis & Coppins, 2009), though this may vary depending on regional context (Ellis *et al.*, 2009; Ellis & Coppins, 2010). The pollution regime is changing however, and a decline in SO_2 levels has been accompanied by increasing N-deposition (Woodin, 1989), so that the range expansion of bryophytes and lichens into formerly polluted areas (Seaward, 1998) should be interpreted against the species-specific response to variability in different N-types (Mitchell *et al.*, 2005; Davies *et al.*, 2007).

The climate change response must therefore be treated as part of a complex and dynamic process, in which species distributions are controlled by an amalgam of drivers which vary spatially and temporally. Against this background, there is tentative evidence for a direct climate impact. First, monitoring in the Netherlands has indicated that as SO_2 pollution has declined, the recovering lichen flora has skewed biogeographic affinities, with 83% of 'increasing' lichens having wide-tropical distributions, compared to an increase of 14% for arctic-alpine/boreo-montane lichens. No wide-tropical species decreased in abundance, while 50% of arctic-alpine/boreo-montane species had declined (Van Herk *et al.*, 2002). The trend includes an increase in lichen species which have *Trentepohila* as a symbiotic partner (Aptroot & Van Herk, 2007) and which tend to be more common in the tropics.

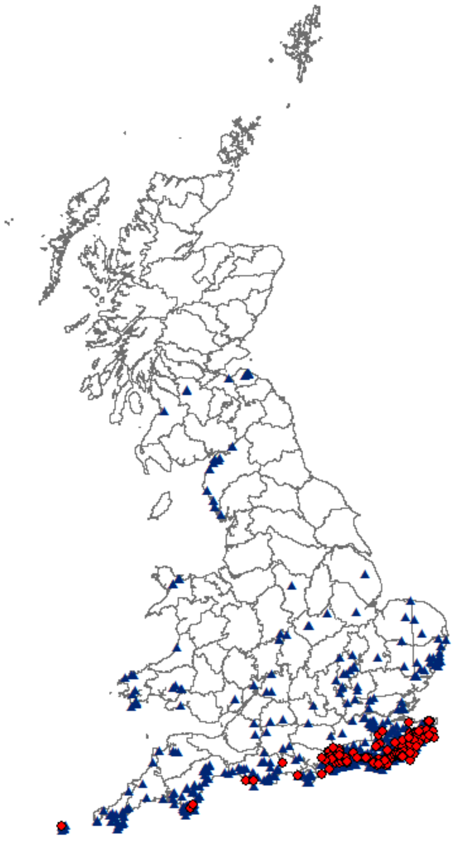

Figure 2. Records for the distribution of *Flavoparmelia soredians* for the 1960s (red circles) and since 1990 (blue triangles). A distinct northward shift may be partly explained by a decline in SO_2 pollution, though climate warming is likely to be a factor for this southern species. Data courtesy of the NBN and the British Lichen Society Mapping Scheme.

Second, there are species within the British flora for which their recent expansion is best explained by climate warming, while acknowledging also a facilitative effect of shifts in the pollution regime and local habitat factors; this includes the liverworts *Cololejeunea minutissima* and *Colura calyptrifolia* (Bates & Preston, 2011). Similar trends are beginning to emerge for lichen distributions also, with the northward spread of warm-temperate species, e.g. *Flavoparmelia soredians* (Fig. 2).

3. Habitat Assessment of Climate Change Sensitivity

General trends in species biogeography (see Section 2, above) are accompanied here by assessments for specific habitats within which bryophytes and lichens are a major component.

3.1 Montane Ecosystems

Bryophytes and lichens are characteristic elements of the British montane vegetation, and are dominant components in several vegetation types of the NVC (Averis *et al.*, 2004):

- Snow-beds: U8, *Carex bigelowii-Polytrichum alpinum* sedge-heath; U11, *Polytrichum sexangulare-Kiaeria starkei* snow-bed; U12 *Salix herbacea-Racomitrium heterostichum* snow-bed.

- Montane Heath: H13 *Calluna vulgaris-Cladonia arbuscula* heath; H14 *Calluna vulgaris-Racomitrium lanuginosum* heath; H19 *Vaccinium myrtillus-Cladonia arbuscula* heath; H20, *Vaccinium myrtillus-Racomitrium lanuginosum* heath; U9*: Juncus trifidus-Racomitirium lanuginosum* rush-heath; U10, *Carex bigelowii-Racomitrium lanuginosum* moss-heath.

- Hepatic Mats: H20, *Bazzania tricrenata-Mylia taylorii* sub-community; H21, *Mastigophora woodsii-Herbertus aduncus* subsp. *hutchinsiae* sub-community.

- Flushes and Springs: M7 *Carex-curta-Sphagnum russowii* mire; M31, *Anthelia julacea-Sphagnum denticulatum* spring; M32, *Philonotis fontana-Saxifraga stellaris* spring, M33 *Pohlia wahlenbergii* var. *glacialis* spring.

Bioclimatic modelling for European plants has indicated that montane species may be disproportionately sensitive to climate change (Thuiller *et al.*, 2005), a finding which is supported by bioclimatic modelling for British vascular plants in montane habitats (Berry *et al.*, 2002; Berry *et al.*, 2003). The extent of this exposure to climate change appears to increase in down-scaled model projections which are applied at a local scale (Trivedi *et al.*, 2008b). It is therefore important to note that a suite of montane bryophyte and lichen species occur in Britain in single or very few locations, and as isolated populations, and these should be considered extremely vulnerable to climate change, e.g. the bryophytes *Marsupella arctica* and *Scorpidium turgescens*, and lichens including *Brodoa intestiniformis*, *Fulgensia bracteata*, and *Nephroma arcticum*.

