

Future Non-Analogue Climates for Scotland's Temperate Rainforest

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ABSTRACT *Temperate rainforest is restricted to a globally rare set of climatic conditions. Scotland has among the best remaining examples of intact temperate rainforest in Europe, characterised ecologically by a unique assemblage of epiphytic bryophytes and lichens. Given climatic control on rainforest distribution and ecology, climate change is a probable risk to Scotland's rainforest. This study investigated climate change impacts for 20 target sites, classified based on (i) bioclimatic conditions, and (ii) epiphytic diversity, into contrasting rainforest and more continental (non-rainforest) examples. Space-for-time matching identified climate analogues within the European conservation forest network, which at present have a climate similar to that expected of the target sites during the 2080s (WorldClim datasets). The results show that 2080s analogues for sites in more continental north-eastern Scotland occur in Wales and southern England. However, Scottish rainforest sites were their own 'best analogues' through to the 2080s, despite the fact that their climate is projected to change significantly; they had no suitable future analogue within Europe's conservation forest network. These contrasting regional patterns highlight the need for a flexible approach to species conservation during climate change, including a strategy to cope with ecological uncertainty in Scotland's zone of oceanic rainforest.*

KEY WORDS: bryophyte, climate change, epiphytes, lichen, woodland ecology, WorldClim

Introduction

Tropical rainforests are celebrated as among the most diverse ecosystems on the planet and they are of global significance in their delivery of ecosystem services (Foley *et al.* 2007). However, the tropical rainforest is one component in a spectrum of rainforest types. Holdridge's Life Zones partition rainforest systems into different 'super-humid' provinces, based on the relationship between potential evapotranspiration and annual precipitation. Along synchronous latitudinal–altitudinal temperature axes these include tropical, sub-tropical, warm-temperate, cool-temperate, and boreal rainforest, positioned from lowland to subalpine. The higher-latitude categories of temperate and boreal rainforests are globally rare, covering < 1% of the global land surface, and they are also highly disjunct. For example, 15% of the total bioclimatic space for temperate/boreal rainforests occurs in western Europe (DellaSala 2011) and is remote from comparable regions in western

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North America, New Zealand, or Japan. A defining feature of temperate/boreal rainforests is their association with a spatially restricted set of terrestrial climatic conditions, which has been specified as having four key attributes (Alaback 1991): (i) over 1400 mm annual precipitation, (ii) at least 10% of which occurs in the summer, (iii) a summer isotherm less than 16°C, and (iv) with seasonality caused by low winter temperatures. Temperate/boreal rainforests are also characterised by and can be mapped based on a unique set of ecological characteristics (DellaSala 2011), the most obvious of which is their extraordinary diversity of moisture-demanding bryophytes and lichens (Figure 1). Epiphytic (tree-dwelling) bryophytes and lichens define the ecological structure of Europe's rainforests (DellaSala 2011; Coppins & Coppins 2012), and are important to its ecosystem function, for example in the capture and recycling of growth limiting nutrients (McCune 1993; Antoine 2004).

There are three major threats to the epiphytic diversity and therefore ecological status of European temperate/boreal rainforests. First, European rainforest has been reduced in extent by widespread deforestation since the mid-Holocene (MEA 2005). Characteristic rainforest epiphytes can be dependent on forest ecological continuity for their persistence (Coppins & Coppins 2002; Whittet & Ellis 2013); these species recover only slowly into regenerated forest and thus become restricted to fragmented 'old-growth' rainforest stands. Second, even where old-growth forest stands have survived in the rainforest bioclimatic zone, the associated epiphytes can be threatened by high levels of transboundary air pollution (MEA 2005), which can cause catastrophic loss of sensitive bryophytes and lichens (Hawksworth & Rose 1970; Van Herk *et al.* 2003). Additionally, given the fundamental importance of climate in structuring the rainforest ecosystem, this paper explores the role of human-induced climate change as a third potential threat to temperate/boreal rainforests, with a focus on epiphytes as an ecological risk factor. It asks: (i) what is the distance to the nearest site that is an analogue for the expected climate in the 2080s, and representing therefore the 'velocity' of climate change? And (ii), this question is asked for sites in Europe's forest conservation network, making it relevant to the biogeographic response of epiphytes.



Figure 1 Oceanic epiphytes, including *Degelia atlantica* (grey) and *Lobaria virens* (green), on hazel at Morven in western Scotland.

