Ancient woodland indicators signal the climate change risk for dispersal-limited species

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ABSTRACT

The climate change risk to biodiversity operates alongside a range of anthropogenic pressures. These include habitat loss and fragmentation, which may prevent species from migrating between isolated habitat patches in order to track their suitable climate space. Predictive modelling has advanced in scope and complexity to integrate: (i) projected shifts in climate suitability, with (ii) spatial patterns of landscape habitat quality and rates of dispersal. This improved ecological realism is suited to data-rich model species, though its broader generalisation comes with accumulated uncertainties, *e.g.* incomplete knowledge of species response to variable habitat quality, parameterisation of dispersal kernels *etc*. This study adopts ancient woodland indicator species (lichen epiphytes) as a guild that couples relative simplicity with biological rigour. Subjectively-assigned indicator species were statistically tested against a binary habitat map of woodlands of known continuity (>250 yr), and bioclimatic models were used to demonstrate trends in their increased/decreased environmental suitability under conditions of 'no dispersal'. Given the expectation of rapid climate change on ecological time-scales, no dispersal for ancient woodland indicators becomes a plausible assumption. The risk to ancient woodland indicators is spatially structured (greater in a relative continental compared to an oceanic climatic zone), though regional differences are weakened by significant variation (within regions) in woodland extent. As a corollary, ancient woodland indicators that are sensitive to projected climate change scenarios may be excellent targets for monitoring climate change impacts for biodiversity at a site-scale, including the outcome of strategic habitat management (climate change adaptation) designed to offset risk for dispersal-limited species.

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1. Introduction

Recent reviews have suggested that the magnitude and velocity of global climate change during the 21st Century will be unprecedented on palaeoecological time-scales encompassing the Quaternary (Moritz and Agudo, 2013) and Cenozoic (Diffenbaugh and Field, 2013), respectively. An emerging climate change threat to biodiversity acts in combination with an amalgam of anthropogenic pressures (Sala et al., 2000). In particular, this includes habitat loss and fragmentation, which can reduce the likelihood of a species migrating between isolated habitat patches, in order to track suitable climate space (Travis, 2003); local populations may be extirpated *in situ*, increasing the overall risk of extinction.

Given that habitat loss/fragmentation and a species' dispersal capacity are key parameters in determining climate change risk, conservation research has attempted to couple these factors within bioclimatic models (sometimes referred in more general terms as species distribution models, or SDMs). Predictive bioclimatic modelling quantifies the constraints to a species' 'realised' climatic space for a baseline environment, comparing these constraints to climate change scenarios in order to project the shift in suitable climate space for a future period (Pearson and Dawson, 2003; Peterson et al., 2011). Various methods have been applied to more closely approximate the real-world implications of climate change, though with a requirement to overcome two problems: (i) accurately mapping the spatial configuration of suitable habitat across a landscape, and (ii) achieving a dynamic range-shifting model by incorporating the dispersal rates of a species. These parameters (habitat patterns and dispersal rates) have been presented with various degrees of accuracy, and either in isolation or combination. For example, shifting from simplistic to more complex approaches, and focussing on trees as a common functional guild for comparing between models: (i) bioclimatic-controlled range-shifts have been used to estimate patterns of loss/gain in tree species occurrence at large-scales (50 × 50 km grids), under the outer boundaries of no or unlimited dispersal (Thuiller et al., 2006), (ii) generic differences in

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habitat quality (*e.g.* proportion forested area at 1 km^2) have been coupled with a continuum of dispersal kernels, though which were not species-specific, to test an average migration response of trees to climate change scenarios (Iverson et al., 2004), (iii) individual tree species have been characterised according to their specific life-history traits, *e.g.* competition for light, and dispersal parameters (*e.g.* competition-colonisation trade-off), and a dynamic forest response simulated under baseline and climate change scenarios to predict migration rates and distributions of contrasting species given a known habitat structure (Meier et al., 2012). As exemplified here, bioclimatic modelling is transitioning from correlative towards more process-orientated mechanistic models (Ellis, 2011), which incorporate physiology, population demographics including interspecific interactions, and meta-population dynamics (Huntley et al., 2010; Mokany and Ferrier, 2011). However, this ecological realism comes with a requirement for well characterised systems, currently achievable for only a limited suite of biodiversity as model species, such as butterflies (Wilson et al., 2010), and/or deeply nested sets of assumptions which leads to extremely high model complexity (*cf.* Bugmann and Cramer, 1998; Lischke et al., 2006; Meier et al., 2012).

This paper presents bioclimatic modelling for lichen epiphytes which are ancient woodland indicator species, a system which can combine simplicity of approach with ecological realism. The indicators used are forest/woodland species which because of both niche-specialism, and limited dispersal or establishment, are proposed to be restricted in the landscape to sites with long periods of habitat continuity. On this basis, the distribution of potential habitat can be reasonably well characterised (ancient woodland), and the advantage of an easy to parameterise boundary of no dispersal becomes a plausible biological assumption across many species, given projections of rapid climate change at ecological time-scales (Diffenbaugh and Field, 2013; Moritz and Agudo, 2013). Ancient woodland indicators thus combine both relative simplicity and biological rigour when dealing with dispersal to track suitable climate space. Coupled with bioclimatic modelling to examine spatial patterns of threat, ancient woodland indicator species are shown to be excellent indicators of climatic risk for dispersal-limited forest/woodland species more broadly, and may be useful in gauging the effectiveness of direct actions to moderate such risk.