3.1.1 Snow-Beds

Niche-specialist bryophytes are dominant in the sward beneath late-lying snow-beds, which provide the primary habitat for BAP bryophyte species such as *Andreaea nivalis*, *Marsupella arctica* and the Schedule 8 species *Gymnotrium apiculatum*, as well as niche-specialist and rare lichen species, e.g. *Cladonia maxima* and *C. trassii*.

This habitat is expected to be among the most vulnerable to climate change: 1. Snow-beds are spatially restricted in Britain; 2. Alongside warming temperatures, UKCP09 scenarios project a decline in mean snowfall of 65-80 % over montane areas by the 2080s (Jenkins *et al.*, 2010); 3.

There is an observed decline in snow patch extent and duration for Scotland (Watson *et al.*, 1994; Cameron *et al.*, 2012); 4. Climate projections have indicated that snow-bed bryophyte vegetation will shift towards upland grassland (Trivedi *et al.*, 2008a); 5. Repeat surveys for 27 snow-beds in Scotland (1990/91 and 2007/8) have tentatively demonstrated a vegetation shift, towards a community typical of more open conditions (Rothero *et al.*, 2011), including the increasing abundance of *Juncus trifidus* and a decrease in the snow-bed liverwort *Moerkia blyttii*; 6. Snow-beds represent the first example of a notified feature (Site of Special Scientific Interest) which has, as a consequence of climate change, been designated as having 'unfavourable status' during Site Condition Monitoring (Dr David Genney, SNH; personal communication).

Assessment of Climate Change Threat: Very Likely; High Agreement, Medium Evidence

3.1.2 Montane Heath

Bryophyte (*Racomitrium lanuginosum*) and lichen species (*Cladonia arbuscula* and *C. uncialis*) associated with montane heath are projected to lose suitable bioclimatic space under climate change scenarios (Trivedi *et al.*, 2008a). However, the relative importance of direct climate impacts has been brought into question for local circumstances, with factors such as wind-speed and species interactions also playing a key role in shaping the vegetation of lichen-rich heath communities (Crabtree & Ellis, 2010).

Climate impacts will occur against a background of additional stresses on montane heath habitats, which have as a consequence declined substantially towards the south of their range, e.g. in Wales and the Lake District (Thompson & Brown, 1992). Observational and experimental studies have demonstrated that montane heath systems are degraded by heavy grazing (Britton *et al.*, 2005) and N-deposition (Britton *et al.*, 2005; Armitage *et al.*, 2012). However, these pressures may be less important in explaining community structure than climate (Armitage *et al*., 2014), which is consistent with the interpretation for repeat monitoring studies, that homogenisation of the montane vegetation and losses for *Racomitriu*m and heathland lichens such as the arctic-alpine *Flavocetraria nivalis* (Britton *et al.*, 2009; Ross *et al.*, 2012) can partly be attributed to climate warming and summer dryness (Ross *et al.*, 2012).

Assessment of Climate Change Threat: Likely; Medium Agreement, Medium Evidence

3.1.3 Hepatic Mats

A northern hepatic mat community (dominated by liverworts) is restricted to a climate zone in the western British mountains, characterised by frequent and high annual rainfall, with low evapotranspiration in a mild climate (Averis, 1992). The component liverwort species have an oceanic boreo-montane distribution (Hill & Preston, 1998), including European endemics and species with continental disjunctions (Hill & Preston, 1998; Rothero, 2003; Hodd & Skeffington, 2011). This hepatic mat community has an analogue in a unique assemblage of terricolous and saxicolous microlichens which are associated with the oceanic mountains of western Britain (Fryday, 2002).

Given a dependency of oceanic-montane hepatic and lichen communities on the interaction of rainfall and temperature, exploring their sensitivity using climate change scenarios is subject to the same uncertainties experienced for oceanic epiphytic lichens, i.e. changing seasonal values (see Section 2.1.4, above). However, results indicate that bioclimatic space may be lost through a shift northwards for hepatic mat communities in western Ireland (Hodd & Skeffington, 2011; Hodd *et al*., 2014), with a vulnerability to bioclimatic shifts because species reproduction is limited to short-distance asexual fragmentation (Rothero, 2003; Hodd & Skeffington, 2011; Hodd *et al*., 2014). This predictive modelling is supported by monitoring over a 50 year period to indicate changed composition for hepatic mat communities in western Scotland including a decline in specialist liverworts attributed in part to warmer and drier climatic conditions (Flagmeier *et al*., 2014). There are important opportunities to reduce other pressures on the habitat which may arise locally through over-grazing (Hodd & Skeffington, 2011) and burning (Rothero, 2003), aiming to increase habitat resilience to climate impacts.

Assessment of Climate Change Threat: Likely; Medium Agreement, Medium Evidence

3.1.5 Springs and Flushes

Montane springs and flushes are dominated by bryophytes, and provide the habitat for BAP species including *Splachnum vasculosum* and *Tayloria lingulata*, and rarities such as *Scapania paludosa*. These habitats will be subject to climate change impacts on montane hydrology, with UKCP09 projections indicating warmer summer temperatures and reduced summer precipitation (Jenkins *et al.*, 2010) and pointing to potential water deficits. This impact includes a loss of integrity for late-lying snow-beds (see Section 3.1.1, above) which may provide a perennial source of drainage water for many high mountain spring and flush habitats.

