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Response of British lichens to climate change scenarios: Trends and uncertainties in the projected impact for contrasting biogeographic groups

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ABSTRACT

Projection of species-response to climate change scenarios is a key tool in conservation strategy. Previous studies have projected climate change impacts for animal and vascular plant species using the 'bioclimatic envelope' approach. In this study we apply the principles of the bioclimatic envelope approach to examine the response of 26 lichen species whose distributions are well characterised within the British Isles. Lichen species were subjectively selected based on their contrasting distributions, and their ecological traits, which fulfilled as closely as possible the assumptions of the bioclimatic envelope method. We used a split-sampling approach to model the species-response to present-day climate using confirmed records and pseudo-absences as input data, and testing each model against an 'independent' calibration dataset. Predictive models were projected using standard climate change scenarios comprising the UKCIP02 data. Projections indicate broad trends in the response of species placed into contrasting biogeographic groups, and point to the potential for significant change in the spatial distribution of the British lichen flora. We highlight putative threats to montane and Boreal elements of the lichen flora, and emphasise significant uncertainty in projected response of the UK's internationally important oceanic flora.

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1. Introduction

Understanding and predicting the response of species to climate change is essential to long-term conservation strategy (Hannah et al., 2002a,b). Research to examine the species-response to climate change should draw on complementary datasets from large-scale modelling (prediction), observation and verification (via monitoring), and the functional analysis of ecological response, e.g. changed species interactions and

reproductive potential. Predictive modelling is a powerful tool which has been widely used to create an initial understanding of climate impacts (e.g. Berry et al., 2002; Araújo et al., 2004; Hamann and Wang, 2006; Thuiller et al., 2006). Monitoring studies may be used to confirm or refute the results from predictive modelling, and have begun to document the signature effect of recent climate change (Hughes, 2000; Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003). This projected and observational data

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should be consistent with, and explained by, functional ecological processes controlling the species or community response to changed climate (Brooker, 2006; Ibáñez et al., 2006). Experimental studies designed to examine the response of vegetation structure and function to simulated climate change may thus provide fundamental support for larger-scale predictive models.

The 'bioclimatic envelope approach' is a common application of predictive modelling used to examine climate impacts (cf. Pearson and Dawson, 2003; Heikkinen et al., 2006). Nevertheless, its application in conservation, e.g. incorporating habitat structure (Pearson et al., 2004; Luoto et al., 2007) and dispersal parameters (Araújo et al., 2004; Midgley et al., 2006; Thuiller et al., 2006), has been restricted to a limited range of species, predominantly animals and vascular plants. Mainstream research to date has neglected to expand this predictive tool to encompass a wider range of biodiversity at the heart of international conservation strategy (cf. Heywood, 1995). Advances in the bioclimatic envelope approach have been largely methodological, and have tested variations in statistical design and modelling (Thuiller, 2003; Thuiller et al., 2003; Segurado and Araújo, 2004; Luoto et al., 2005; Thuiller et al., 2004; Araújo et al., 2005a; Araújo and Guisan, 2006; Pearson et al., 2006). In combination with method development tested against a small biodiversity sub-set, active conservation may benefit equally from the examination of species in previously neglected though diverse biological groups. For example, algae, mosses and liverworts, and fungi including lichens, are highly diverse and comprise >86% of 'botanical' diversity (based on estimates in Hammond, 1995), they are functionally important in many ecosystems (Cornelissen et al., 2007), though there is a scarcity of research examining their putative response to climate change.

This paper seeks to expand the climate modelling debate away from an exclusive focus on vascular plants and a limited range of animals by examining the projected response of Britain's lichens to climate change scenarios. Lichens are the symbiotic association between a fungal species (typically contributing most biomass to the lichen thallus) and a photosynthetic partner (i.e. an alga or cyanobacteria); the lichen response to climate change concerns fungal species which are phylogenetically distinct from, and have physiological constraints different to those of animals and plants (cf. Hale, 1983; Deacon, 2005). However, lichens are also representative of 'poikilohydric' organisms (e.g. also including bryophytes), which lack advanced vascular tissue and whose physiologies are, therefore, closely coupled to ambient environmental conditions. We may expect the climatic response of many lichens (and other poikilohydric taxa) to be affected by conditions of atmospheric moisture and temperature and not by soil moisture (e.g. Prentice et al., 1992), previously adopted as an explanatory variable for vascular plant climatic response (Berry et al., 2002; Pearson et al., 2004, 2006). The British Isles contain ca 1900 lichen species (ca 45% of European lichen diversity: Mackey et al., 2001; Coppins, 2002), making lichens one of Britain's most important contributions to international biodiversity and a key group in UK conservation strategy (UK BAP, 1999; Coppins, 2003; Gibby, 2003). Nevertheless, the application of predictive

modelling to Britain's lichens presents a series of methodological and data issues that are common to specialist groups more generally (i.e. algae, mosses, liverworts and fungi) and which may explain their frequent neglect by non-specialist researchers.

1. Many lichen species are incompletely sampled across their range, and some are likely to have been inaccurately identified. If using collective data sets (i.e. derived from mapping schemes), it is necessary to make a carefully informed qualitative judgement of the species for which modelling is most appropriate: i.e. species that are expected to be well recorded and correctly identified.
2. Where reliable distribution maps are available 'false absences' are nevertheless a problem. Even 'well recorded' lichen species are unlikely to have been detected at all sites across a landscape, and the lack of a confirmed presence is not a reliable indicator of a species' absence. Lichens (which are generally less easily or intensively recorded than vascular plants or certain animals) may be especially prone to false absences, causing biased model estimates and misleading results. Thus, confirmed presences can rarely be compared to known absences (Ellis et al., 2007), and a suite of alternative absence data based on likelihoods may be preferred to presence-only modelling (Zaniewski et al., 2002).
3. The assumptions of the bioclimatic envelope model – i.e. that a species' distribution is in equilibrium with the climate – is rarely tested (cf. Hampe, 2004; Pearson and Araújo, 2005), and choice of model-species depends instead on qualitative knowledge of a species' traits. Trait information is published for vascular plants (e.g. Grime et al., 1988) though for cryptogams this information is less easily accessible to non-specialist researchers.

We attempted to overcome these problems through the *a priori* selection of lichen species appropriate to bioclimatic modelling, and prudent application of analytical methods (e.g. use of pseudo-absences, with nonparametric regression). Our results are used to explore the projected impact of climate change on lichen biodiversity; the modelled responses of selected lichen species are assessed in terms of directional change (i.e. projected increase or decrease in range) and magnitude of range shift. Strong trends in the response of species are highlighted and suggestions are made for their verification. Additionally, we draw attention to a number of uncertainties, which we suggest would benefit from functional analysis and monitoring.

2. Materials and methods

We subjectively selected 26 species, representing five biogeographic patterns common to the British lichen flora (Coppins, 1976). Distribution patterns for the selected species correspond to broadly recognised climatic zones (Coppins, 1976), and are thought not to have been significantly impacted by the extent of severe air-pollution (Hawksworth and Rose, 1970; Seaward, 1998; Van Herk et al., 2003 – see maps in NEG-TAP (2001)); we assume that the present-day distributions of selected species are in equilibrium with the climate. Species

distributions were based on confirmed presences (1960–2006) within 10 km grid-squares, collated through the British Lichen Society mapping scheme (e.g. Seaward, 1995–1999; cf. also www.thebls.org.uk). Species selection was carefully considered based on >35 y experience of Britain's lichen flora (BJC) and we believe this represents the most appropriate sub-sample of British lichen diversity for bioclimatic modelling. Species were selected according to the availability of records and ease of identification, ensuring, therefore, that distribution maps were as comprehensive and reliable as possible, which precluded taxonomically difficult or under-recorded species. To fulfil as closely as possible the assumptions of the bioclimatic envelope model, we selected lichen species that have non-specialist substratum requirements, and which occur in habitats that are potentially widely distributed throughout Britain. First, the putative biogeographic groups were determined statistically through clustering analysis. Second, the species-response to climate was modelled using pseudo-absences (Zaniewski et al., 2002; Engler et al., 2004), weighted according to a species-specific probability distribution, and projected using standard climate change scenarios (i.e. UKCIP02 data: Hulme et al., 2002). The UKCIP02 scenarios have previously been applied to a wider spectrum of Britain's biodiversity (Berry et al., 2005, 2007) and enable a broad comparison of climatic sensitivity and vulnerability between lichens and contrasting biological groups (Berry et al., 2002, 2005, 2007).

2.1. Climatic variables

We used UK Met Office modelled data-sets (Perry and Hollis, 2005) as present-day (baseline) climate data at 5 km grid-square resolution: estimated monthly and annual climatic averages for (i) number of days with rainfall >1 mm, (ii) average, maximum and minimum monthly temperatures (°C) and (iii) precipitation (mm). Estimated climate data incorporate factors such as aspect, altitude, topography, and urban and coastal effects, and are the verified averages derived for 5 km grid-squares based on point data for the period 1961–2000 at 540 and 4400 monitoring stations across Britain (temperature and precipitation, respectively). A suite of 13 climatic variables was calculated for individual 5 km grid-squares across Britain (though excluding the geographically out-lying Orkney and Shetland Islands): mean annual temperature (°C), mean seasonal temperatures, temperatures of the warmest and coldest months of the year, annual temperature range, total annual precipitation (mm) and seasonal precipitation.

The 13 climatic variables were recalculated for climate change scenarios corresponding to the UKCIP02 analysis (Hulme et al., 2002); scenarios comprised two greenhouse gas emission levels (low and high emissions) for a period during the 2050s. These data match with the Intergovernmental Panel on Climate Change (IPCC) B2 and A1F1 SRES scenarios, respectively (Nakicenovic, 2000; Hulme et al., 2002). The climate change scenarios encompassed in the UKCIP02 data provide a common starting point for assessing climate change impacts in the UK (Hulme et al., 2002) and are consistent with previous analyses of climate impacts on Britain's biodiversity (Berry et al., 2005, 2007).