Methods

Twenty target sites were selected for the study. These were all ancient woodlands with > 260 yr of continuity (Roberts *et al.* 1992) designated as Sites of Special Scientific Interest (SSSIs) within the UK conservation network, and which have been comprehensively surveyed for their bryophyte and lichen epiphytes (Ellis *et al.* 2015b). The target sites are known to include contrasting epiphyte community types aligned along a climatic gradient from western to eastern Scotland (Figure 2(a); Table 1). Baseline climatic data (1960–2000) for each of the target sites included the monthly averages and totals for temperature (°C) and precipitation (mm) respectively. These climatic data were derived from instrumental records contributing to WorldClim spatial interpolation and statistical downscaling to achieve a resolution of 30 seconds, or c. 1 km² (Hijmans *et al.* 2005). The baseline data



Figure 2 (a) The distribution of 20 climatically and ecological contrasting target sites in Scotland (cf. Table 1). (b) The distribution of 3842 potential analogue sites, across the European conservation forest site network, 3. The trajectory of 2080s analogue sites linked to the target sites, the circular area for Scotland's west coast shows the temperate rainforest sites which were each other's best 2080s analogues.

Table 1 Summary information on the locality, climatic (WorldClim) and vegetation conditions for 20 target sites with well-characterised epiphyte communities (Ellis *et al.* 2015b), distributed along the transition from oceanic (temperate rainforest) to more continental climates

sample site code and name	lat; long	NVC: dominant woodland type	ann. precip. (mm)	summer precip. (%)	July T. (°C)
OCEANIC					
EW: Ellary woods	55.91; -5.62	W11b: Oak-Birch woodland	1609	20	14.6
TAY: Tainish NNR	56.00; -5.63	W17b: Oak-Birch woodland	1628	20	14.6
LB: Loch Ba woods	56.47; -5.94	W4b, W11b: Birch woodland, and Oak-Birch woodland	1790	20	14.2
IB: Inninmore Bay woods	56.52; -5.74	W7a: Ash-Alder woodland	1837	20	13.9
DR: Druimbuidhe woods	56.65; -5.92	W17b: Oak-Birch woodland	1748	20	14.3
AR: Ariundle woods	56.72; -5.52	W4b: Birch woodland	1777	20	14.5
GC: Glen Creran woods	56.58; -5.22	W9a: Ash woodland	1858	19	14.6
CC: Coille Coire Chuilc	56.41; -4.70	W18b: Pine woodland	1863	18	13.9
CONTINENTAL					
GT: Glen Tarff woods	57.10; -4.67	W9, W11: Ash woodland, and Oak-Birch woodland	1366	19	14
EN: East Loch Ness woods	57.20; -4.56	W17: Oak-Birch woodland	1223	20	14.2
IN: Inchvuilt wood	57.39; -4.91	W18d: Pine woodland	1376	20	13.5
SF: Strath Farrer NNR	57.41; -4.76	W18d: Pine woodland	1193	20	14.1
CW: Cawdor wood	57.51; -3.91	W16: Oak-Birch woodland	735	26	14.9
KF: Kinveachy Forest	57.22; -3.84	W18b and W18d: Pine woodland	1039	22	14
TA: Torr Alvie woods	57.15; -3.86	W11: Oak-Birch woodland	899	23	15.8
IV: Invertromie woods	57.07; -4.01	Aspen (no NVC community equivalent)	990	22	15.3
GQ: Glen Quoich	57.02; -3.50	W18: Pine woodland	1029	22	12.6
BF: Bolfracks wood	56.60; -3.91	W7c: Ash-Alder woodland	1138	21	14.2
BA: Birks of Aberfeldy	56.60; -3.86	W9a, W9b: Ash woodland	1046	21	14.6
MW: Milton NNR	56.64; -3.36	W9a: Ash woodland	804	23	14.1

were matched to climate change scenarios for the same sites. The climate change scenarios were derived from the HADCM3 general circulation model (Johns *et al.* 2003) for the A2a (high energy requirements) scenario (Nakićenović & Swart 2000), implemented within the IPCC 4th Assessment Report. This scenario data was statistically downscaled contributing to the WorldClim resource (Hijmans *et al.* 2005) and made available by the International Centre for Tropical Agriculture (CIAT) and the CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS) (<http://www.ccafs-climate.org/>).