2. Materials and methods

For datasets made available at different resolutions and for alternative cartographic projections, spatial matching used ArcGIS v. 10.1 (ESRI, 2012) and R (R Development Core Team, 2013) for data aggregation and compatibility within ArcMap.

2.1. Identification of ancient woodland indicators

A proposed list of lichen epiphyte indicators of woodland ecological continuity for Britain has been published by Coppins and Coppins (2002), based on field experience combined with archival studies of woodland history, and building on earlier work by Rose (1974, 1976). These indicators are partitioned into biogeographic regions, with the focus for this study being a relatively clean-air region of northern Britain, and including therefore a western category encompassing both the 'West of Scotland Index of Ecological Continuity' (WSIEC) and the 'Eu-Oceanic Calcifuge Index of Ecological Continuity' (EUOCIEC), contrasted with an eastern category, referred to as the 'East of Scotland Index of Ecological Continuity' (ESIEC). A number of putative indicator species are relevant to both the western and eastern categories, *e.g. Lopadium disciforme, Nephroma parile.*

Given the expert-led though subjective nature of the proposed indicator lists, the selection of lichen species was refined in two ways, both of which utilise the UK's ancient woodland inventory (Roberts et al., 1992; Walker and Kirby, 1987). The hypothesis was that indicator species applied within their regional context should show a significant association with Class 1 ancient woodlands (sites which have existed in the landscape ≥250 yr) if they are constrained by two defining elements of ecological continuity (Whittet and Ellis, 2013): (i) microhabitat specialisation towards structures associated with old woodland stands, and (ii) long-term persistence of these microhabitats within a site, across multiple generations of trees. Acknowledging that not all Class 1 sites will retain these combined features, logically, it is only from among the Class 1 ancient woodland resource that the co-occurrence of these features can be drawn (Whittet and Ellis, 2013).

First, we adopted indicator species whose confirmed presences from field inventory data had previously been shown to be significantly skewed towards Class 1 ancient woodland sites within their appropriate biogeographic context, when accounting for spatial sampling bias among recorders (Whittet and Ellis, 2013).

Second, we applied field recorded inventory data for 84 isolated woodland sites which had formerly been surveyed by an expert lichenologist (see Ellis et al., 2009, for site details), recording a total of 554 epiphyte species. Surveyed sites were isolated woodlands within a single continuity category, and therefore scored exclusively as either Class 1 ancient woodland (>250 yr continuity), or more recently regenerated sites. To accommodate species relevant to contrasting biogeographic categories, we divided Scotland into two regions with a boundary corresponding broadly to the limits of the WSIEC and EUOCIEC in western Scotland, and the ESIEC in eastern Scotland (Fig. 1). The western region was delimited using the 'temperate rainforest' bioclimatic zone, adopting climatic thresholds defined by Alaback (1991): (i) annual precipitation >1400 mm, (ii) 10% of annual precipitation during the summer, and (iii) a mean July isotherm <16 °C. The eastern region accommodated the remaining woodlands outside the temperate rainforest boundary. Indicator species analysis (Dufrêne and Legendre, 1997) was performed separately for sites falling within each of these regions, in order to account for species that are common across woodlands in one region (*e.g.* in western Scotland), though which become significant indicator species in a climatically contrasting biogeographic region (Coppins and Coppins, 2002). Analysis was implemented in PC-ORD v. 6 (McCune and Mefford, 2011), with species significance estimated using a permutation test with 10,000 randomisations.

2.2. Baseline bioclimatic modelling

Baseline distributional data for the statistically significant indicator epiphytes (1961–2010) was sampled from across the British Isles at a 10 km grid-scale, using the British Lichen Society Database which at the time of analysis included >1.2 million individual records (Simkin, 2012).

Species distributions were compared to baseline climate, pollution and landscape habitat variables. Climatic values for the period 1961–2006 were derived from gridded datasets interpolated by the UK Met Office at a 5 km resolution (Perry and Hollis, 2005). To avoid statistical problems of high spatial autocorrelation within our study regions (Ellis and Coppins, 2009, 2010) a subset of variables was used to represent multivariate climate space: (i) annual precipitation (mm), (ii) summer precipitation (mm), (iii) winter precipitation (mm), (iv) mean annual temperature (°C), and (v) mean temperature of the coldest month (°C). Pollution data were made available at a 5 km scale by the Centre for Ecology and Hydrology (RoTAP, 2012): total deposition for (i) acidity (keq ha^{-1} yr^{-1}), (ii) nitrogen (kg N ha^{-1} yr^{-1}), (iii) reduced nitrogen, NH$_x$ (kg N ha^{-1} yr^{-1}), (iv) oxidised nitrogen, NO$_x$ (kg N ha^{-1} yr^{-1}),