2.2. Biogeographic groups

Species were divided into biogeographic groups by cluster analysis based on geographic distribution, and ordination was used to examine the relationship between the species distributions and climatic variables. First, species presences were compared across geographic space using Sørensen similarity with flexible beta linkage ($\beta = -0.25$) to construct a dendrogram (McCune and Mefford, 1999; McCune and Grace, 2002). Potential biogeographic groups were delimited at contrasting hierarchical levels and five distinct associations were recognised. Second, species associations in geographic space were examined using detrended correspondence analysis (DCA, implemented using PC-Ord v. 4: McCune and Mefford, 1999). The importance of baseline climatic variables in explaining species variation was estimated indirectly as the correlation coefficient (r) between axis site scores and their respective values for the different climatic variables. The coefficients were summarised as vectors (McCune and Grace, 2002).

2.3. Pseudo-absences

Recorded presences were compared for each lichen species to an equivalent number of randomly generated pseudo-absences (Zaniewski et al., 2002; Engler et al., 2004). However, the spatial application of pseudo-absences was weighted by a decay factor based on the estimated likelihood of a species' absence at increasing distances from the centre of its British range. The central point of a species' range was calculated as the centre of minimum distance (C: Burt and Barber, 1996):

$$C = \text{minimum value for } \sum d_{ic} \quad (1)$$

where d_{ic} is the distance between a single point of occurrence (i.e. a record in a 10 km grid-square, i) and a central point (C) that has a minimum summed distance to all values of i . Values of C were estimated using an iterative algorithm to implement step-by-step improvement and continued until estimated values of C reached a sufficiently low tolerance, i.e. <0.000001. The shortest distances between each recorded presence and the centre of minimum distance (C) were tabulated. A decay factor (Df) was calculated as the inverse of the proportion of sites with recorded presences at increasing distances from C:

$$Df = 1 - [(100/n) * y]/100 \quad (2)$$

where n is the number of possible presences (i.e. 10 km grid-squares) within a given distance (x) from C, and y is the actual number of records within the same distance x . Values of Df at increasing distances ($x - C$) were summarised using a suite of fourteen standard response-curves supported by the program Genstat v. 7.1 (Genstat, 2003: VSN International Ltd., Oxford). Two examples are shown below, the exponential, Eq. (3), and quadratic-by-quadratic, Eq. (4):

$$Y = a + b * (r^x) \quad (3)$$

$$Y = a + (b + c * X)/(1 + d * X + e * X * X) \quad (4)$$

where Y is the modelled value of Df (constrained to ≤ 1), values of a , b , c , d and e are the model constants, and X is the distance $x - C$. Models were assessed and selected by aiming to

minimise the probability ($p \leq 0.5$), maximise the value of R^2 , and ensuring residuals from the fitted curve were normally distributed. The random application of pseudo-absences was, therefore, weighted by species-specific values of Y for grid-squares with values of $x - C$. Sets of presences and pseudo-absences for a given species were split into two equal groups comprising: (i) a training set used as input data (response variable) to generate a predictive model and (ii) a randomly selected test set retained as 'independent observations', used to compare the predicted with observed presence-absences and thereby evaluate the predictive ability of the model.

2.4. Species-response

Confirmed presences and pseudo-absences (10 km grid-scale) were compared to climatic variables derived for each 5 km grid-square occurring centrally within 10 km units. Thus, presence and pseudo-absences were compared to the 13 climatic variables simultaneously using the program *Hyperniche v. 1beta* (McCune and Mefford, 2004) to create multiple 'best models' by nonparametric multiplicative regression, implemented using a local mean with Gaussian weighting (NPMR: McCune, 2006). A stepwise free-search was used to seek a range of models with different combinations of predictors, and default values adopted for all remaining search criteria (McCune and Mefford, 2004). An optimum model was selected for each species, using a Bayes factor to express model improvement over a 'naïve' model (i.e. $\log_{10}B$), and using a 'leave-one-out' strategy of cross-validation to prevent over-fitting (McCune and Mefford, 2004; McCune, 2006). Selected models were assessed using a Monte Carlo randomisation test, with 1000 runs to evaluate model fit, and assuming an equivalent number of explanatory variables. The utility of each statistically significant optimum model was assessed by comparing predicted likelihood of occurrence to the separate data 'test-set', comprising confirmed presences and pseudo-absences excluded from model development and retained as 'independent observations' for model diagnostics. Predicted values were compared to the test-set as the area under the receiver operating curve (AUC: Swets, 1988; Pearce and Ferrier, 2000). This measure is independent of species prevalence within a sample (Pearce and Ferrier, 2000) and is widely accepted as an appropriate diagnostic measure for the discrimination ability of predictive models (e.g. Thuiller et al., 2005a), though subject to the caveats outlined by Araújo et al. (2005b).

Having chosen optimum models for individual species, and tested their statistical significance and discrimination ability, the importance of selected predictor variables was expressed as their tolerance (t), standardised as the proportion of the predictor variable's range (s). The relative importance of individual climatic variables was then estimated by summing the sensitivity value (i.e. $1 - s$) across the 26 species-specific models.

Our *a priori* selection of NPMR to model the species-response is based on: (i) the method's flexibility to characterise interacting factors unbounded by the simplified assumptions of linear models (McCune, 2006), and (ii) its better performance in tests compared against several other statistical techniques frequently used in climate response studies (e.g.

theoretical curve fitting (GLMs) and additive models (GAMs): Fosaa et al., 2004; Segurado and Araújo, 2004; Luoto et al., 2005; Randin et al., 2006). Additionally, tests of NPMR have included data specifically relevant to the environmental response of lichens (McCune, 2006). We believe the aims of this study were more likely to be achieved by using a method that has been carefully tested and shown to perform well in model inter-comparisons, rather than adopt the recently advocated ensemble forecasting approach (Araújo et al., 2005a; Araújo and New, 2006), which would introduce additional uncertainty and model variability through the pooling of untested models, or by including models that have been shown to less effectively capture the species-response.

2.5. Model projection

Climate-response models for individual species were used to project the likelihood of occurrence in 5 km grid-squares across the geographic range of the study area. However, model application was limited to 5 km grid-squares whose input data satisfied the minimum threshold for an acceptable model (McCune, 2006), i.e. input values above a minimum neighbourhood size ($= n * 0.05$). The projection of species data was, therefore, constrained to grid-squares whose climate occurred within limits set by the data-range used to generate the predictive model, preventing erroneous application of the model beyond the boundaries of the base-line dataset. This identification of an 'unmodelled range' is particularly important since models were constructed using data restricted to the extent in Britain of each species' world-wide distribution (cf. Thuiller et al., 2004; Randin et al., 2006).

The likelihood of occurrence was projected for individual species based on present-day modelled climate data (Perry and Hollis, 2005), and the UKCIP02 scenarios for the 2050s under high and low emissions (Hulme et al., 2002). AUC defined thresholds were used to estimate species presence based on projected likelihoods in each of the 5 km grid-squares. Species presences were plotted for the three scenarios (present-day, 2050s low and high emissions) using ArcGIS v. 9 (ESRI Inc, 1999–2005). The cumulative number of species projected to jointly occur in an individual grid-square (i.e. likelihood of occurrence $>$ AUC threshold) was plotted for those species that were associated together in a given biogeographic group. These projections were compared to the cumulative number of species in each grid-square whose likelihood of occurrence could not be known, i.e. with climatic data outside the limits of the predictive model (unmodelled range).

Large-scale climate impacts were estimated for individual species by plotting percent loss against percent gain of bioclimatic space, measured in 5 km grid-squares within the statistical range of the predictive models (i.e. projected bioclimatic space): comparing present-day with 2050s low and 2050s high scenarios.

3. Results

3.1. Biogeographic groups

Examination by cluster analysis indicates that the 26 selected lichen species are suitably represented by five biogeographic

groups, nested within three major divisions: Northern, Southern and Oceanic (Fig. 1). These associations support the subjective selection of species, chosen to represent contrasting biogeographic groups and highlighted by their distributional ranges in Britain (Fig. 2). Northern-montane (Fig. 2a): species whose distributions form aggregated occurrences in montane regions of Britain: e.g. the Cairngorms, the western Scottish Mountains, the Lake District and Snowdonia. Occurrences outwith these montane regions are rare though correspond with locations in Britain’s uplands (i.e. northern Pennines, Scottish borders). Northern-Boreal (Fig. 2b): species with a broad distribution pattern across Britain, though which nevertheless tend to be clustered in the relatively more continental region of north-east Scotland. The species in this group are relatively frequent within the Straths of north-east Scotland (i.e. Strathspey and Deeside) and mostly rare elsewhere. Southern-widespread (Fig. 2c): species which occur throughout the southern region of Britain, becoming aggregated towards the south coast and increasingly scattered northward. Oceanic-northern (Fig. 2d): species aggregated along the western seaboard of Scotland, rarely occurring far inland, and occurring only as isolated occurrences further south. Oceanic widespread (Fig. 2e): species aggregated along the entire western seaboard of Britain and rarely occurring away from the Atlantic coast, i.e. only scattered occurrences towards eastern and more inland regions.