Assessment of Climate Change Threat: Likely; Medium Agreement, Limited Evidence

3.2 Woodland Ecosystems

Epiphytic and ground-flora bryophytes and lichens are critical to understanding the ecology and conservation of British woodlands. While woodland structure (e.g. tree species composition and demography) might be similar among sites in different bioclimatic regions, the bryophyte and lichen flora can be dramatically different, revealing contrasting biogeographic affinities and suggesting macroclimatic sensitivity.

However, alongside any direct climate change impact, future changes in woodland composition, either as a climatic response (Berry *et al*., 2012) or through tree disease (Pautasso *et al*., 2013), could have an important effect on epiphyte communities (Ellis *et al*., 2014). It is also possible that future mitigation and adaptation in woodland management, e.g. an emphasis on carbon-sequestration, wood-fuel products and amenity value in multi-functional woodlands, could have a detrimental effect on Britain's epiphyte flora. Such land-use transitions need to be carefully managed, taking full account of the importance of woodlands for bryophyte and lichen diversity; as such, goals to increase the extent and connectivity of native woodland have the potential to buffer climate impacts.

3.2.1 Sub-Boreal Woodland

The birch, pine, aspen and juniper woodlands in north-east Scotland include epiphytic lichens with restricted distributions in Britain, and which are representative of a relatively more continental and boreal climate, e.g. *Melanohalea septentrionalis* and *Vulpicida pinastri*. Although it is difficult to identify an analogue suite of sub-boreal bryophytes by matching global biogeographies to the British flora (Table 1), species with restrictions to north-east Britain include the BAP species *Buxbaumia viridis* and *Orthotrichum gymnostomum*.

As with oceanic species, bioclimatic modelling for sub-oceanic epiphytes has provided contrasting results, with the suggestion that increased summer dryness may favour the occurrence of certain species, e.g. *Lecanora populicola* (Ellis *et al.*, 2007a), while the 'sub-boreal' climate associated with the occurrence of other lichen epiphytes may decline, especially in outlying areas such as mid-central Wales and north-east England (Ellis *et al.*, 2007b). Thus, boreal species such as *Vulpicida pinastri*, which is associated with areas of deep snow-lie in the forests of Scandinavia, are expected to decline with warmer winters, though an equally important factor in Britain may be the loss of juniper scrub as its preferred habitat (Binder & Ellis, 2008). Observational evidence based in southern Scandinavia has nevertheless demonstrated a range shift for *V. pinastri* of c. 151 km to the north-east (Lättman *et al.*, 2009), suggesting climatic sensitivity when comparing distributions for 1986 and 2003. Based on historic mapping and herbarium records, it has been possible to infer an apparent decline in England of *V. pinastri* during the 20th Century, despite an increase in recording effort over the same period (Ellis & Binder, 2007). This example for *V. pinastri* is consistent with predictive modelling for > 380 epiphyte species, which suggests a decline in environmental suitability for sub-boreal woodland species located in north-eastern Scotland, based on UKCP09 projections through to the 2080s (Ellis *et al*., 2014; Ellis *et al*., 2015).

Assessment of Climate Change Threat: Likely; Medium Agreement, Medium Evidence

3.2.2 Temperate Rainforest

Britain’s temperate rainforest is characterised by its unique bryophyte and lichen flora, and is internationally important (Coppins & Coppins, 2005; Rothero, 2005).

The assemblage of lichen epiphytes associated with woodland habitats along the hyper-oceanic west coast of Britain includes three elements: 1. Widespread species, which do not define the rainforest system; 2. Oceanic specialists, which define the rainforest system, and which are only recorded from hyper-oceanic climates, including the BAP lichen species *Graphis alboscripta* and *Pseudocyphellaria norvegica*; 3. Facultatively oceanic species. This last category includes species which are most abundant in hyper-oceanic woodland habitats during the present-day, but which may have been widespread in relatively more continental regions prior to the loss of primary, old-growth forest, e.g. the *Lobarion* alliance of species (Rose, 1988). Monitoring tentatively suggests that representative species of the *Lobarian* alliance have stable or declining populations in Britain, with limited recruitment (Wolseley & James, 2000), though this may be attributed to multiple factors (pollution, or woodland and surrounding land use), which interact with climate change, e.g. increased periods of water stress. Facultatively oceanic species tend to be associated in sub-optimal climates with ancient woodland (Ellis *et al.*, 2009), which is expected to include ‘old-growth’ microhabitats that buffer macroclimatic unsuitability (Lisewski & Ellis, 2010; Ellis, 2013) and provide refugia for establishment and growth. This underscores the critical link between micro- and macroclimatic conditions, and recent work has demonstrated this interaction with respect to riparian woodland, whereby the oceanic lichen epiphyte *Nephroma parile* may shift its ‘preferred’ position with respect to distance from a watercourse, along a macroclimatic gradient (Belinchon *et al*., 2015). There is as a consequence an important opportunity for proactive management to increase the resilience of oceanic bryophyte and lichen populations to climate change. This may be achieved by increasing the extent and complexity of woodland sites to promote microhabitat heterogeneity (ensuring refugia for establishment in sub-optimal climates: Ellis 2013), or ensuring a sufficient width of riparian and stream/riverside buffer zone woodland in order to enable populations to adjust to changing macroclimates, in addition to maintaining ecological continuity for the viability of dispersal-limited species.

Assessment of Climate Change Threat: About as Likely as Not; Medium Agreement, Limited Evidence

3.3 Wetland and Coastal Ecosystems

Wetland and coastal ecosystems are considered together. They each provide examples of habitats in which the direct species response to climate change may be less important that indirect impacts operating through a loss of habitat integrity.

