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Quantifying the role of multiple landscape-scale drivers controlling epiphyte composition and richness in a conservation priority habitat (juniper scrub)

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ABSTRACT

Recent concern over human-induced climate warming has activated bioclimatic research projecting the species-response to climate change scenarios. However, climate change is one of a range of human-induced environmental drivers controlling biodiversity, and for many species should be considered together within a framework of relevant stresses and threats. This paper critically assesses the sensitivity of epiphyte assemblages to regional gradients in climate, pollution regime and landscape-scale habitat structure (woodland extent and fragmentation). We examine lichen epiphytes associated with juniper scrub (a conservation priority habitat in Europe), sampled across a network of protected sites in Britain (Special Areas of Conservation). Results point to significant differences in associated epiphyte diversity between conservation priority sites. Historic woodland structure was identified as of greater importance than present-day woodland structure in controlling species composition and richness, pointing to an extinction debt among lichen epiphytes. Climatic setting was important in controlling species composition, but not species richness. However, we demonstrate that pollution regime exerts the dominant controlling force for epiphyte assemblages across regional gradients. As a corollary, we caution that for many species groups – for example those sensitive to pollutants, or landscape structure – an exclusive focus on climate is restricting, and that climate change models should expand to include a range of multiple interacting factors.

1. Introduction

The emergence of human-induced climate change as a threat to biodiversity (Root et al., 2003; Rosenzweig et al., 2008) adds further ecological complexity to an existing framework of anthropogenic stresses, e.g. pollution impacts and habitat loss or degradation. Bioclimatic studies have typically focussed on the predictive species-response to climate change scenarios (Thuiller et al., 2005; Araújo and New, 2006). However, for many species groups, the effect of climate should be considered together with additional factors known to control large-scale patterns in assemblage composition and diversity (cf. Pearson et al., 2004; Ellis and Coppins, 2007a; Ellis et al., 2009). The pollution regime resulting from industrial processes is one of the most powerful biodiversity drivers (McNeely, 1992), and, through fluid spatial pathways (transport by water, or air), may operate at a scale comparable with regional climate. Similarly, the effects of habitat loss and fragmentation have direct consequences for species' landscape-scale distributions (Pullan, 2002). For many organisms, their climatic sensitivity should be integrated with sensitivity to the pollution regime and the impact of changed habitat, aiming to provide a quantitative assessment of multiple threats. In contrast to the large number of studies which have focussed on the effects of individual drivers of biodiversity change (e.g. climate, pollution or habitat loss), studies to critically assess the relative sensitivity of species to a combination of known landscape-scale drivers are surprisingly rare. In order to assess the role of three key biodiversity drivers – climate, pollution and habitat modification – this paper examines spatial patterns of lichen epiphyte diversity and composition, aiming to partition the epiphyte response to regional trends in climatic setting, pollution regime and habitat structure.

Lichen epiphytes contribute importantly to forest biodiversity and ecosystem function (Dietrich and Scheidegger, 1997; Cornelissen et al., 2007). Lichens (as with mosses and liverworts) are poikilohydric organisms, responding directly to ambient climatic conditions, and there is growing concern over the potential impact on lichens of human-induced climate change. A comprehensive understanding of the climatic-response of lichens is problematic because of their additional sensitivity to a wide range of the most common pollutants (Van Dobben et al., 2001). Lichens have been used accordingly as a bioindicator for a variety of pollutants, including SO_2 (Hawksworth and Rose, 1970) and nitrogen (Van Herk, 1999; Van Herk et al., 2003). Pollution indices have, in their turn, been criticised for neglecting to account for 'natural' under-lying

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differences between lichen assemblages in response to climatic sensitivity over relatively small spatial-scales (Ellis and Coppins, 2006). Imposed on the lichen response to climatic variation and pollution regime is sensitivity to the under-lying habitat structure (e.g. extent and fragmentation). Habitat structure impacts epiphyte assemblages through meta-population dynamics (dispersal/colonisation likelihood into available patches: Gu et al., 2001; Löbel et al., 2006a), as well as controlling the habitat availability for specialist species through increased heterogeneity in more extensive woodland stands (Gignac and Dale, 2005). The importance of climate, pollution and habitat quality in controlling lichen assemblages is symptomatic of a key issue in conservation; for many species, potentially confounded relationships between climate, pollutants and landscape-scale habitat have yet to be adequately resolved.

This paper describes epiphytes associated with juniper scrub (*Juniperus communis* L.) in mainland Britain. Juniper has suffered a long-term decline in the British Isles and on the European mainland (Preston et al., 2002; Braithwaite et al., 2006), is classified as a priority species in the UK's Biodiversity Action Plan (UK BAP, 1999), and is a dominant component in several Annex I habitats comprising the European Habitats Directive (McLeod et al., 2005). The British Isles are characterised by steep climatic gradients, ranging from the hyper-oceanic north and west, to the more continental east and south-east (Perry and Hollis, 2005). British biodiversity has suffered widely from severe exposure to industrial pollution over a period of centuries (Mallanby, 1967; Woodin, 1989; Coppins et al., 2001), and British woodland habitats have undergone long-term modification over centuries and millennia (Birks, 1988). The British scenario thus provides an opportunity to examine the extent to which a key group in terms of biodiversity conservation (lichens) varies between conservation sites which have been designated for a higher-level feature (i.e. the juniper on which the lichen epiphytes occur). Using partial-redundancy analysis, variation in epiphyte diversity and composition was partitioned for conservation priority sites into components explained specifically by climate, pollution regime and habitat extent and fragmentation. Our results provide a novel quantification of sensitivity to multiple landscape-scale drivers, for species occupying a habitat of significant conservation concern.