First, the climate of the target sites was compared at the baseline and for the 2080s high emissions scenario (2070–2099), using ordination by Principal Components Analysis (data standardised and centred) to summarise patterns of spatial and temporal climatic variability. Ordination was performed in CANOCO v. 4.5 (Ter Braak & Šmilauer 2002). Second, we aimed to find analogue sites within the European conservation forest network whose

present climate most closely matches the expected future (2080s) climate of the target sites, and from this to estimate the ‘velocity’ of climate change (see Hamann *et al.* 2015). We calculated the root mean square error (RMSE) for the monthly values of temperature and precipitation, compared between each target site in the 2080s, and all other potential analogue sites at the baseline. The analogues were drawn from 3842 localities within the European Habitats Directive which were notified either for a broad habitat feature (i.e. Special Areas of Conservation) or a species of conservation concern, and which had $\geq 70\%$ woodland cover for a spatial area of at least 10 ha (Figure 2(b)). The mean RMSE was calculated separately for each variable (i.e. temperature or precipitation) and month. These RMSE values were then normalised with respect to their means (RMSE_p). The normalised scores were summed for each target-to-analogue comparison, across the variables and months (\sum RMSE_p), and the summed values ranked to find the comparison with the lowest \sum RMSE_p, that is, the analogue site with a climate most similar to that of the target site in the 2080s.

Results

Ordination of target sites by PCA explained 66.2% and 28.3% of variation in precipitation and temperature along axes one and two, respectively (94.5% cumulative), and demonstrated spatial and temporal variability when comparing the baseline and 2080s climates (Figure 3). There were two broad climatic groups (Figure 3(a); Table 1). The ordination separated western and more oceanic sites corresponding to the temperate rainforest climate (Alaback 1991), referred to as Group I sites, from drier and relatively more continental north-eastern sites referred to as Group II. Subdivisions separated each of the main groupings (Groups Ia and IIa) from climatically outlying pinewood sites that were either oceanic but montane and had cooler winter temperatures (Group Ib), or which were dry continental, montane and cooler (Group IIb). At the scale of analysis used here the relative climatic differences between the target sites were retained through to the 2080s (Figure 3(b)), with an expected trend towards warmer temperatures across all seasons.

Space-for-time matching, to compare the target sites with 3842 potential analogues from a European conservation forest network (Figure 2(b)), indicated that – despite the clear environmental difference under scenarios of climate change – all of the oceanic sites (Group I sites) had their closest 2080s analogues from within the same Group I designation (Figure 2(c); Table 1), with a mean \sum RMSE_p score of 0.429 ± 0.056 . This represented a greater climatic difference than for the analogues of the more continental sites (see below). The Druimuidhe woods site (DR) was its own closest 2080s analogue as well as the closest analogue for oceanic sites coded LB, IB, AR, and GC (Figure 2(a); Table 1). The Taynish NNR site (TAY) was its own closest 2080s analogue, and the closest analogue for oceanic site coded EW (Figure 2(a); Table 1). The closest 2080s analogue for the Coille Coire Chuilc site was the oceanic site coded GC (Figure 2(a); Table 1).

In contrast, the closest 2080s analogues for the Group IIa sites were positioned in Wales and southern England (Figure 2(c); Table 1), with a mean \sum RMSE_p score of 0.378 ± 0.091 . However, 2080s analogues for the montane Group IIb pinewood sites were located from among the lowland Group IIa sites. The closest analogue for both the Kinveachy Forest site (KF) and the Glen Quoich site (GQ) was the lowland site coded BA (Figure 2(c); Table 1), with \sum RMSE_p scores of 0.379 and 0.389, respectively.