3.3.1 Wetlands

Bioclimatic studies have indicated that wetland habitats may suffer decreased water availability, as particularly highlighted for south-east England (Dawson *et al.*, 2003). Along with changing woodland structure (see Section 3.2, above), this habitat-type serves to emphasise the potential indirect consequence of climate change. Thus, wetland bryophyte species with a southerly distribution, rather than simply expanding their range northwards (see Section 2.1.3, above), may be threatened *in situ* by a loss of suitable wetland habitat. This is the case for the liverwort *Leiocolea rutheana* var. *laxa*, which occurs in a calcareous fen in East Anglia, and which the preliminary results of DNA barcoding (see Section 1.2.1, above) indicate to be a distinct species (Dr David Long, RBGE; personal communication).

Bryophytes, in particular *Sphagnum* species, are critically important in the structure and function of British ombrotrophic peatlands, which are also the habitat for BAP species, e.g. *Sphagnum balticum*, and in drier sub-communities rare lichens including *Cladonia stygia*. Bioclimatic models focussed on individual *Sphagnum* species have projected relatively small climate change impacts through to 2050 (for UKCP09: Smart *et al*. 2010), though in contrast, studies focussed at the ecosystem scale (UKCIP02 high emissions scenarios) have indicated a massive loss of bioclimatic space (up to c. 84 %) for British blanket peats (Gallego-Sala *et al.*, 2010), representing a significant threat to associated bryophytes and lichens. Climate change impacts might be ameliorated by reversing additional factors which compromise peatland hydrology, such as afforestation and drainage, and reducing impacts on the vegetation such as intensive burning and over-grazing.

Assessment of Climate Change Threat: Likely; Medium Agreement, Medium Evidence

3.3.2 Stabilised Dune and Shingle Systems

Stabilised dune and shingle systems are locally dominated by bryophyte and lichen communities (e.g. within H11, *Carex vulgaris-Carex arenaria* heath) and are important for the occurrence of rare species such as the declining ‘sand-dune *Bryums*’ (Rothero, 2003), represented by the BAP species, *Bryum calophyllum*, *Bryum marratii* and *Bryum warneum*, as well as providing important habitat for lichens including the BAP species *Peltigera malacea*.

Stabilised coastal systems are marginal habitats in Britain, increasingly fragmented and trapped between extensive coastal development (e.g. housing estates, caravan parks, golf courses etc), and often subject to associated pressures from human use. The lack of natural buffer zones makes these ecosystems vulnerable in the future to rising sea levels and the impact of storm surges, which may increase in magnitude in the seas around Britain (Lowe & Gregory, 2005).

Assessment of Climate Change Threat: Likely; Low Agreement, Limited Evidence

4. Conclusions

1. In terms of regional distributions, there is emerging evidence for a species-specific bryophyte and lichen response to climate change, through the expansion of species with southern ranges northwards. This is consistent with predictions from bioclimatic models, though this evidence remains extremely tentative and needs to account for a dynamic process of shifting patterns in response to pollution and land use change.

2. There are convincing examples of montane habitats where projections from bioclimatic modelling are complemented by direct evidence for a climate impact, leading to the loss of bryophyte and lichen species from plant communities; this is especially the case for snow-beds in Scotland, and to a lesser extent *Racomitrium* and lichen-rich ericaceous heath.

3. The climatic response remains unresolved for some of the most important bryophyte and lichen communities, especially for oceanic montane hepatic mats and lichens, and temperate rainforest systems.

4. In all cases examined, there are important opportunities to build resilience into the bryophyte and lichen flora by off-setting negative impacts and discounting uncertainty, e.g. reducing additional pressures such as grazing, burning and N-pollution for montane systems, and increasing woodland extent, microhabitat heterogeneity and temporal continuity during forest management.

5. There are many systems for which climate impacts are indirect, operating through changed ecosystem status (e.g. peatland water tables), where threat is related to accumulating pressures on an already vulnerable ecosystem (e.g. coastal dune and shingle systems), or because of the potential for indirect threats of human adaptation, e.g. the impact of altered flow regimes on obligately aquatic species as a consequence of hydro-schemes or increased extraction in water stressed environments.

6. Despite evidence for possible climate change impacts, in many cases the actual vulnerability of species remains unknown. This could be improved through:

   a. A functional understanding of the ways in which bryophytes and lichens respond to microhabitat conditions, which may interact with macroclimatic gradients, and including the potential of species to acclimate to climatic variation (Lange & Green, 2005);
   b. Understanding how dispersal and gene flow across landscapes may be limited (Pohjamo *et al.*, 2008) or else (i) provides opportunities for migration among fragmented habitats to track climate change, or (ii) allows *in situ* adaptation where populations are locally adapted to contrasting climatic regimes (Murtagh *et al.*, 2002; Gerdol & Vincentini, 2011).

References

Alpert, P. & Oechel, W.C. (1985) Carbon balance limits the microdistribution of *Grimmia laevigata*, a desiccation-tolerant plant. *Ecology*, **66**, 660-669.

Anderson, B.J. & Ohlemüller, R. (2011) Climate change and protected areas: how well do British rare bryophytes fare? *Bryophyte ecology and climate change* (ed. by Z. Tuba, N.G. Slack and L.R. Stark), pp. 409-425. Cambridge University Press, Cambridge.

Antoine, M.E. (2004) An ecophysiological approach to quantifying nitrogen fixation by *Lobaria oregana*. *The Bryologist*, **107**, 82-87.

Aptroot, A. & Van Herk, C.M. (2007) Further evidence of the effects of global warming on lichens, particularly those with *Trentopohlia* phycobionts. *Environmental Pollution*, **146**, 293-298.

