The biogeography of climate change risk for Scotland’s woodland biodiversity: epiphytes

Christopher J. Ellis and Sally Eaton
Royal Botanic Garden Edinburgh, Edinburgh, Scotland

ABSTRACT
The biodiversity threat of human-induced climate change occurs because shifts in temperature, precipitation, etc. are expected to be large and rapid, while at the same time species vulnerability is increased because of habitat loss and fragmentation, weakening an effective ecological response to climate change. Here, we map both the species exposure to climate change – a decline in suitable climatic condition for areas with diverse lichen epiphyte assemblages – and vulnerability measured as the landscape extent of native woodland, which can provide microclimatic refugia. Choropleth maps for Scotland reveal regional contrasts in the risk for lichen epiphytes; a difference between northeast Scotland, with high exposure to climate change but lower potential vulnerability, and western Scotland with a lower (or more ambiguous) exposure, but high vulnerability because of landscapes with smaller and isolated woodlands. The analysis is general and large scale, relating to species biogeography, but helps to identify key actions at smaller, habitat scales.

ARTICLE HISTORY
Received 5 February 2018
Accepted 17 September 2018

KEYWORDS
Biodiversity; choropleth map; climate change; risk analysis; woodland

Introduction
Climate change is a natural process that has occurred throughout Earth’s history. The unique threat to biodiversity of human-induced climate change is explained by two interacting features: (i) an unprecedented rate and magnitude of projected climate change (Diffenbaugh & Field, 2013; Moritz & Agudo, 2013), and species sensitivity to this (Pearson & Dawson, 2003; Thomas et al., 2004), combined with (ii) extensive habitat loss. Species populations in reduced and isolated habitat patches will tend to be smaller and pushed closer to a minimum viable population size (Boyce, 1992; Shaffer, 1981). They will be at increased risk of stochastic population extinction (Matthies, Bräuer, Maibom, & Tscharntke, 2004), while deterioration in suitable climate will increase deterministic extinction risk, e.g. lowering population growth rates (cf. Dalgleish, Koons, Hooten, Moffet, & Adler, 2011; Rande, 1993; Sletvold, Dahlgren, Øien, Moen, & Ehrén, 2013). Smaller populations with lower genetic diversity (Leimu, Mutikainen, Koricheva, & Fischer, 2006) may have reduced capacity to adapt to climate change, including in fragmented habitats through genetic rescue (Hoffman & Sgrò, 2011; Jump & Peñuelas, 2005),

© 2018 Royal Scottish Geographical Society
as well as the limited ability for migration to track suitable climate space (Schwartz, 1992; Travis, 2003). The direct sensitivity of a species to large-scale climate change has been characterised as its exposure, while the conditions enabling a biological response (habitat and/or population size and connectivity) represent aspects of vulnerability (Ellis, 2013), both of which – exposure and vulnerability – are key elements in risk assessment (Crichton, 1999; Cardona et al., 2012).

This study aimed to map two simple proxies for climate change risk to biodiversity. First, relating to exposure, the degree to which an assemblage of species may lose suitable climate space in a landscape. Second, relating to vulnerability, the extent and covarying fragmentation (Smith, Koper, Francis, & Fahrig, 2009) of key habitat structure in the same landscape. By way of example, the study focuses on epiphytic lichens in Scotland.

**Methods**

The methods applied here build on previously published large-scale analyses of baseline environmental suitability (envS) and response to environmental change including climate change scenarios (Sexton, Harris, & Murphy, 2010) for lichen epiphytes in Britain (Ellis et al., 2014; Ellis, Eaton, Theodoropoulos, Coppins, et al., 2015). In summary (cf. Table 1), MAXENT (Elith et al., 2011; Phillips, Anderson, & Schapire, 2006) was used to generate robust bioclimatic models for species ≥30 occurrence records as epiphytes at a 10 km grid scale for a baseline period 1961–2010. Species occurrence was compared to climate (temperature, precipitation) and pollution variables (SO2, forms of nitrogen), and landscape extent of ancient woodland (Ellis et al., 2014; Ellis, Eaton, Theodoropoulos, Coppins, et al., 2015). Background environmental data was used for the entire study area (Britain), to help avoid clamping issues (extrapolation) when projecting to baseline climate for a regional subset (Scotland), with 10-fold cross-validation used to implement training and test datasets for model evaluation. On this basis, 382 individualistic species models had diagnostic values of cross-validated AUC > 0.7 (Pearce & Ferrier, 2000; Swets, 1988). The subsequent analysis of risk proceeded in two stages.