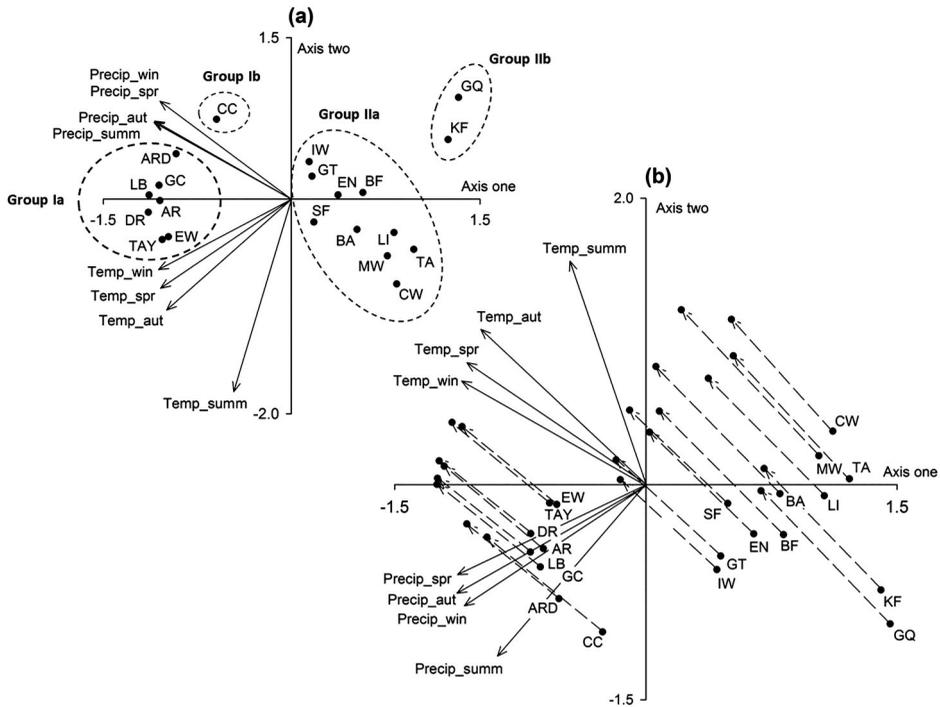


Figure 3 (a) Ordination by principal components analysis (PCA), to summarise climatic variability across the 20 target sites (cf. Table 1 and Figure 2(a)). (b) Including the shift between the baseline and 2080s climate for the target sites (dashed arrows). Vectors from the origin of the plot show the direction of change for the seasonal climate variables (precipitation and temperature averages).

Discussion

Compared to other European regions, Scotland retains large areas of ancient woodland with ecological continuity (Roberts *et al.* 1992; Patterson *et al.* 2014), in a relatively clean air environment (NEGTA 2001; RoTAP 2012). Because of its position at the oceanic margins of Europe, it has some of the finest remaining examples of European epiphyte-rich temperate rainforest (Ellis *et al.* 2015b). Although Scotland's environment has been previously examined within the context of global climate change (Werritty & Sugden 2012), and bioclimatic modelling (Pearson & Dawson 2003; Peterson *et al.* 2011) has been used to explore the response of British epiphytes to climate change scenarios (Ellis *et al.* 2007, 2014, 2015a), this paper takes an alternative approach to previous work. The study tested space-for-time matching for 20 target sites in Scotland, across a European conservation forest network. The target sites were climatically contrasting, and with respect to their epiphytes they were known to capture the ecological transition from internationally important temperate rainforest on Scotland's oceanic west coast, through to relatively more continental systems in north-eastern Scotland (Ellis *et al.* 2015b). A search was made for analogue sites whose present climate was a match for the climate of target sites in the 2080s. This was based on the application of a single climate model analysis (HADCM3, statistically downscaled in the WorldClim resource) for a scenario that was

towards the upper boundary of estimated climate impacts in the IPCC 4th Assessment Report (A2a), but not representing the most extreme scenario (A1FI) for the intensified use of fossil fuels (Nakićenović & Swart 2000). Climate projections from the HADCM3 are close to the mean for the IPCC 4th Assessment Report; HADCM3 values for equilibrium climate sensitivity and transient climate response were within 0.14 and 0.65 standard deviation units of the overall means calculated for the 23 complementary general circulation models (using data in Table 8.2 of Randall *et al.* 2007). More recent projections underpinning the IPCC 5th Assessment Report reveal patterns of projected climate change similar to those of the 4th Assessment when taking into account differences among climate change scenarios (IPCC 2013). Thus, the direction and magnitude of climate change used here seems to be robust in relation to recent developments in climate modelling, while the pathway of climate change (the extent of greenhouse gas emissions) represents an upper boundary but not the extreme case for conservation planning. Analogue 2080s climates were located for the continental target sites, at southerly distributed sites in Britain. However, the best analogues for rainforest sites were locally positioned within their same region despite the effects of climate change. Thus, the climatic comparison between baseline and 2080s analogues was less well matched for the rainforest system (Group I), compared to the continental system (Group II) where analogues could be located at distance within present European climate space.

The study was focussed on the practical implications of climate change, as this relates to the distribution of protected habitat for epiphytes. Consequently, the space-for-time matching did not examine all pairwise 1 km grid squares across Europe, and so it is not possible to definitively state an absence of 2080 analogues within all of European climate space, for Scotland's rainforest. However, the study did focus on a very broad geographic subsample of forest sites across Europe, including oceanic but relatively warmer sites in Wales and southwest England, and especially along the Atlantic coastlines of northern France, Spain, and Portugal. The forest sites included in the analysis are therefore among the most relevant in terms of epiphyte conservation and its strategic planning for climate change.