The broad recognition of these five groups is putatively explained by regional climatic variation. Species with a Northern-montane and -Boreal distribution are separated from those with a Southern or Oceanic distribution along DCA axis two (Fig. 3). Site scores along axis two ($\Delta = 0.576$; 3.2% variation explained, $n = 1452$) are negatively correlated with temperature: for all temperature variables (excluding temper-

ature range), r varies between -0.497 (mean temp. of the warmest month) and -0.59 (mean annual temp.), and in all cases $p < 0.001$ with 1450 df. This is consistent with generally cooler temperatures in montane regions and to the north of Britain, compared to the relatively mild conditions along Britain’s highly oceanic west coast and in the warmer south (Ordnance Survey, 1986). Further biogeographic divisions are apparent along DCA axis one ($\Delta = 0.566$; 19.3% variation explained, $n = 1452$), which is negatively correlated with precipitation: for all precipitation variables, r varies between -0.625 (total precip.) and -0.587 (summer precip.), and in all cases $p < 0.001$ with 1450 df. Precipitation co-varies with temperature range, which is positively related to axis one scores: $r = 0.476$, $p < 0.001$ with 1450 df. Accordingly, species in the Northern-montane group (cooler and wetter) are separated from the Northern-Boreal group (cooler and drier), while species in the Oceanic group (warmer and wetter) are separated from species in the Southern group (warmer and drier).

3.2. Species-response models

Estimated likelihood of a species’ absence at increasing distances from the spatial centre of its range in Britain was effectively modelled using exponential regression and quadratic-by-quadratic curves (examples in Fig. 4). These models capture two contrasting trends. First, a linear decline in observed occurrence away from the centre of a species’ range (Fig. 4a) is consistent with an aggregated distribution and decay in recorded presences away from a species’ distributional centre. Second, an initial increase in occurrence away from the centre of a species’ range, followed by a decrease in occurrence beyond this minimum (Fig. 4b). This latter trend is explained by species with an aggregated distribution along the

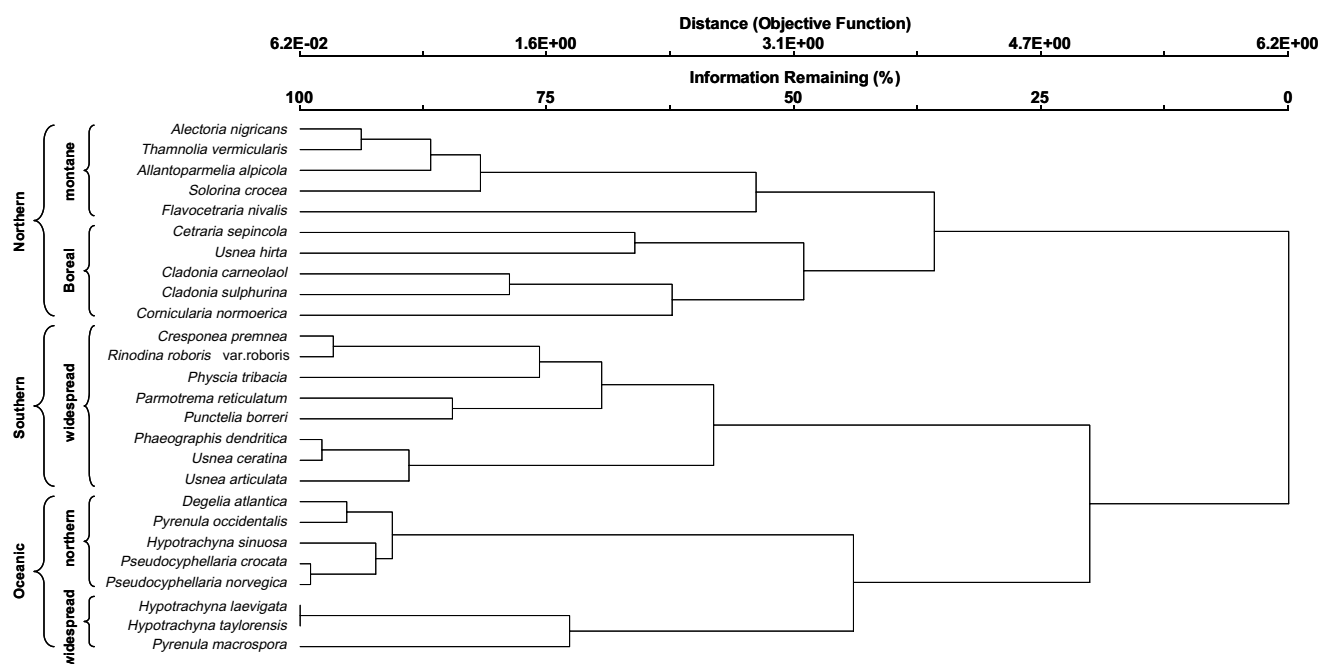


Fig. 1 – Results of cluster analysis by flexible beta linkage ($\beta = -0.25$), used to identify associations in the geographic distribution (10 km scale) of selected British lichen species (percent chaining = 1.77). Five biogeographic groups are nested within three major divisions: Northern, Southern and Oceanic.

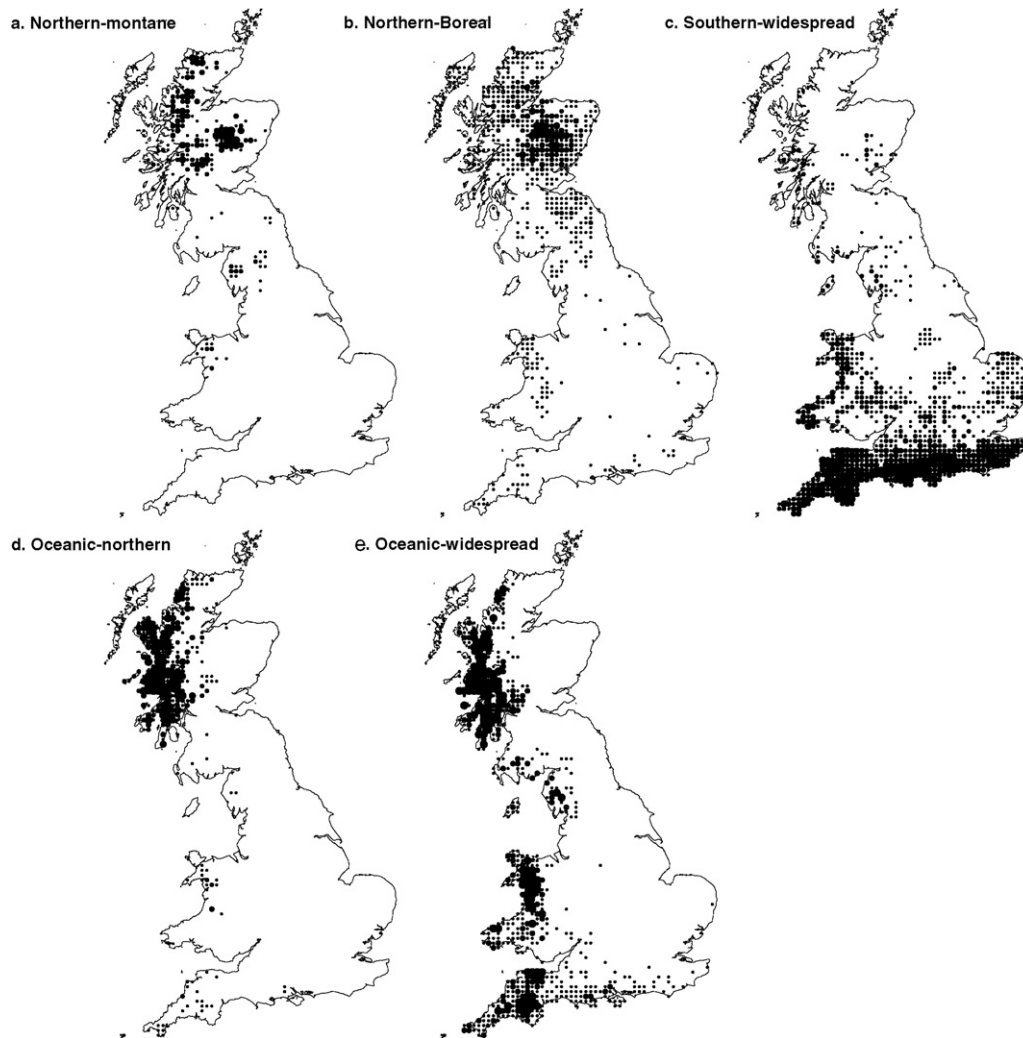


Fig. 2 – Spatial distribution within mainland Britain of lichen species associated into five biogeographic groups (Fig. 1). Symbols represent single 10 km grid-squares and are size-scaled, thereby indicating the joint co-occurrence of all species included within a biogeographic group (•) to the occurrence of a single species only (◦).

south coast of England, though with clumped occurrences in Wales and eastern England also; accordingly, the centre of distribution occupied a region of lower density records between these aggregations (Fig. 2c).

The use of decay factors to generate pseudo-absences resulted in species models with high values of $\log_{10}B$, well supported by Monte Carlo randomisation tests (Table 1). Comparison of projected likelihoods with the test-set retained as ‘independent observations’ suggests all the models performed well, with good predictive ability (Table 1): i.e. AUC values between 0.79 and 0.94. The sum of sensitivity values for explanatory variables included in the optimum models points to the relative importance of temperature and precipitation during autumn and winter (opposed to spring and summer), and the importance of temperature range and the temperature of the warmest month (Fig. 5).