The first stage aimed to identify the parts of Scotland’s landscape having the highest baseline envS for lichen epiphytes, and which might be delimited as priority areas for conservation. Previous published results strongly suggest that these would be areas with (i) low historic and baseline values for SO2 and nitrogen pollutants (Hawksworth & Rose, 1970; Van Herk, Mathijsen-Spiekman, & De Zwart, 2003; Wolseley, James, Theobald, & Sutton, 2006), and (ii) a high spatial extent of ancient woodland, allowing for the observation that certain lichen species are restricted to woodland stands with old growth properties (Coppins & Coppins, 2002; Whittet & Ellis, 2013). Thus, MAXENT envS values were summed among species, for each of 912 10 km grid squares representing Scotland’s land surface, calculated as percentiles and values >75th percentile plotted to show the areas of highest envS for lichen epiphytes.

Second, within the high envS areas two attributes were assessed. The degree of exposure to anticipated future environmental change, including lower SO2 pollution (Vestreng, Myhre, Fagerli, Reis, & Tarrasón, 2007) and changing climate (Jenkins et al., 2010; Sexton et al., 2010). Exposure was calculated for each grid square as species 2080s envS relative to the baseline envS (positive or negative trend in
ΔenvS) and summing values for any species experiencing a decline (negative ΔenvS). These values were then ranked over the grid squares and divided into three percentile classes <25th, 25th–75th and >75th. The vast majority of modelled species, with a few notable exceptions (e.g. Lecanora conizeoides: Bates, Bell, & Massara, 2001), experience an increase in envS in response to lower SO2 pollution (Ellis, Eaton, Theodoropoulos, Coppins, et al., 2015), and negative ΔenvS can be assumed as an epiphyte exposure to climate change. This approach contributes to a risk estimate for threatened species, but any species losses incurred could be offset by compositional turnover if species declines are compensated by other species increasing in their envS and probable occurrence, so that richness remains the same. To test for potential compositional turnover, the percentile values of ΔenvS for threatened species were compared to the mean ΔenvS for all species, for an equivalent grid square, estimating the possibility for net turnover and compositional change. Thus, a percentile ΔenvS value for threatened species was hypothesised to represent no net change in species richness if the mean ΔenvS for all species equalled zero, i.e. declining values of environmental suitability for some species are offset by gains for other species.

To assess the degree of vulnerability the native woodland survey of Scotland (NWSS) was used as a template for habitat structure (Patterson, Nelson, Robertson, & Tullis, 2014). NWSS values for extent of native woodland were summed per 10 km grid square; we tested for collinearity of habitat extent with fragmentation, through correlation with mean woodland area (Smith et al., 2009). Values for extent were ranked and divided.

### Table 1. List of environmental variables used to model lichen species occurrence in Scotland, using MAXENT (Ellis et al., 2014).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Units</th>
<th>Source</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Response</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Explanatory</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Climate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pollution</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acidity</td>
<td>Keq ha⁻¹ yr⁻¹, 2004–2006</td>
<td>Centre for Ecology and Hydrology</td>
<td>RoTAP (2012)</td>
</tr>
<tr>
<td>Total-nitrogen</td>
<td>Kg N ha⁻¹ yr⁻¹, 2004–2006</td>
<td>Centre for Ecology and Hydrology</td>
<td>RoTAP (2012)</td>
</tr>
<tr>
<td>NH₅</td>
<td>Kg N ha⁻¹ yr⁻¹, 2004–2006</td>
<td>Centre for Ecology and Hydrology</td>
<td>RoTAP (2012)</td>
</tr>
<tr>
<td>NOx</td>
<td>Kg N ha⁻¹ yr⁻¹, 2004–2006</td>
<td>Centre for Ecology and Hydrology</td>
<td>RoTAP (2012)</td>
</tr>
<tr>
<td>SO₂ 2</td>
<td>ppb, 1987</td>
<td>Centre for Ecology and Hydrology</td>
<td>RoTAP (2012)</td>
</tr>
<tr>
<td>Habitat Extent</td>
<td>Ancient Woodland</td>
<td>Conservation Agencies</td>
<td>Roberts et al. (1992)</td>
</tr>
</tbody>
</table>

Note: Choice of variables was based on previous research to identify the structure of covariation within a particular effect-type (climate, pollution) and to select orthogonal examples of each (Ellis & Coppins, 2010; Ellis, Yahr, & Coppins, 2011).
into percentiles <25th, 25th–75th and >75th. Values for lichen epiphyte exposure (negative envS in response to climate change) and vulnerability (extent/fragmentation of native woodland in the landscape) were visualised using a bivariate choropleth plot.