Armitage, H.F., Britton, A.J., van der Wal, R., Pearce, I.S.K., Thompson, D.B.A. & Woodin, S.J. (2012) Nitrogen deposition enhances moss growth, but leads to an overall decline in habitat condition of mountain moss-sedge heath. *Global Change Biology*, **18**, 290-300.

Armitage, H.F., Britton, A.J., van der Wal, R. & Woodin, S.J. (2014) The relative importance of nitrogen deposition as a driver of *Racomitrium* heath species composition and richness across Europe. *Biological Conservation*, **171**, 224-231.

Averis, A. (1992) Where are all the hepatic mat liverworts in Scotland? *Botanical Journal of Scotland*, **46**, 191-198.

Averis, A., Averis, B., Birks, J., Horsfield, D., Thompson, D. & Yeo, M. (2004) *An Illustrated Guide to British Upland Vegetation*. Joint Nature Conservation Committee, Peterborough.

Bates, J.W. & Preston, C.D. (2011) Can the effects of climate change on British bryophytes be distinguished from those resulting from other environmental changes? *Bryophyte Ecology and Climate Change* (ed. by Z. Tuba, N.G. Slack and L.R. Stark), pp. 371-407. Cambridge University Press, Cambridge.

Beckett, R.P. (1995) Some aspect of the water relations of lichens from habitats of contrasting water status studied using thermocouple psychrometry. *Annals of Botany*, **76**, 211-217.

Belinchon, R., Yahr, R. & Ellis, C.J. (2015) Interactions among species with contrasting dispersal modes explain distributions for epiphytic lichens. *Ecography*, in press.

Bell, D., Long, D.G., Forrest, A.D., Hollingsworth, M.L., Blom, H.H. & Hollingsworth, P.M. (2012) DNA barcoding of European *Herbertus* (Marchantiopsida, Herbertaceae) and the discovery and description of new species. *Molecular Ecology Resources*, **12**, 36-47.

Berry, P.M., Dawson, T.P., Harrison, P.A. & Pearson, R.G. (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography*, **11**, 453-462.

Berry, P.M., Dawson, T.P., Harrison, P.A., Pearson, R.G. & Butt, N. (2003) The sensitivity and vulnerability of terrestrial habitats and species in Britain and Ireland to climate change. *Journal of Nature Conservation*, **11**, 15-23.

Berry, P.M., Jones, A.P., Nicholls, R.J. & Vos, C.C. (2007a) *Assessment of the Vulnerability of Terrestrial and Coastal Habitats and Species in Europe to Climate Change*. Annex 2 – Planning for Biodiversity in a Changing Climate. BRANCH Project Final Report, Natural England.

Berry, P.M., O'Hanley, J.R., Thomson, C.L., Harrison, P.A., Masters, G.J. & Dawson, T.P. (eds) (2007b) *Modelling Natural Resource Responses to Climate Change (MONARCH)*. MONARCH 3 Contract Report. UKCIP Technical Report, Oxford.

Berry, P., Onishi, Y. & Paterson, J. (2012) *Understanding the Implications of Climate Change for Woodland Biodiversity and Community Functioning*. Forestry Commission (UK), Edinburgh.

Binder, M.D. & Ellis, C.J. (2008) Conservation of the rare British lichen *Vulpicida pinastri*: changing climate, habitat loss and strategies for mitigation. *The Lichenologist*, **40**, 63-79.

Britton, A.J., Pearce, I.S.K. & Jones, B. (2005) Impacts of grazing on montane heath vegetation in Wales and implications for the restoration of montane areas. *Biological Conservation*, **125**, 515-524.

Britton, A.J., Beale, C.M., Towers, W. & Hewison, R.L. (2009) Biodiversity gains and losses: evidence for homogenisation of Scottish alpine vegetation. *Biological Conservation*, **142**, 1728-1739.

Cameron, I., Watson, A. & Duncan, D. (2012) Two Scottish snow patches survive until winter 2011/12. *Weather*, **67**, 162-164.

Coppins, B.J. (1976) Distribution patterns shown by epiphytic lichens in the British Isles. *Lichenology: Progress and Problems* (ed. by D.H. Brown, D.L. Hawksworth and R.H. Bailey), pp. 249-278. Academic Press, London.

Coppins, B.J. & Coppins, A.M. (2005) Lichens - the biodiversity value of western woodlands. *Botanical Journal of Scotland*, **57**, 141-153.

Crabtree, D. & Ellis, C.J. (2010) Species interaction and response to wind speed alter the impact of projected temperature change in a montane ecosystem. *Journal of Vegetation Science*, **21**, 744-760.

Davey, M.C. & Rothery, P. (1997) Interspecific variation in respiratory and photosynthetic parameters in Antarctic bryophytes. *New Phytologist*, **137**, 231-240.

Davies, L., Bates, J.W., Bell, J.N.B., James, P.W. & Purvis, O.W. (2007) Diversity and sensitivity of epiphytes to oxides of nitrogen in London. *Environmental Pollution*, **146**, 299-310.

Dawson, T.P., Berry, P.M. & Kampa, E. (2003) Climate change impacts on freshwater wetland habitats. *Journal for Nature Conservation*, **11**, 25-30.

del Prado, R. & Sancho, L.G. (2007) Dew as a key factor for the distribution pattern of the lichen species *Teleschistes lacunosus* in the Tabernas Desert (Spain). *Flora*, **202**, 417-428.

Dilks, T.J.K. & Proctor, M.C.F. (1979) Photosynthesis, respiration and water content in bryophytes. *New Phytologist*, **82**, 97-114.