The study was also based on the assumption that a standardised set of climate data with sufficient European breadth, that is, derived from WorldClim's data resource (Hijmans *et al.* 2005), provides a robust proxy for the baseline climate (Figure 4), as well as capturing the direction and magnitude of climate change. For oceanic rainforest sites, the absolute values for precipitation derived from WorldClim were on average lower than local interpolated estimates by the UK's Met Office (Perry & Hollis 2005); the mean annual precipitation for oceanic rainforest sites in WorldClim was 1764 ± 98 mm, compared to equivalent Met Office estimates of 2138 ± 554 mm. The higher mean precipitation and large standard deviation for the Met Office figures is explained by a single very large difference for the oceanic-montane Coille Coire Chuilc site, which has an estimated baseline annual precipitation of 1863 mm in WorldClim and 3163 mm using Met Office data. Deviation in precipitation values is an acknowledged problem for WorldClim, in global regions with high precipitation (Hijmans *et al.* 2005), and the difference observed here is also consistent with a known WorldClim error rate for mountainous regions. Nevertheless, the WorldClim derived values do correlate significantly with Met Office values for oceanic sites (Pearson's product-moment $r = 0.838$, $P < .01$ with 6 df). For the more continental sites, estimates of precipitation were more similar between WorldClim (1069 ± 201 mm) and Met Office values ($1150 \pm$

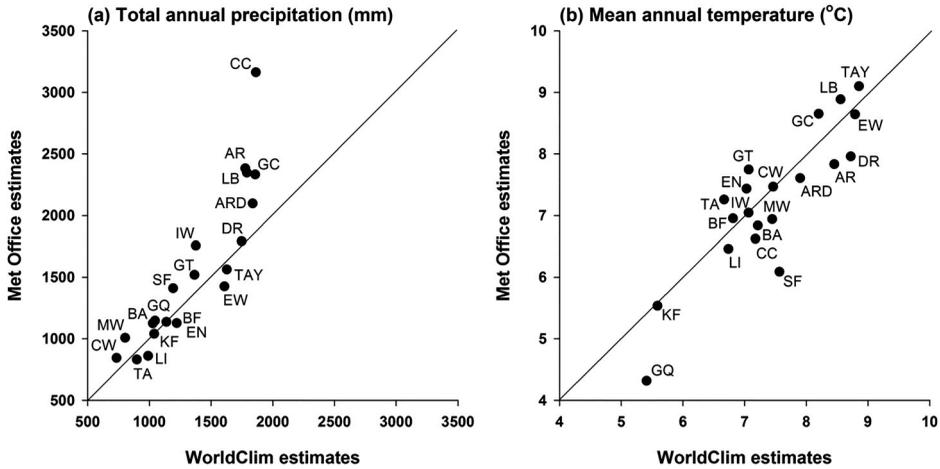


Figure 4 Comparison of estimated baseline climate values from the WorldClim project (1960–2000), with equivalent values derived from spatial interpolation by the UK's Met Office (1961–2006). Deviation away from the line of equity highlights the potential for regional underestimates of precipitation in areas with the highest values (panel (a)).

283 mm), again with a significant correlation ($r=0.868$, $P < .001$ with 10 df). Overall, the WorldClim values were consistent with the longitudinal oceanic-continental gradient across Scotland (Jenkins *et al.* 2008). The temporal pathway of climate change projected by HADCM3 and statistically downscaled in the WorldClim resource matched with a consensus for consistent warming in Scotland through the twenty-first century (Werritty & Sugden 2012).

For ten of the target sites located in a more continental 'non-rainforest' climatic zone, suitable analogues for 2080s climate were located in Wales and southern England. This is consistent with the results of previous bioclimatic modelling (Ellis *et al.* 2007, 2014, 2015a), which has highlighted a climate change risk posed to epiphytes with distributions centred in north-eastern Scotland, for example, *Cetraria sepincola*, and the projected expansion of suitable bioclimatic space for southern elements of the British flora northwards into Scotland, for example, *Cresponia premnea*, or *Punctelia borerri*. The use of space-for-time matching suggests that – under high greenhouse gas emissions through to the 2080s – the approximate distance required for locally adapted populations to track analogue climate space would be an average of 508 km. This equates to c. 60 km per decade. In the context of conservation practice; first, this result raises the question as to whether suitable 'stepping-stone' habitats will be available within Britain's fragmented woodland landscape (Lawton 2010; Gimona *et al.* 2012), and especially within the protected site network, to facilitate species migration to track climate change (Travis 2003). It has been shown that epiphytic species may be dispersal-limited over the distances and time-scales considered here (Sillett *et al.* 2000; Öckinger *et al.* 2005). Second, even if suitable habitat was configured for effective migration, the trajectory of analogue climates intersects severely polluted environments in midland and northern England, and the Scottish central belt, which would make ostensibly suitable habitat unavailable for stepping-stone colonisation (Ellis & Coppins 2010).