**Results**

With respect to lichen epiphyte baseline environmental suitability (envS), the highest accumulated values (Figure 1(a)) occurred at distance from pollution sources (north of Scotland’s urbanised, post-industrial central belt), and especially towards the central west coast of Scotland, though also including the southern Highlands, the Great Glen and the upland valleys of northeast Scotland (e.g. Deeside, Strathspey, Findhorn). There were scattered areas of high envS outside these regions, including in the Scottish borders.

Focussing on areas with the highest envS, the broad picture of biodiversity risk had two aspects (Figure 1(b)). First, the exposure to climate change was high in the northeast of Scotland, with a relatively strong negative ΔenvS when comparing baseline to 2080s scenarios. The trend in ΔenvS for species exposed to climate change was also negatively correlated with mean ΔenvS across all species (Figure 2), indicating that the areas of highest climate change exposure were also the least likely to be compensated by species turnover. However, the overall climate risk was estimated to be lower in the northeast because of large native woodland extents with the potential to reduce vulnerability (Figure 3(a)). Overall risk was, therefore, highest toward the west of Scotland, which in general had

![Figure 1](image-url). (a) The cumulative values of environmental suitability (envS) per 10 km grid square, for 382 lichen epiphytes; areas with optimum environmental conditions (>75th percentile) are highlighted in black. (b) Choropleth plot to show the intersection of climate change exposure (declining envS under a 2080s climate change scenario), and vulnerability considered as the loss and fragmentation of native woodland in the landscape.
moderate values of exposure to climate change, and a potential for compositional turnover in maintaining richness (Figure 2), but coupled with increased vulnerability for threatened species because of lower extents and high fragmentation of native woodland in the landscape (Figure 3(a)). Used as a proxy for vulnerability, native woodland extent was correlated with mean woodland area as a measure of fragmentation (Figure 3(b)).

Figure 2. Relationship between the percentile values of negatively shifted environmental suitability (negative $\Delta envS$) for lichen epiphytes exposed to climate change, and the balance between negative and positive (mean) $\Delta envS$ across all species for equivalent 10 km grid squares.

Figure 3. (a) The relationship between the extent of native woodland in the landscape, and a longitudinal gradient in Scotland: $r = 0.453, P < .001$ with 226 df. (b) The relationship between native woodland extent ($\approx$ habitat loss) and the mean size of woodland remnants ($\approx$ habitat fragmentation): $r = 0.668, P < .001$ with 226 df.
**Discussion**

This study attempted to make two broad observations: first, to examine the regional pattern of baseline environmental suitability (envS) for lichen epiphytes, and second to explore relative degrees of species risk determined as the exposure and vulnerability to climate change. Our assessments of climate change were based on previously published bioclimatic models (Ellis et al., 2014), which quantified species environmental responses for Britain, and projected these to a delimited region (Scotland) under baseline and future climate change scenarios. This avoids some extrapolation problems, for example by including warmer climates in the model baseline (southern England), which then fall within the range of future projected climate in Scotland (though see our caveats for western Scotland, below).

The projection of baseline envS aimed to reconstruct from the extensive sampling of species distributions (Simkin, 2012) the conditions and locations that favour epiphyte diversity. These conditions – low pollution, high extents of ancient woodland for relevant species – are consistent with drivers of species loss reconstructed for historic landscapes (Ellis et al., 2011, 2018), as well as spatial inference to explain distribution patterns for post-industrial landscapes (Coppins & Coppins, 2002; Hawksworth & Rose, 1970; Van Herk et al., 2003; Whittet & Ellis, 2013; Wolseley et al., 2006). High values of envS match consistently in Scotland to a relatively clean air environment (RoTAP, 2012), coupled with areas that have more extensive ancient, mixed semi-natural woodland (Roberts, Russel, Walker, & Kirby, 1992). There appear to be outlying areas with high envS that are potentially anomalous, such as in the Scottish borders. Comparison of bioclimatic models with and without bias layers to control for sampling effort have supported the robustness of occurrence records in Britain when reconstructing regional distributions (Bogomazova, 2018); however, small outlying areas with high envS may remain influenced by localised sampling bias (Bogomazova, 2018), such as locations in southeast Scotland close to taxonomic institutes in Edinburgh (Dennis & Thomas, 2000; Sastre & Lobo, 2009).

Our methodology of estimating climate change exposure measured a decline in envS across species, when comparing the baseline to 2080s projections (ΔenvS), and uncompensated by potential gains in suitability for alternate species in the same landscape (i.e. compositional turnover). The focus is therefore on a threat to extant biodiversity. This threat appears to be consistent with an overall loss of species, rather than being offset by compositional turnover, since the percentile values for species with negative ΔenvS were negatively correlated with the mean values of ΔenvS for all species.