Ellis, C.J. (2013) A risk-based model of climate change threat: hazard, exposure and vulnerability in the ecology of lichen epiphytes. Botany, **91**, 1-11.

Ellis, C.J. & Binder, M.D. (2007) Inferred shift in the British distribution of *Vulpicida pinastri* using herbarium and mapping data. *Bulletin of the British Lichen Society*, **101 (Winter)**, 4-10.

Ellis, C.J. & Coppins, B.J. (2007) Changing climate and historic-woodland structure interact to control species diversity of the '*Lobarion*' epiphyte community in Scotland. *Journal of Vegetation Science*, **18**, 725-734.

Ellis, C.J. & Coppins, B.J. (2009) Quantifying the role of multiple landscape-scale drivers controlling epiphyte composition and richness in a conservation priority habitat (juniper scrub). *Biological Conservation*, **142**, 1291-1301.

Ellis, C.J. & Coppins, B.J. (2010) Integrating multiple landscape-scale drivers in the lichen epiphyte response: climatic setting, pollution regime and woodland spatial-temporal structure. *Diversity and Distributions*, **16**, 43-52.

Ellis, C.J., Coppins, B.J. & Dawson, T.P. (2007a) Predicted response of the lichen epiphyte *Lecanora populicola* to climate change scenarios in a clean-air region of northern Britain. *Biological Conservation*, **135**, 396-404.

Ellis, C.J., Eaton, S., Theodoropoulos, M., Coppins, B.J., Seaward, M.R.D. & Simkin, S. (2014) Response of epiphytic lichens to 21st Century climate change and tree disease scenarios. Biological Conservation, **180**, 153-164.

Ellis, C.J., Eaton, S., Theodoropoulos, M., Coppins, B.J., Seaward, M.R.D. & Simkin, S. (2015) *Lichen Epiphyte Scenarios. A Toolkit of Climate and Woodland Change for the 21st Century*. Royal Botanic Garden, Edinburgh. http://rbg-web2.rbge.org.uk/lichen/scenarios/index.php

Ellis, C.J., Yahr, R. & Coppins, B.J. (2009) Local extent of old-growth woodland modifies epiphyte response to climate change. *Journal of Biogeography*, **36**, 302-313.

Ellis, C.J., Coppins, B.J., Dawson, T.P. & Seaward, M.R.D. (2007b) Response of British lichens to climate change scenarios: trends and uncertainties in the projected impact for contrasting biogeographic groups. *Biological Conservation*, **140**, 217-235.

Fisher, P.J. & Procter, M.C.F. (1978) Observations on a season's growth in *Parmelia caperata* and *P. sulcata* in south Devon. *The Lichenologist*, **10**, 81-89.

Flagmeier, M., Long, D.G., Genney, D.R., Hollingsworth, P.M., Ross, L.C. & Woodin, S.J. (2014) fifty years of vegetation change in oceanic-montane liverwort-rich heath in Scotland. *Plant Ecology & Diversity*, **7**, 457-470.

Fryday, A.M. (2002) Distribution and importance of the lichen vegetation of the Scottish Highlands. *Botanical Journal of Scotland*, **54**, 133-151.

Gallego-Sala, A.V., Clark, J.M., House, J.I., Orr, H.G., Prentice, I.C., Smith, P., Farewell, T. & Chapman, S.J. (2010) Bioclimatic envelope model of climate change impacts on blanket peatland distribution in Great Britain. *Climate Research*, **45**, 151-162.

Gerdol, R. & Vincentini, R. (2011) Response to heat stress of populations of two *Sphagnum* species from alpine bogs at different altitudes. *Environmental and Experimental Botany*, **74**, 22-30.

Gilbert, O.L. (1968) Bryophytes as indicators of air pollution in the Tyne Valley. *New Phytologist*, **67**, 15-30.

Gilbert, O.L. (1970) A biological scale for the estimation of sulphur dioxide pollution. *New Phytologist*, **69**, 629-634.

Hawksworth, D.L. & Rose, F. (1970) Qualitative scale for estimating sulphur dioxide air pollution in England and Wales using epiphytic lichens. *Nature*, **227**, 145-148.

Hill, M.O. & Preston, C.D. (1998) The geographical relationships of British and Irish bryophytes. *Journal of Bryology*, **20**, 127-226.

Hodd, R.L., Bourke, D. & Skeffington, M.S. (2014) Projected range contractions of European protected oceanic montane plant communities: focus on climate change impacts is essential for their future conservation. *PLOSOne*, **9**, e95147.

Hodd, R. & Skeffington, M.S. (2011) Mixed northern hepatic mat: a threatened and unique bryophyte community. *Field Bryology*, **104**, 3-11.

Jenkins, G., Murphy, J.M., Sexton, D.M.H., Lowe, J.A., Jones, P. & Kilsby, C. (2010) UK Climate Projections: Briefing Report. In, p. 56

Kelly, L.J., Hollingsworth, P.M., Coppins, B.J., Ellis, C.J., Harrold, P., Tosh, J. & Yahr, R. (2011) DNA barcoding of lichenized fungi demonstrated high identification success in a floristic context. *New Phytologist*, **191**, 288-300.

Kershaw, K.A. & Dzikowski, P.A. (1977) Physiological-environmental interactions in lichens. VI. Nitrogenase activity in *Peltigera polydactyla* after a period of desiccation. *New Phytologist*, **79**, 417-421.

Kranner, I., Beckett, R., Hochman, A. & Nash, T.H. (2008) Desiccation tolerance in lichens: a review. *The Bryologist*, **111**, 576-593.