2. Methods

Areas of juniper scrub were sampled from across Britain to reflect potential biogeographic variability in their lichen epiphytes (Fig. 1). The majority of stands examined (18 out of 26 sites) have been designated as Special Areas of Conservation (SACs) within the European Habitats Directive (McLeod et al., 2005). A focus on SACs enabled an assessment of epiphyte variability within the conservation network; however, additional juniper sites were selected to increase resolution when examining between-site variation in epiphyte assemblages. Additional sites lying outwith the conservation network were selected as among the most important in terms of their national status, from the published literature (cf. Ward, 1973) and by canvassing expert opinion (e.g. Mr Douglas McKean (RBGE), pers comm.). Sites were visited between June 2005 and July 2006. All lichen epiphytes associated with juniper were inventoried: lichen species which could not be determined in the field were returned to RBGE for herbarium examination using standard light microscopy with chemical spot tests, and thin layer chromatography (Orange et al., 2001).

2.1. Climatic setting

Climate data for each of the juniper study sites was derived from UK Met Office modelled data at a 5-km grid-square scale (Perry and Hollis, 2005): estimated monthly and annual climatic averages for average, maximum and minimum monthly temperatures (°C) and precipitation (mm). Estimated climate data are the verified averages derived for 5 km grid-squares based on point data for the period 1961–2000 at 540 and 4,400 monitoring stations across Britain (temperature and precipitation, respectively). A suite of 13 climatic variables was calculated for individual 5 km grid-squares corresponding to juniper study sites: 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. Climatic variation compared between sampled juniper sites was summarised using principal components analysis, PCA (CANOCO v. 4.5: ter Braak and Šmilauer, 2002). Climate data were standardised and centred to equalise variables measured on different scales (Lepš and Šmilauer, 2003). Climatic indices were used as a proxy for site-by-site climatic differences. Four climatic indices were tested, and their explanatory power quantified as R^2 and significance (P) when compared to orthogonal PCA axes: (i) Lang's 'rain factor', RF = P/T, (ii) de Martonne's 'humidity index', HI = P/[T + 10], (iii) Dantin & Ravenga's 'aridity index', AI = [100.T]/P, and (iv) Amann's 'hygrothermy', Hy = $[P_{cm}.T]/[t_H - t_C]$ (cf. Seaward, 1975; Tuhkanen, 1980). Where P is annual precipitation in mm (or cm, P_{cm}), T is annual mean temperature (°C), t_H is mean temperature during the warmest month, and t_C is mean temperature during the coldest month. Selection of an appropriate index sought (i) to maximise cumulative R^2 when compared against ordination axes, and (ii) to minimise the difference in % variation explained, compared between orthogonal PCA axes and equivalent R^2 values.

2.2. Woodland structure

Local woodland surrounding each juniper study site was quantified for two time-periods: modern and historic. The extent and fragmentation of modern woodland was estimated for the period 1994–2004, based on Editions B & C of the Ordnance Survey's 1:50,000 'Landranger' map series and for historic woodland over a period during the 19th Century (1869–1886) based on the Ordnance Survey's First (1-in.) Series. Positioning each juniper stand as a central node, woodland extent and fragmentation were estimated at two scales (1 km^2 or 4 km^2), for the modern and historic landscape, according to methods previously described by Ellis and Coppins (2007b). Areas of juniper scrub cannot be exclusively identified on modern or historic maps, and 'local woodland' included all native broadleaf, mixed and pinewood (with or without juniper), though excluded commercial plantations of non-native trees.

2.3. Pollution regime

The environmental loading of key pollutants was derived using modelled values at a 1 ha scale, using model output specifically applicable to woodland and hedgerow habitats (NEGTAP, 2001; cf. www.apis.ac.uk): SO_2 (μg m^3), acid deposition (keq ha^{-1} yr^{-1}), nitrogen deposition (kgN ha^{-1} yr^{-1}), ammonia (μg m^3), nitrogen oxides (μg m^3) and ozone (ppb h, accumulated as a threshold >40 ppb, or AOT40). The pollution regime compared between sampled juniper sites was summarised using PCA (CANOCO v. 4.5). Pollution data were log-transformed prior to analysis, and data were standardised and centred (Lepš and Šmilauer, 2003).

2.4. Statistical analysis

In an exploratory constrained ordination (including all explanatory factors), the species composition of samples (study sites) was analysed using detrended canonical correspondence analysis (DCCA). Species turnover, measured as the gradient length, was less than three units (2.984 for axis one, $F = 1.282$, $P = 0.0034$)