3.3. Projected response

The projected response of species contrasts strongly between Northern and Southern groups. Ten species categor-

ised as Northern-montane (Fig. 6a) and Northern-Boreal (Fig. 6b) each show a consistent and strong decrease in projected range, compared between the modelled present-day climatic setting and the 2050s climate change scenarios, with significant loss of climate space compared to little or no gain (Fig. 7). In both cases there are few areas over which the model cannot be suitably projected based on the present-day climate (reflecting constraints to model flexibility imposed by the number and spatial arrangement of confirmed presences), though this unmodelled range increases from the south under future climate change scenarios (Fig. 6a and b). In contrast, the group of eight species categorised as Southern-widespread (Fig. 6c) show a consistent increase in projected range northwards. There are areas to the north of Britain over which the species models cannot be suitably projected based on the present-day climate, though these northern unmodelled grid-squares decrease under climate change scenarios, as equivalent areas increase from the south-east (Fig. 6c). Even allowing for the unmodelled range, the results nevertheless point to a potentially large increase in bioclimatic space for Southern-widespread

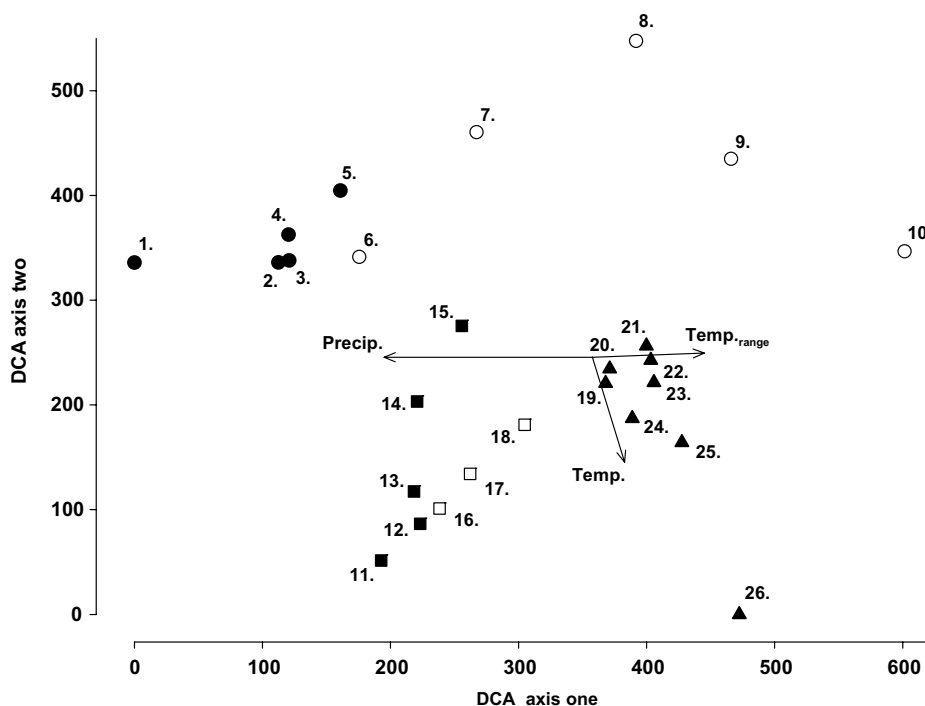


Fig. 3 – Results of detrended correspondence analysis (DCA) to compare the geographic occurrence of 26 lichen species in 10 km grid-squares. Species scores are identified according to their putative biogeographic groups (cf. Fig. 1): ‘●’ is Northern-montane, 1 = *Alectoria nigricans*, 2 = *Thamnolia vermicularis*, 3 = *Allantoparmelia alpicola*, 4 = *Solorina crocea* and 5 = *Flavocetraria nivalis*; ‘○’ is Northern-Boreal, 6 = *Cornicularia normoerica*, 7 = *Cladonia carneola*, 8 = *Cladonia sulphurina*, 9 = *Cetraria sepincola* and 10 = *Usnea hirta*; ‘■’ is Oceanic-northern, 11 = *Pseudocyphellaria norvegica*, 12 = *Hypotrachyna sinuosa*, 13 = *Pseudocyphellaria crocata*, 14 = *Degelia atlantica* and 15 = *Pyrenula occidentalis*; ‘□’ is Oceanic-widespread, 16 = *Hypotrachyna taylorensis*, 17 = *Hypotrachyna leavigata* & 18 = *Pyrenula macrospora*; ‘▲’ is Southern-widespread, 19 = *Phaeographis dendritica*, 20 = *Usnea ceratina*, 21 = *Cresponea premnea*, 22 = *Usnea articulata*, 23 = *Rinodina roboris* var. *roboris*, 24 = *Parmotrema reticulatum*, 25 = *Punctelia borrieri* and 26 = *Physcia tribacea*. Separate variables within classes for temperature (excluding temperature range) and precipitation strongly covaried ($r = 0.753 - 0.999$ and $r = 0.927 - 0.994$, for temp. and precip., respectively); vectors (positioned centrally), therefore, summarise correlations between DCA axes one and two and the temperature and precipitation variables combined.

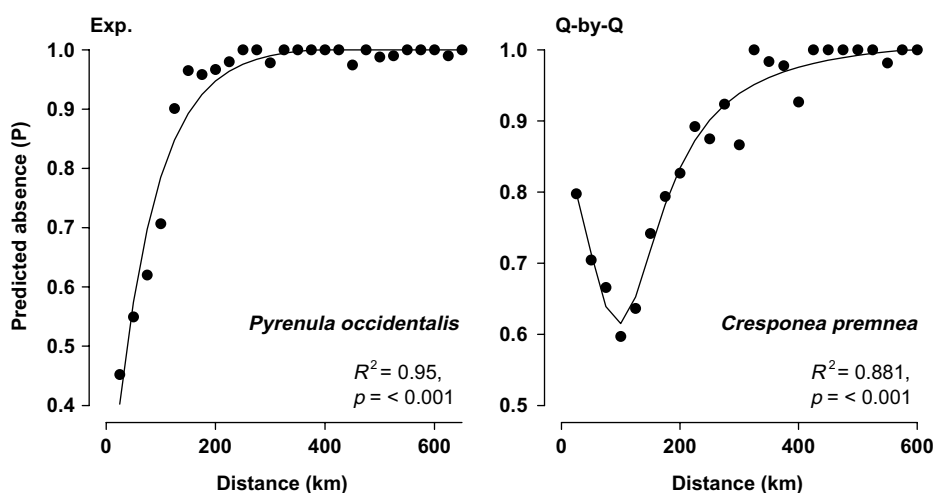


Fig. 4 – Results of analyses to describe a species’ predicted absence (P) in 10 km grid-squares measured at increasing distance from the centre a species’ range in Britain. Patterns were summarised using standard parametric models – exponential (exp) and quadratic-by-quadratic (Q-by-Q). Model values of (P) were used as distance-controlled weightings, applied to generate randomised pseudo-absences for each species.

Table 1 – Results of model development by NPMR to predict species-response to climate for 26' lichens (for a description of NPMR see McCune, 2006)

Lichen species	Nonparametric multiplicative regression			Predictive diagnostics		
	Explanatory variables	Tolerance (s)	log ₁₀ B	Monte Carlo p	AUC ± 1 SE	s – s threshold
<i>Alectoria nigricans</i>	Temp _{.aut} Precip _{.spr}	0.753 (0.1) 86.78 (0.15)	13.2	<0.001	0.87 ± 0.034	0.47
<i>Allantoparmelia alpicola</i>	Temp _{.warm} Precip _{.spr}	0.911 (0.1) 153.65 (0.3)	13.07	<0.001	0.89 ± 0.032	0.61
<i>Cetraria sepincola</i>	Temp _{.win} Temp _{.range}	0.65 (0.1) 0.52 (0.1)	18.49	<0.001	0.9 ± 0.027	0.61
<i>Cladonia carneola</i>	Temp _{.sum} Precip _{.sum}	0.429 (0.05) 40.6 (0.1)	13.57	<0.001	0.79 ± 0.051	0.69
<i>Cladonia sulphurina</i>	Temp _{.aut}	0.796 (0.1)	34.03	<0.001	0.84 ± 0.015	0.61
<i>Cornicularia normoerica</i>	Temp _{.warm} Temp _{.range}	0.483 (0.05) 0.768 (0.15)	48.83	<0.001	0.94 ± 0.013	0.6
<i>Cresponea premnea</i>	Temp _{.aut} Temp _{.range} Precip _{.win}	0.474 (0.05) 0.708 (0.15) 91.41 (0.1)	39.41	<0.001	0.91 ± 0.015	0.58
<i>Degelia atlantica</i>	Temp _{.range} Precip _{.win}	0.256 (0.05) 152.41 (0.2)	46.34	<0.001	0.96 ± 0.011	0.7
<i>Flavocetraria nivalis</i>	Temp _{.sum}	0.737 (0.1)	3.41	<0.001	0.85 ± 0.049	0.59
<i>Hypotrachyna laevigata</i>	Temp _{.warm} Precip _{.sum} Precip _{.win}	0.43 (0.05) 45.57 (0.1) 83.33 (0.1)	48.11	<0.001	0.94 ± 0.013	0.65
<i>Hypotrachyna sinuosa</i>	Temp _{.win} Precip _{.sum}	1.46 (0.2) 23.37 (0.05)	19.31	<0.001	0.88 ± 0.029	0.72
<i>Hypotrachyna taylorensis</i>	Temp _{.mean} Precip _{.total}	0.872 (0.15) 156.78 (0.05)	30.5	<0.001	0.94 ± 0.014	0.69
<i>Parmotrema reticulatum</i>	Temp _{.aut} Precip _{.aut}	0.794 (0.1) 42.15 (0.05)	25.74	<0.001	0.90 ± 0.018	0.57
<i>Phaeographis dendritica</i>	Temp _{.aut} Temp _{.win} Precip _{.win}	0.39 (0.05) 0.432 (0.05) 121.95 (0.15)	41.39	<0.001	0.95 ± 0.013	0.59
<i>Physcia tribacia</i>	Temp _{.warm} Temp _{.aut} Temp _{.range} Precip _{.win}	1.25 (0.15) 0.799 (0.1) 0.54 (0.1) 125.21 (0.15)	49.4	<0.001	0.93 ± 0.013	0.34
<i>Pseudocyphellaria crocata</i>	Temp _{.range} Precip _{.aut}	0.946 (0.15) 99.92 (0.105)	22.18	<0.001	0.93 ± 0.025	0.76
<i>Pseudocyphellaria norvegica</i>	Temp _{.range} Precip _{.aut}	0.659 (0.15) 101.49 (0.1)	18.91	<0.001	0.94 ± 0.029	0.82
<i>Punctelia borleri</i>	Temp _{.aut} Precip _{.aut}	0.709 (0.1) 40.96 (0.05)	27.99	<0.001	0.94 ± 0.017	0.72
<i>Pyrenula macrospora</i>	Temp _{.win} Precip _{.win}	0.456 (0.05) 46.59 (0.05)	64.55	<0.001	0.86 ± 0.016	0.68
<i>Pyrenula occidentalis</i>	Precip _{.aut}	92.38 (0.1)	22.19	<0.001	0.92 ± 0.023	0.58
<i>Rinodina roboris v. roboris</i>	Temp _{.aut} Precip _{.aut} Precip _{.win}	0.746 (0.1) 49.73 (0.05) 46.32 (0.05)	52.47	<0.001	0.95 ± 0.011	0.55
<i>Solorina crocea</i>	Temp _{.aut}	0.858 (0.1)	9.75	<0.001	0.89 ± 0.039	0.55
<i>Thamnomia vermicularis</i>	Temp _{.warm} Precip _{.aut}	0.899 (0.1) 211.32 (0.2)	16.47	<0.001	0.92 ± 0.025	0.51