Lange, O.L. & Green, T.G.A. (2005) Lichens show that fungi can acclimate their respiration to seasonal changes in temperature. *Oecologia*, **142**, 11-19.

Lange, O.L., Kilian, E. & Ziegler, H. (1986) Water vapor uptake and photosynthesis of lichens: performance differences in species with green and blue-green algae as phycobionts. *Oecologia*, **71**, 104-110.

Lange, O.L., Büdel, B., Meyer, A. & Kilian, E. (1993) Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. *The Lichenologist*, **25**, 175-189.

Lättman, H., Milberg, P., Palmer, M.W. & Mattson, J.-E. (2009) Changes in the distribution of epiphytic lichens in southern Sweden using a new statistical method. *Nordic Journal of Botany*, **27**, 418-418.

Lisewski, V. & Ellis, C.J. (2010) Epiphyte sensitivity to a cross-scale interaction between habitat quality and macroclimate: an opportunity for range-edge conservation. *Biodiversity and Conservation*, **19**, 3935-3949.

Long, D.G., Paton, J.A., Squirrel, J., Woodhead, M. & Hollingsworth, P.M. (2006) Morphological, ecological and genetic evidence for distinguishing Anastrophyllum joergensenii Schiffn. and A. alpinum Steph. (Jungermanniopsoda: Lophoziaceae). *Journal of Bryology*, **28**, 108-117.

Lowe, J.A. & Gregory, J.M. (2005) The effects of climate change on storm surges around the United Kingdom. *Philosophical Transactions of the Royal Society A*, **363**, 1313-1328.

MacFarlane, J.D. & Kershaw, K.A. (1977) Physiological-environmental interactions in lichens. IV. Seasonal changes in the nitrogenase activity of *Peltigera canina* (L.) Willd var. *praetextata* (Floerke in Somm.) Hue, and *P. canina* (L.) willd var. *rufescens* (weiss) Mudd. *New Phytologist*, **79**, 403-408.

Mitchell, R.J., Truscot, A.M., Leith, I.D., Cape, J.N., Van Dijk, N., Tang, Y.S., Fowler, D. & Sutton, M.A. (2005) A study of epiphytic communities of Atlantic oak woods along an atmospheric nitrogen deposition gradient. *Journal of Ecology*, **93**, 482-492.

Muir, P.S., Shirazi, A.M. & Patrie, J. (1997) Seasonal growth dynamics in the lichen *Lobaria pulmonaria*. *The Bryologist*, **100**, 458-464.

Murtagh, G.J., Dyer, P.S., Furneaux, P.A. & Crittenden, P.D. (2002) Molecular and physiological diversity in the bipolar lichen-forming fungus *Xanthoria elegans*. *Mycological Research*, **106**, 1277-1286.

Pautasso, M., Aas, G., Queloz, V. & Holdenrieder, O. (2013) European ash (*Fraxinus excelsior*) dieback – a conservation biology challenge. *Biological Conservation*, **158**, 37–49.

Poelt, J. (1987) Das gesetz der relativen standortskonstanz bei den flechten. *Bot. Jahrb. Syst.*, **108**, 363-371.

Pohjamo, M., Korpelainen, H. & Kalinauskaite, N. (2008) Restricted gene flow in the clonal hepatic *Tricocolea tomentella* in fragmented landscapes. *Biological Conservation*, **141**, 1204-1217.

Preston, C.D., Harrower, C.A. & Hill, M.O. (2011) Distribution patterns in British and Irish liverworts and hornworts. *Journal of Bryology*, **33**, 3-16.

Proctor, M.C.F. (2011) Climatic responses and limits of bryophytes: comparisons and contrasts with vascular plants. *Bryophyte Ecology and Climate Change* (ed. by Z. Tuba, N.G. Slack and L.R. Stark), pp. 35-54. Cambridge University Press, Cambridge.

Proctor, M.C.F., Oliver, M.J., Wood, A.J., Alpert, P., Stark, L.R., Cleavitt, N.L. & Mishler, B.D. (2007) Desccation-tolerance in bryophytes: a review. *The Bryologist*, **110**, 595-621.

Rincon, E. & Grime, J.P. (1989) An analysis of seasonal patterns of bryophte growth in a natural habitat. *Journal of Ecology*, **77**, 447-455.

Rose, F. (1988) Phytogeographical and ecological aspects of *Lobarion* communities in Europe. *Botanical Journal of the Linnean Society*, **96**, 69-79.

Ross, L.C., Woodin, S.J., Hester, A.J., Thompsom, D.B.A. & Birks, H.J.B. (2012) Biotic homogenization of upland vegetation: patterns and drivers at mutiple scales over five decades. *Journal of Vegetation Science*, **23**, 755-770.

Rothero, G. (2003) Bryophyte conservation in Scotland. *Botanical Journal of Scotland*, **55**, 17-26.

Rothero, G. (2005) Oceanic bryophytes in Atlantic oakwoods. *Botanical Journal of Scotland*, **57**, 135-140.

Rothero, G., Birks, J., Genney, D., Grytnes, J.-A. & Long, D. (2011) Climate change and its consequences on bryophyte-dominated snowbed vegetation. *The Changing Nature of Scotland* (ed. by S.J. Marrs, S. Foster, C. Hendrie, E.C. Mackey and D.B.A. Thompsom), pp. 435-440. TSO Scotland, Edinburgh.

Scheidegger, C. (1991) Phyogeography of the genus *Buellia* (*Physciaceae*, *Lecanorales*) in Mediterranean Europe. *Bot. Chron.*, **10**, 211-220.