These results for the more continental target sites contrast with the situation for rainforest sites, which have their 2080s analogues located over short distances within the baseline rainforest zone. This is consistent with two observations from previous bioclimatic modelling. First, bioclimatic models have suggested that the future climatic conditions of western Scotland may strengthen the occurrence of oceanic temperate rainforest epiphytes (Ellis & Coppins 2007; Ellis 2014), assuming greater warmth with consistent wetness (Jenkins *et al.* 2010). This receives support from the observation that oceanic species are either representatives of genera that have tropical affinities and may be cold-sensitive (e.g. *Hypotrachyna*, or *Pyrenula* species), or include nitrogen-fixing cyanolichens requiring liquid water for photosynthetic activation (Lange *et al.* 1986, 1993) and which may benefit from increased rates of nitrogen-fixation in a warmer environment (Antoine 2004). Second, bioclimatic models have highlighted a surprising degree of local variability in the projected response of epiphytes to climate change over relatively small scales (Ellis 2014), explained partly by the complex topography of western Scotland. This is consistent with the more general notion that analogue climate space may be located over shorter distances in topographically heterogeneous landscapes (Loarie *et al.* 2009). Nevertheless, the results presented here do highlight key uncertainties inherent with the problem of non-analogue climates, and in particular the extrapolation from baselines into novel areas of climate space without adequate reference points (Williams & Jackson 2007; Fitzpatrick & Hargrove 2009). This places a demand on the improved verification of species response. Given climatically controlled growth for certain epiphytes (Larsson & Gauslaa 2011; Merinero *et al.* 2015), coupled with the observation that experimental growth rates can be projected onto macroclimatic surfaces to explain large-scale species distribution patterns (Eaton & Ellis 2012), experiments could be used to characterise a species' functional response (e.g. growth rates) to simulated novel climates. Additionally, seasonal transitions, such as wetter winters and drier summers (Jenkins *et al.* 2010; Werritty & Sugden 2012), may interact with annual cycles of solar insolation (Reu *et al.* 2014) to shift the balance of photosynthesis and respiration (Cabrajic 2009), and affecting ecological fitness in ways that cannot be characterised through the analysis of annual average values within existing European climate space.

In summary, this study has highlighted a need for contrasting regional strategies in the response to climate change. The response for a majority of species in Scotland's more continental non-rainforest sites might be conceptualised as the shift between local extinctions and colonisations in a spatially dynamic metapopulation (Mustin *et al.* 2009; Hodgson *et al.* 2012). Ultimately there may be weakened metapopulation viability for species (Hanski *et al.* 1996) where climate becomes less suitable and population sizes decline across their entire current range (north-eastern 'continental' species), with shifted latitudinal distributions for others (southern species). The species at risk of decline may be protected by efforts to improve local habitat quality and increase population sizes. For species undergoing migration to track changing climate space, there can be clearly defined landscape-scale planning in which dispersal is linked across multiple suitable sites among regions. This brings into focus a conflicted use of resources, either in attempting to conserve threatened species in a region such as north-eastern Scotland, or to encourage turnover in community composition, through landscape management that facilitates the arrival of southerly distributed species. For a majority of rainforest epiphytes in western Scotland the existing baseline sites may represent their entire suitable habitat resource now and possibly into the future. However, to hedge against uncertainty given the future non-analogue status of the rainforest environment, it would be judicious to increase the extent and quality of sites

within this core region, rather than planning for large-scale distributional shifts. The conclusion is that climate change will demand flexible national conservation strategies, depending ultimately on the interaction of a species' biology with regional pathways of future climate change. However, prioritising the delivery of these alternative strategies depends on the balance between values placed on nature – contrasting, for example, internationally important rainforest epiphytes with nationally important species in continental north-eastern Scotland (that also occur more extensively in Scandinavia) – and current confidence in the degree of risk, which appears high for species restricted to continental north-eastern Scotland but is more equivocal for Scotland's internationally important rainforest epiphytes.

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