Table 1 – continued

Lichen species	Nonparametric multiplicative regression			Predictive diagnostics		
	Explanatory variables	Tolerance (s)	log ₁₀ B	Monte Carlo p	AUC ± 1 SE	s – s threshold
<i>Usnea articulata</i>	Temp. _{aut}	1.03 (0.15)	19.76	<0.001	0.94 ± 0.018	0.68
	Temp. _{win}	1.07 (0.15)				
	Precip. _{aut}	43.62 (0.05)				
	Precip. _{win}	85.53 (0.1)				
<i>Usnea ceratina</i>	Temp. _{aut}	0.737 (0.1)	39.21	<0.001	0.93 ± 0.015	0.66
	Precip. _{aut}	49.53 (0.05)				
	Precip. _{win}	46.47 (0.05)				
<i>Usnea hirta</i>	Temp. _{warm}	0.425 (0.05)	29.85	<0.001	0.87 ± 0.023	0.51
	Temp. _{aut}	0.382 (0.05)				
	Precip. _{spr}	112.35 (0.25)				

Tolerance is the range of an explanatory variable equal to one standard deviation of the Gaussian weighting function, and sensitivity (s) is the tolerance expressed as a proportion of total range in the modelled explanatory variable. Diagnostic tests using area under the receiver operating curve (AUC) assess the discrimination ability of optimum models and identify a threshold value for projected presence-absence.

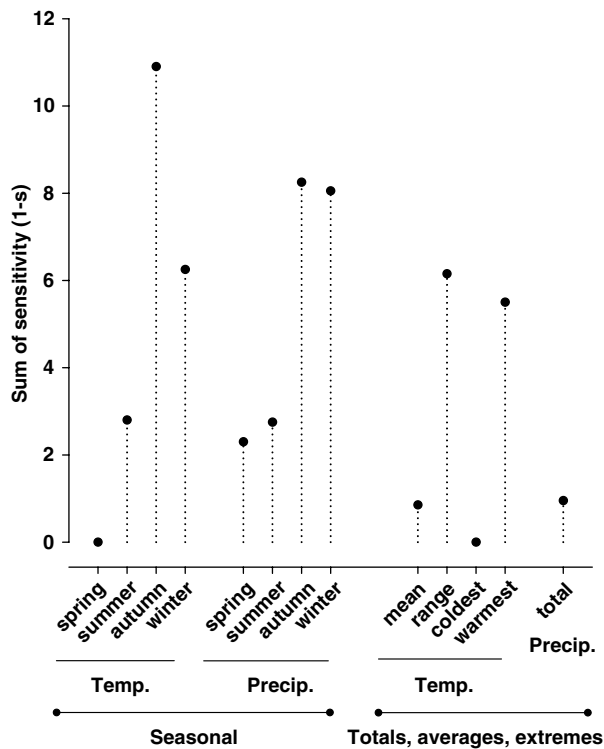


Fig. 5 – Sum of sensitivity values for the climate variables selected as explanatory factors, and used to describe the species-response of 26 lichens based on nonparametric multiplicative regression (NPMR).

species, compared between the present-day and the 2050s climate change scenarios (Fig. 7).

Projected impacts on Oceanic species are less well characterised than for the Northern and Southern-widespread groups. Species categorised as Oceanic-northern (Fig. 6d) show a consistent loss in projected range between the modelled present-day climatic setting and the 2050s climate change scenarios, though the magnitude of this shift is less

than for species comprising the Northern groups (Fig. 7). Two species categorised as Oceanic-widespread (Fig. 6e) show little or no change in the availability of bioclimatic space, while a third species (*Pyrenula macrospora*) shows an increase in projected range, compared between the modelled present-day climatic setting and the 2050s climate change scenarios (Fig. 7).

4. Discussion

This study provides the first comprehensive examination of projected climate change impacts on lichens based on an established methodology (the bioclimatic envelope approach) previously applied to a range of British animals and vascular plants (Berry et al., 2002, 2005, 2007). Our approach is one example of ecological niche-based modelling and is subject to a well documented range of assumptions and caveats (see Pearson and Dawson, 2003; Hampe, 2004; Araújo et al., 2005b; Heikkinen et al., 2006; Botkin et al., 2007). Additionally, the extent to which projected impacts might reflect the actual future distribution of species should be assessed against a range of confounding factors, e.g.: (i) inherent uncertainty under-pinning the climate change scenarios used in model projection (Hulme et al., 2002), (ii) the ability of species to migrate into suitable habitat in response to changing climate (Travis, 2003; Pearson and Dawson, 2005), (iii) the opportunity for evolutionary adaptation of species in situ (Franks et al., 2007) and (iv) climate interactions with smaller-scale factors, including local habitat quality (Warren et al., 2001; Ellis and Coppins, 2007), and species interactions (Davis et al., 1998; Harrington et al., 1999) incorporating the potential effect of colonising or invasive species that are currently absent from the British flora (Dukes and Mooney, 1999; Walther, 2000). Previous methodological studies have identified opportunities to reduce inherent uncertainties; accordingly: (i) the selected lichen species have well-defined range margins in Britain and low-moderate prevalence (Fig. 2), and may, therefore, be suited to bioclimatic modelling (Brotons et al., 2004; Segurado and Araújo, 2004; Luoto et al., 2005), (ii) split-sampling was used in an attempt to partially control for spatial-autocorrelation

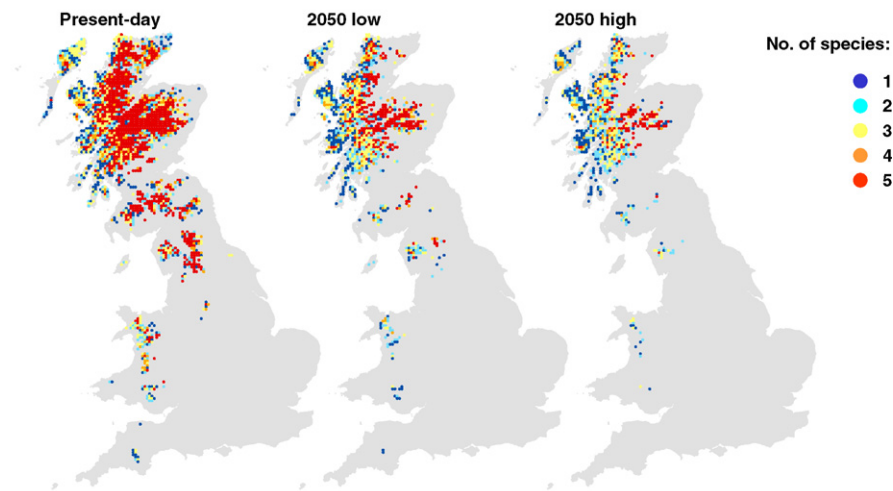
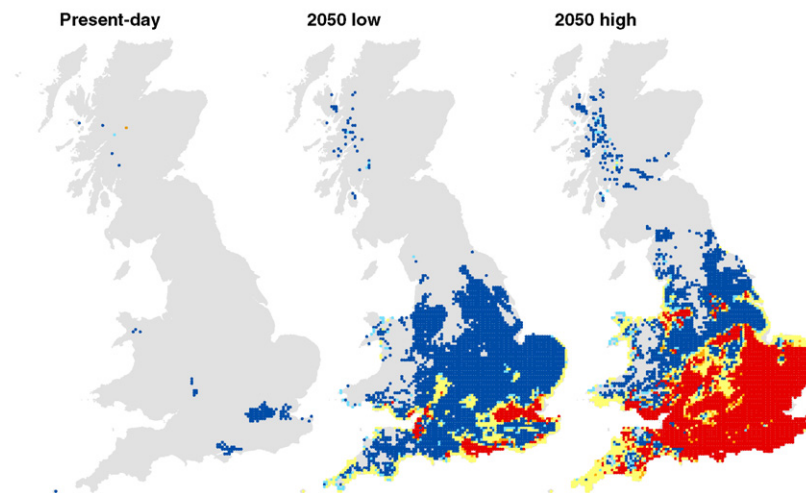
a Projected bioclimatic range:**Unmodelled range:**

Fig. 6 – Projected bioclimatic range and ‘unmodelled’ range applied using modelled climate variables for the present-day, and UKCIP02 scenarios for the 2050s low and high emissions: (a) Northern-montane species, (b) Northern-Boreal species, (c) Southern-widespread species, (d) Oceanic-northern species and (e) Oceanic-widespread species.