Seaward, M.R.D. (1998) Time-space analysis of the British lichen flora, with particular reference to air quality surveys. *Folia Cryptogamica Estonica*, **32**, 85-96.

Smart, S.M., Henrys, P.A., Scott, W.A., Hall, J.R., Evans, C.D., Crowe, A., Rowe, E.C., Dragosits, U., Page, T., Whyatt, J.D., Sowerby, A. & Clark, J.M. (2010) Impacts of pollution and climate change on ombrotrophic Sphagnum species in the UK: analysis of uncertainties in two empirical niche models. *Climate Research*, **45**, 163-177.

Souza-Egipsy, V., Valladares, F. & Ascaso, C. (2000) Water distribution in foliose lichen species: interactions between method of hydration, lichen substances and thallus anatomy. *Annals of Botany*, **86**, 595-601.

Thompson, D.B.A. & Brown, A. (1992) Biodiversity in montane Britain: habitat variation, vegetation diversity and some objectives for conservation. *Biodiversity and Conservation*, **1**, 179-208.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threatens plant diversity in Europe. *Proceedings of the National Academy of Sciences*, **102**, 8245-8250.

Trivedi, M.R., Morecroft, M.D., Berry, P.M. & Dawson, T.P. (2008a) Potential effects of climate change on plant communities in three montane nature reserves in Scotland, UK. *Biological Conservation*, **141**, 1665-1675.

Trivedi, M.R., Berry, P.M., Morecroft, M.D. & Dawson, T.P. (2008b) Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Global Change Biology*, **14**, 1089-1103.

Van Herk, C.M., Aptroot, A. & Van Dobben, H.F. (2002) Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *The Lichenologist*, **34**, 141-154.

Waite, M. & Sack, L. (2010) How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. *New Phytologist*, **185**, 156-172.

Watson, A., Davison, R.W. & French, D.D. (1994) Summer snow patches and climate in northeast scotland, U.K. *Arctic and Alpine Research*, **26**, 141-151.

Wolseley, P.A. & James, P.W. (2000) Factors affecting changes in species of *Lobaria* in sites across Britain 1986-1998. *Forest, Snow and Landscape Research*, **75**, 319-338.

Woodin, S.J. (1989) Environmental effects of air pollution in Britain. *Journal of Applied Ecology*, **26**, 749-761.

Table 1. Comparison of bioclimatic models for vascular plants and lichens with distinct range boundaries in Britain, with the distribution for suites of bryophytes, liverworts and lichen epiphytes that show equivalent distributions (cf. Hill & Preston, 1988; Preston *et al*., 2011).

BIOCLMATIC MODELS						**APPROXIMATE SPATIAL MATCH**					
Vascular Plants: Berry *et al.* (2002)			**Lichens: Ellis *et al.* (2007)**			**Lichen Epiphytes: Coppins (1976)**		**Mosses & Liverworts:**		**Liverworts:**	
Grouping	**Example species**		**Grouping**	**Example species**		**Grouping**	**Example Species**	**Grouping**	**Example Species**	**Grouping**	**Example Species**
Widely distributed	*Erica tetralix* *Galium aparine*	→	Not assessed			Widespread	*Arthonia radiata* *Ramalina farinacea*	Wide-boreal Wide-temperate	*Hylocomnium splendens* *Polytrichum commune*	*Pellia epiphylla* cluster (Boreal-temperate)	*Frullania dilatata* *Lophocolea bidentata*
Northern	*Loiseleuria procumbens* *Blysmus rufus*	↓	Northern montane	*Flavocetraria nivalis* *Solorina crocea*	↓	No analogue		Arctic-montane	*Andreaea alpestris* *Pohlia ludwigii*	*Moerckia blytii* cluster (Arctic, boreo-arctic) *Scapania degenii* cluster (Arctic, boreo-arctic) *Marsupella condensata* cluster (Arctic, boreal)	*Harpanthus flotovianus* *Jungermannia borealis* *Leiocolea heterocolpos* *Scapania cuspiduligera* *Cephalozia ambigua* *Gymnotrium apiculatum*
			Northern boreal	*Cetraria sepincola* *Cladonia sulphurina*	↓	Northern	*Pseudevernia furfuracea* *Vulpicida pinastri*	No analogue		No analogue	
Southern	*Atriplex portulacoides* *Sanguisorba officianalis*	↑	Southern widespread	*Punctelia borreri* *Usnea ceratina*	↑	Southern	*Flavoparmelia soredians* *Lecanactis premnea*	Mediterranean	*Bryum donnianum* *Fossombronia caespitiformis*	*Lophocolea heterophylla* cluster (Temperate, southern-temperate, Mediterranean-Atlantic)	*Lunularia cruciata* *Marchantia polymorpha*
			Oceanic widespread	*Hypotrachyna laevigata* *Pyrenula macrospora*	→	General western	*Hypotrachyna taylorensis* *Menegazzia terebrata*	Hyper-oceanic elements		Harpalejeunea molleri (Hyper-oceanic, southern-temperate)	*Plagiochila punctate* *Frullania teneriffae*
			Oceanic northern	*Pseudocyphellaria norvegica* *Pyrenula occidentalis*	↓	Scottish-Hibernian	*Leptogium hibernicum* *Thelotrema petractoides*	Oceanic boreo-montane		Harpalejeunea molleri (Hyper-oceanic, southern-temperate)	As above

KEY:

☐ Groups for which a spatial match in their British distribution and climatic sensitivity is attempted

↑ Increase in extent of bioclimatic space

→ No change in extent of bioclimatic space

↓ Decrease in extent of bioclimatic space