Towards the northeast of Scotland, the exposure to climate change is high. This is explained by warming and the loss of suitable climate space for an assemblage of relatively Boreal- or continental-climate associated species including *Cetraria sepincola* and *Lecanora populincola* (Ellis, Eaton, Theodoropoulos, Coppins, et al., 2015) or *Vulpicida pinastri* (Binder & Ellis, 2008). However, there are extensive areas of native woodland within the same landscapes. Assuming this woodland resource is managed towards the protection of biodiversity, it may have potential to reduce vulnerability to climate change. The exposed species are biogeographically at a trailing range edge, and given Britain’s island situation there will be a net loss of climate space in Scotland, rather than a contiguous spatial shift. Reduction in vulnerability is not afforded by long-distance migration to track suitable climate space. Instead, reduced vulnerability would reflect opportunity to migrate...
within and among native woodland stands, responding to the heterogeneity of microclimates associated with Scotland’s complex topography. This topographic variability offers the potential to maintain larger and more resilient populations and metapopulations (Hanski, Moilanen, & Gyllenberg, 1996) if a sufficient range of microclimatic refugia can persist under macroclimatic change (Dobrowski, 2010; Rull, 2009). Furthermore, well-wooded landscapes may harbour larger more connected populations that can more effectively adapt or acclimate to climate change. More and larger populations may include those that are differently adapted (Nadyeina et al., 2014) or acclimated through patterns of photobiont selectivity (Dal Grande, Widmer, Wagner, & Scheidegger, 2012; Werth & Sork, 2010), representing opportunity for gene flow or photobiont switching. However, the reduced vulnerability for northeast Scotland is measured only in relative terms against the situation in western Scotland. The highest extents of woodland in northeast Scotland remain low in absolute terms, <17% of the landscape (Figure 2(a)), and a robust ecological response to climate change is uncertain. Nevertheless, a focus on resilience to climate change for northeast Scotland would include the maintenance as well as diversification of existing woodland structure, to create structurally more complex stands across broad landscape and topographic gradients, with higher native tree diversity and a greater range of tree ages from regenerating to senescent veteran trees and deadwood (Dettki & Esseen, 1998; Kuusinen & Siitonen, 1998; Lesica, McCune, Cooper, & Hong, 1991). This would be expected to increase epiphyte population sizes, species genetic diversity, and offset the exposure to climate change through the provision of microclimatic refugia (Ellis, 2018). This transition in northeast Scotland could include the possibility to re-naturalise areas of old plantation pine (Pinus sylvestris) through commercial management that better recreates natural forest dynamics (Humphrey, Davey, Peace, Ferris, & Harding, 2002), and working towards assisted restoration that repurposes economic forestry for a more diverse or contrasting set of ecosystem services (Chazdon, 2008).

Towards western Scotland, the climate change risk appeared to have a different character. The species exposure to climate change was in general lower, though our coarse-grained model results are subject to caveats that include projected response to non-analogue future climates for oceanic western Scotland (Ellis & Eaton, 2016). The threat of climate change for Scotland’s western, oceanic species remains, therefore, less certain than for species characteristic of northeast Scotland. However, should climate change negatively affect Scotland’s oceanic species the consequences are arguably greater, since the region includes some of Britain’s most important contributions to international biodiversity in terms of its temperate rainforest epiphytes (Ellis, Eaton, Theodoropoulos, & Elliott, 2015; Woods & Coppins, 2012). Furthermore, epiphytes in western Scotland occur in a landscape where the extent of native woodland is less, and fragmentation is higher, increasing species vulnerability to climate change. The recovery of native woodland is an active policy option in Scotland (Anon, 2006) that could reduce species vulnerability, but in order for this to be effective key ecological questions remain, including: (1) What is the appropriate spatial and temporal scale for local woodland recovery in the landscapes of western Scotland, in order to allow remnant populations to expand into regenerating habitat, (2) What are the optimum translocation options for conservation priority species thought unable to colonise passively into recovered woodland?

In summary, we provide a biogeographic case study that combines relatively simple measures related to elements of risk – bioclimatic modelling (climate change exposure)
and habitat mapping (vulnerability) – to identify key spatial areas of climate change risk to biodiversity. We show that this approach can be sensitive to regional discrepancies in the biodiversity response to climate change, highlighting questions at a habitat scale that are appropriate to a given landscape context.

Acknowledgements

We thank two anonymous reviewers for their suggested improvements to a draft manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This material in this work was partly funded (bioclimatic modelling) by the Esmée Fairbairn Foundation, and partly in contribution to Theme 1 (Natural Assets) of the Scottish Government’s Strategic Research Programme.

References