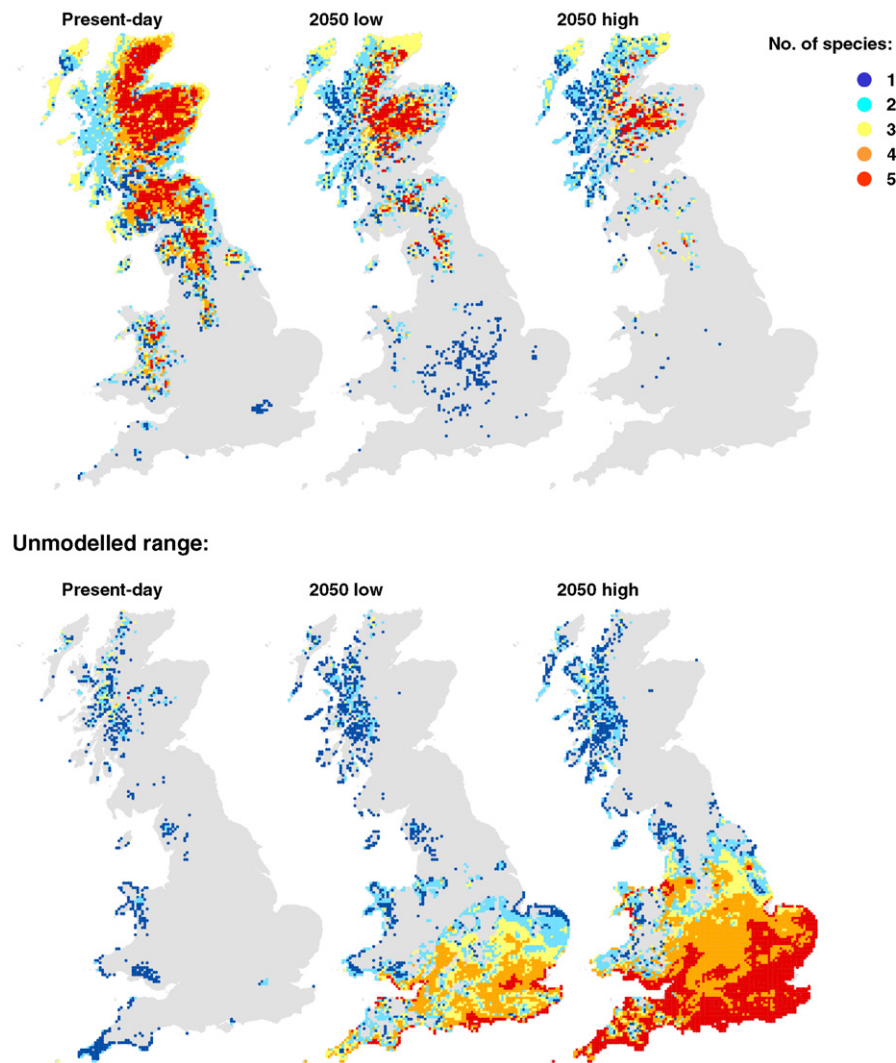
while retaining larger-scale gradients (Diniz-Filho et al., 2003; Segurado et al., 2006), and (iii) analysis was based on nonparametric modelling (Segurado and Araújo, 2004; Araújo et al., 2005b) using a tested methodology (McCune, 2006) with weighted pseudo-absences (Zaniewski et al., 2002).

Notwithstanding inherent uncertainty in the actual response of a species, we believe the use of the bioclimatic envelope approach has provided a valuable initial insight into possible change in the geographic range of lichens, compared between contrasting species groups, and examined using a common frame of reference in the UKCIP02 scenarios. Accordingly, the results provide a cautious indication of possible direction and relative magnitude of change in the availability of bioclimatic space for the 26 species. The study highlights the potential for significant change in the spatial distribution of Britain’s lichen flora, which, if confirmed, would challenge inflexibilities within existing UK conservation strategy (cf. Araújo et al., 2004). The projected response

of lichens should now be confirmed or refuted based on careful monitoring, and tested against an improved functional understanding of lichen population and community response to climate.

4.1. Species bioclimatic response

The selected species were well defined in five contrasting biogeographic groups (Figs. 1–3). Assessed across these groups, the individualistic response of lichen species demonstrated sensitivity to seasonal effects of temperature and precipitation (Fig. 5). This modelled response is consistent with evidence for seasonal growth of lichens measured during field experiments (Fisher and Proctor, 1978; Muir et al., 1997), which is further supported by physiological studies to indicate the climatic control of photosynthesis and respiration (Sundberg et al., 1999; Palmqvist and Sundberg, 2000; Gaioliveira et al., 2004), and N-fixation in lichens (MacFarlane

b Projected bioclimatic range:**Fig. 6 – continued**

and Kershaw, 1977; Antoine, 2004). The additional importance of temperature range (Fig. 5) agrees with a general effect of ‘oceanicity’ on Britain’s lichen flora (oceanicity \approx temperature range and frequency of rainfall – cf. Crawford, 1997; Fryday, 2002). There is a steep gradient in lichen community structure from the more oceanic west coast, with a lower temperature range and more frequent rainfall, to the relatively more continental east, with a greater temperature range (cooler winter temperatures) and less frequent rainfall (Coppins, 1976; Fryday, 2002; Ellis and Coppins, 2006).

4.2. Projected response

The projected bioclimatic response based on the UKCIP02 scenarios strongly indicates a loss of bioclimatic space for Northern species (Fig. 6a and b) and an increase in bioclimatic space for Southern species (Fig. 6c). Projections for Northern-montane species are consistent with experimental evidence demonstrating a decline in lichen occurrence following the simulated effects of climate change (e.g. increased tempera-

ture and nutrient cycling), which may shift the balance of arctic-alpine communities in favour of more competitive species (Chapin et al., 1995; Press et al., 1998; Cornelissen et al., 2001). However, certain of Scotland’s montane lichens (e.g. *Alectoria nigricans*, *Flavocetraria nivalis* and *Thamnolia vermicularis*) occur in prostrate heath where the stature of competitive vascular plants may also be limited by frequent high wind speeds (Grace, 1977). Long-term changes in wind-speed are difficult to identify and predict (Barnett et al., 2006), and are not included in this analysis. However, the fate of lichens occurring in Britain’s prostrate heath communities may depend upon wind speed as an additional control on the growth of vascular plants. This may contrast with saxicolous lichens (e.g. *Allan-toparmelia alpicola*), which are free from competition with vascular plants and might respond directly to climatic parameters.

The projections for Northern-Boreal lichen species match with previous application of bioclimatic models for the lichen *Vulpicida pinastri* (Binder, 2006), a species restricted to north-east Scotland and predicted to decrease in response to war-

C Projected bioclimatic range:

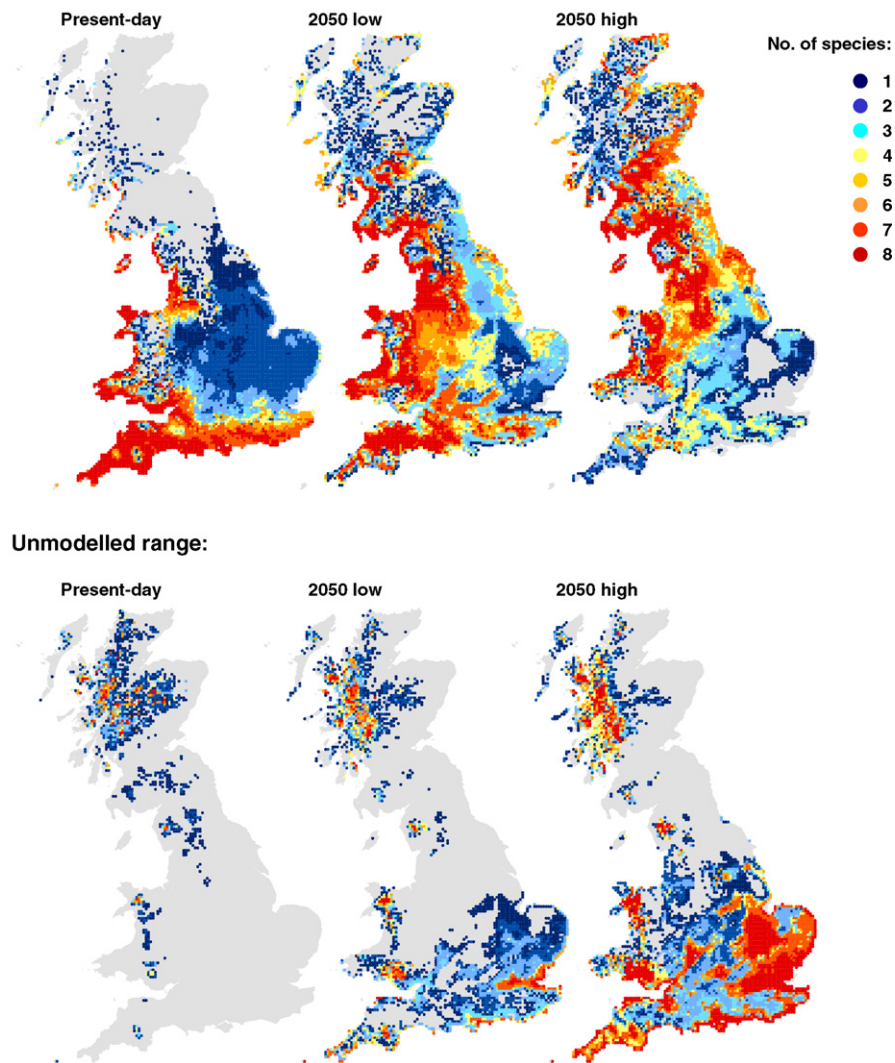
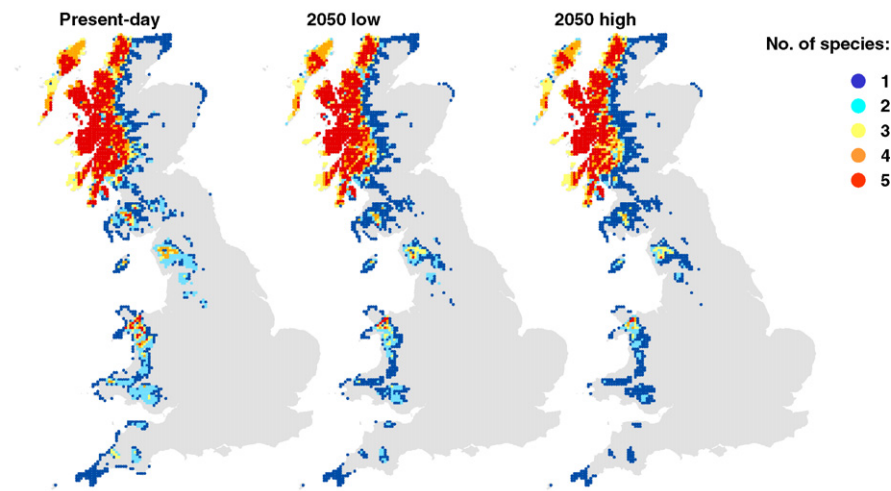
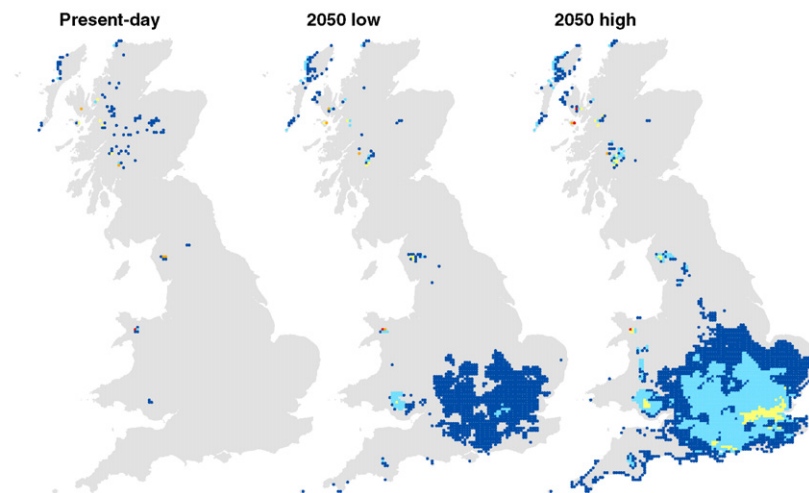


Fig. 6 – continued

mer winters. However, these trends contrast with a projected increase in bioclimatic space for *Lecanora populicola*, also restricted to north-east Scotland, though with a distribution thought to be limited by summer dryness (Ellis et al., 2007). These contrasting projections tentatively caution the potential for non-analogue lichen assemblages, driven by differential response of species that currently occupy a similar geographic range. The individualistic response of species to climate change within well-defined vegetation communities has been reported in earlier studies (Berry et al., 2002). Nevertheless, as a broad pattern, the projected decrease in bioclimatic space for Northern species, and an increase for Southern species, agree with documented shifts in the lichen flora of the Netherlands, where boreo-montane elements are declining and tropical elements are increasing (Van Herk et al., 2002), and are consistent with general trends projected across contrasting biological groups for Britain (Berry et al., 2002, 2005, 2007) and Europe (Thuiller et al., 2005b, 2006).

These losses and gains of suitable climate space inferred through the projection of the individual species models

(Fig. 7) should be assessed in the context of the unmodelled range: i.e. the grid-squares for which future climate scenarios were beyond the threshold of the NPMR models (McCune, 2006). While acceptance of a threshold value ensures models are not erroneously applied beyond their calibration range, the scope of model utility could have been increased by using input data from a wider geographic extent (i.e. recorded presences and pseudo-absences from across continental Europe). However, expansion of this study to include European sites would have necessitated a trade-off in the resolution and accuracy of input data; few European countries have systematically recorded presences of lichens or have quality controlled records at a 10 km grid-square scale as comprehensively as within Britain. A further advantage of split-sampling records for Britain (rather than using European records as input data, and subsequently applying models to a test-set of British records: cf. Berry et al., 2002) is the better capture of a hyper-oceanic climate that has limited or no analogue in continental Europe. This is particularly important with respect to lichens (and other poikilohydric groups), for which

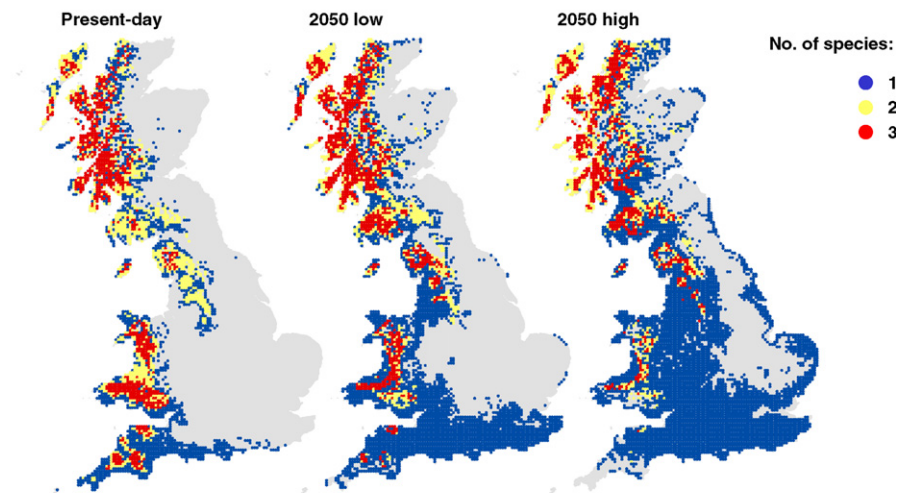
d Projected bioclimatic range:**Unmodelled range:****Fig. 6 – continued**

diversity and conservation importance is often ascribed to Britain's oceanic position in north-west Europe (Fryday, 2002; Rothero, 2005). Previous modelling studies based on European distributions have failed to capture the bioclimatic range for poikilohydric species representative of Britain's oceanic flora (e.g. *Trichomanes speciosum*, cf. Rumsey et al., 1999: Prof. M. Gibby, pers comm.), and it is significant, therefore, that our approach appears to have effectively captured the climatic response of oceanic lichens (Fig. 6d and e).

The unmodelled range can be qualitatively assessed for Northern and Southern species. For both of these groups, grid-squares in which 2050s bioclimatic suitability is not captured by the modelled species-response are concentrated in the south-east of England. Climate change scenarios suggest this region will become drier and warmer (Hulme et al., 2002), a projection that is supported by climate trends based on instrumental records since 1914 (cf. www.ukcip.org.uk). The unmodelled range, therefore, occurs in a region whose projected climate for 2050 is a dry and warm lowland setting. Applying a simple 'space for time' comparison, the Northern

species examined are currently absent from European regions that occupy a climatic setting tending towards that projected for southern England in the 2050s (i.e. lowland southern Europe: cf. Nimis, 1993). We assume, therefore, that these species will be absent from southern England under projected climate change trends, and that the projected loss of bioclimatic space for these species tentatively indicates a genuine threat to their range in Britain. Based upon the spatial trends in the UKCIP02 data, Northern-montane and Northern-Boreal species will be most susceptible to the effects of projected climate change towards their southern range margins (Wales, northern England and the Scottish borders) and towards the west of their range in Scotland. The climate is projected to remain relatively more suitable for this suite of species in the mountains and Straths of north-east Scotland (i.e. the Cairngorm region). In contrast, the present-day bioclimatic range occupied by the suite of Southern species is projected to shift northwards, into Wales, much of northern England, the Scottish borders and the eastern coast of Scotland. A number of these species occur in present-day southern Europe, though

e Projected bioclimatic range:



Unmodelled range:

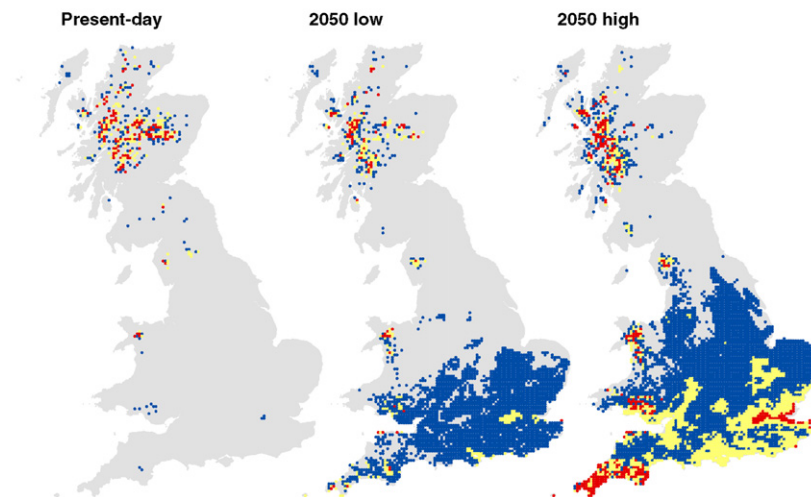


Fig 6. – continued

are associated with a warm and notably humid climate (cf. Nimis, 1993); accordingly, we can be less sure of their projected status if the future climate of southern England becomes both warmer and drier.

Unmodelled grid-squares for the suite of Oceanic lichen species are similarly concentrated in southern England, and the projected dryness in this region is expected to preclude the widespread occurrence of these species under climate change scenarios. While the projected change in climatic suitability for Oceanic species appears to be less pronounced compared to the Northern and Southern species (Fig. 7), there is nevertheless a projected loss in bioclimatic space for Oceanic-northern species, attributable to a potential contraction at the eastern edge of their range in Scotland (Fig. 6d). This contrasts with recent evidence to suggest that the richness of oceanic lichen species comprising the 'Lobarion' community (cf. James et al., 1977; Rose, 1988) may benefit from warmer winters and increased winter rainfall in Scotland (Ellis and Coppins, 2007). Two of the Oceanic-widespread species (*Hypotrachyna*

laevigata and *Hypotrachyna taylorensis*) show little net change in projected bioclimatic space (Fig. 7), though there are potentially important spatial shifts (i.e. a projected decline in Wales, and an increase in south-west Scotland: Fig. 6e). The third Oceanic-widespread species (*P. macrospora*) shows a broad increase in range in southern and western England and along the eastern coast (Fig. 6e). These inter-specific differences within the same biogeographic grouping can be explained as contrasts in the individualistic species-response and especially the relative importance of precipitation compared to temperature. The *Hypotrachyna* species are expected to be more responsive to wetness, which will restrict their eastward distribution under climate change scenarios, compared to *P. macrospora*, which is thought to be relatively more sensitive to temperature and may expand eastwards in response to warming. Nevertheless, the projected impact of climate scenarios is generally less well characterised for the Oceanic species than for species in the Northern and Southern groups, despite effective model discrimination of their present-day distribution (Fig. 6d and e).

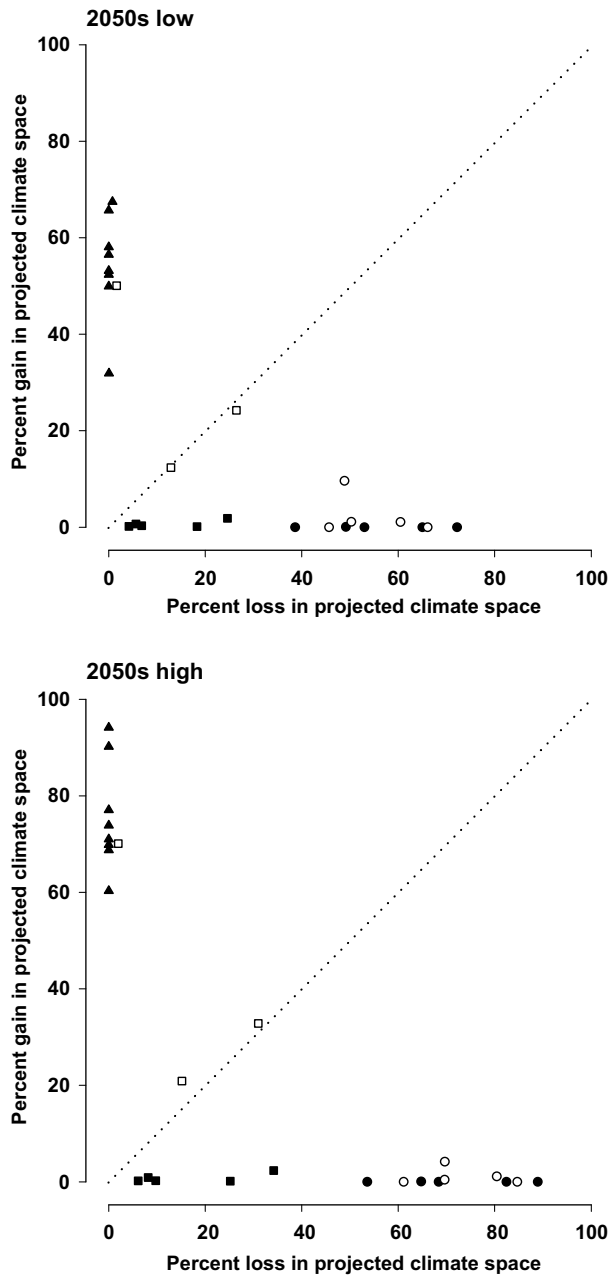


Fig. 7 – Projected loss and gain in bioclimatic space compared between the present-day and 2050s low and high emissions scenarios. Values are compared for species in contrasting biogeographic groups: Northern-montane (●), Northern-Boreal (○), Oceanic-northern (■), Oceanic-widepread (□) and Southern-widespread (▲).

4.3. Summary trends and conservation

General trends in the projected response of lichen species to climate change scenarios (Fig. 6) agree with expected shifts between contrasting northern and southern elements in Britain’s flora and fauna (Berry et al., 2002, 2005, 2007), supported by recent observations demonstrating species range shifts northwards (Parmesan et al., 1999; Thomas and Lennon, 1999). We highlight, therefore, the possibility of climate-induced threat

to Britain’s Northern-montane and -Boreal lichen species, which represent outlying examples of arctic-alpine and continental floristic elements. We hesitantly suggest that conservation efforts to support the continued presence of these species in Britain (e.g. by reducing additional pressures such as habitat loss or hypertrophication) might productively focus on certain montane and upland regions of Scotland, where a suitable bioclimatic range is expected to persist into the 2050s (Fig. 6a and b). However, assessed at contrasting scales, this potential threat to the Northern species of Britain’s lichen flora may present a decision-making challenge. While montane species generally may be disproportionately threatened by climate change (Thuiller et al., 2005a,b), the Northern-montane and -Boreal lichens examined in this study are widespread in Scandinavia and continental alpine zones, and there remains a scarcity of molecular evidence with which to assess the genetic isolation of British populations. Without this information on genetic diversity it may be difficult to balance the cost of attempting to conserve Britain’s geographically peripheral populations of Northern species against a responsibility to enable the northward migration of Southern species (Fig. 6c). The protection of lichen species considered at a European-scale may seek to promote the migration of new species into Britain, by lowering restrictive pollution loads and enabling dynamic vegetation change, for example the development of a warm-climate lichen vegetation in currently degraded environments of lowland south-east England. Additionally, a critical assessment of the UK’s international responsibilities might off-set protection of Northern-montane and -Boreal species in favour of resources spent to protect the Oceanic lichen flora which is restricted to Britain’s Atlantic coast (though this may include certain specialist montane species in oceanic western Scotland: cf. Fryday, 2002). The sensitivity of Britain’s Oceanic lichen flora to climate change impacts is less well characterised than for the contrasting Northern and Southern species, and previous research has demonstrated that the climate-response of oceanic epiphytes (e.g. species in the *Lobarion* community) may depend on an interaction between climate change and the spatial-temporal structure of woodland habitat (Ellis and Coppins, 2007). Oceanic lichen communities along Britain’s west coast provide some of the best European examples of temperate rainforest epiphyte communities (Coppins and Coppins, 2003, 2005), comparable to the rich epiphyte assemblages of north-western North America (Pike et al., 1975; Goward and Spribille, 2005) and New Zealand (Green and Lange, 1991); research to better understand their sensitivity and vulnerability to climate change should be a priority concern.

4.4. Future directions

The results of this study provide a framework for future monitoring, which is now needed to critically assess these model predictions. Accordingly, our results provide only a tentative assessment of projected climate impacts, and it is important to emphasise that the degree to which a species’ actual distribution might track changing climate remains difficult to assess. To minimise this complexity we aimed to select lichen species whose present-day distributions are expected to be in equilibrium with the present-day climate. Nevertheless,

the fragmented nature of habitats in the modern British landscape may present a severe constraint to effective species migration in response to rapid climate change (Travis, 2003). Accordingly, easily dispersed species may track rapid climate change more effectively than those that are dispersal-limited. Previous researchers have pointed to a difference between sexual spore-producing lichen species (e.g. *Cetraria sepincola*, *Degelia atlantica*, and *Pyrenula occidentalis*) and asexual diaspore-producing species (e.g. *A. nigricans*, *F. nivalis* and *Usnea hirta*) in their meta-population dynamics and ability to disperse within- and between habitat patches (Hedenås et al., 2003; Löbel et al., 2006a,b). The effect of climate change and habitat fragmentation may, therefore, be compounded for dispersal-limited asexual species by the negative effects of genetic isolation, i.e. lowered genetic diversity in isolated populations may include reduced influx of novel genetic material and the lowered potential for *in situ* adaptation to changing climate. Additional research is also needed to describe the role of smaller-scale processes (i.e. shifts in establishment or growth rates, species interactions, etc.) which will underlie a pattern of larger-scale range shifts (Brooker, 2006).

Our study has at least highlighted the potential for climate change to cause large shifts in the regional distribution of lichens in Britain: these impacts would contribute additional complexity to a flora that has already undergone significant change in response to pollution and land management (Seward, 1998; Coppins et al., 2001). This well documented sensitivity of lichens to environmental change has been used as an effective tool for the bioindication of pollutants (Hawksworth and Rose, 1970; Van Herk et al., 2003) and in resource management (Coppins and Coppins, 2002), and we suggest lichens may also provide an effective monitoring system for climate impacts. It is thus critically important to ensure existing databases are maintained – e.g. the British Lichen Society mapping scheme, and the Scottish Lichen Database. These provide a rich source of high quality, dated and geo-referenced records, and represent a base-line resource with which to identify the present status and assess past and future change in the British lichen flora.

Acknowledgements

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