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Conservation of the rare British lichen *Vulpicida pinastri*: changing climate, habitat loss and strategies for mitigation

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Abstract: Autecological information targeted towards rare and threatened lichen species is severely lacking. This study adopts the rare British lichen *Vulpicida pinastri* as a case study species and examines its ecological response to emerging threats: climate change and the recurrent loss of its primary habitat (juniper scrub). We used predictive niche modelling to examine the response of *V. pinastri* to a range of present-day climatic variables. A successful model was projected for a period during the 2050s based on IPCC climate change scenarios (UKCIP02 data), and threat was estimated as the proportional change in bioclimatic space. To estimate the potential range now and during the 2050s, projected bioclimatic space was masked by a habitat map equivalent to (i) the present-day distribution of juniper and (ii) theoretical juniper distribution based on existing rates of decline. Our results point to potential range loss of *V. pinastri* with climate warming, exacerbated by the recurrent decline in juniper habitat. This predictive modelling approach was complemented by an assessment of local stand-scale effects. At four sites in north-east Scotland we examined the occurrence and abundance of *V. pinastri* thalli, in response to juniper spatial distribution, and the life-stage and structure of individual shrubs. *Vulpicida pinastri* appeared to be dispersal limited at small-scales, and was significantly more abundant on old and degenerate juniper shrubs. Our results evidence a close relationship between management for habitat quality and effective lichen conservation. Effective conservation of *V. pinastri* must ensure cohorts of older and degenerate juniper shrubs are maintained at sites where the species is expected to be most resistant to long-term climate warming, i.e. in the uplands of north-east Scotland.

Key words: bioclimatic response, *Juniperus communis*, niche-modelling, nonparametric multiplicative regression, UKCIP02.

Introduction

Lichenized fungi are one of Britain's most important contributions to international biodiversity. The British lichen flora is estimated to include >45% of European lichen species (*cf.* Mackey *et al.* 2001; Coppins 2002) rendering lichens a key group in UK conservation (Coppins 2003). Lichen cultivation is poorly researched and notoriously difficult (Gilbert 1977; Bando & Sugino 1995), and the protection of lichen species is thus limited by the unreliability of *ex situ* conservation. Therefore, protection of threatened lichen species is necessarily *in situ*, based on ecologically informed management strategies which aim to ensure the long-term persistence of a suitable habitat regime within the British landscape (Gilbert 1977; Fletcher 2001). While this is sound in principle, in practice ecological information is often severely lacking, and conservation strategies too often rely on guesswork (Coppins 2003). To meet the need for greater autecological information this paper presents a scientific framework for the conservation of a rare British lichen species, *Vulpicida pinastri* (Scop.) Gray (synonym *Cetraria pinastri* (Scop.) Gray). The research described exemplifies ecological analyses targeted towards key threats: climate change and the recurrent loss of primary habitat.

Vulpicida pinastri is distributed widely in Eurasia and North America (Mattsson 1993; Randlane & Saag 2005), though it is

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rare and locally restricted in the British Isles (Fig. 1; Purvis *et al.* 1992). British populations of *V. pinastri* occur towards the edge of the species' biogeographic range, in a setting that is relatively more temperate and oceanic, compared to its circumboreal-montane distribution in continental Eurasia and America (Mattsson 1993; Randlane & Saag 2005). Accordingly, populations of *V. pinastri* at its distributional range-edge in Britain may be constrained by a scarcity of suitable habitat (Brown 1995) as establishment and growth become restricted to a reduced suite of favourable localities in a climatically marginal area (Lennon *et al.* 2002; Lidén & Hilmo 2005). These range-edge populations are important for a variety of reasons:

1. They cross a major political and biogeographic boundary into the UK, rendering the species of significant national concern; the species is considered 'Near Threatened' in the UK according to recent IUCN assessment (Woods & Coppins 2003).
2. The range-edge populations of *V. pinastri* may provide an early indication of large-scale climate warming impacts. In common with the rapid response of other species at distributional boundaries (Grabherr *et al.* 1994; Parmesan & Yohe 2003), studies in continental Europe have indicated a decrease in boreal-montane lichens from marginal sites towards the south of their biogeographic range (possibly including *V. pinastri*: Mattsson *et al.* 2006), and a northward migration of sub-tropical species (van Herk *et al.* 2002).
3. Range-edge populations may tend to be rare and relatively more isolated (Brown 1995), providing a model system for investigating ecological processes underlying the causes of rarity. Thus, in contrast to its wide-spread occurrence on various acidic substrata in boreal and montane Europe (e.g. the bark of *Abies*, *Betula*, *Picea* and *Pinus*, and, less frequently, siliceous rocks and soil: Randlane & Saag 2005), the abundance of *V. pinastri* in Britain is predominantly associated with extensive stands of juniper (*Juniperus communis* L.), for example in north-east Scotland and in Teesdale, where it grows as an epiphyte. Large areas of juniper provide the habitat for the majority of *V. pinastri*'s British populations, including its only large populations (Fig. 1; Fryday 2006), with only rare and fewer thalli recorded elsewhere and on different substrata. Thus, the putative vulnerability of Britain's range-edge population of *V. pinastri*, for example to climate change or pollution effects, may be exacerbated by the continuing wide-spread decline of juniper (Preston *et al.* 2002; Braithwaite *et al.* 2006), itself a priority species in the UK's Biodiversity Action Plan (UK BAP, 1999) and a dominant component in several Annex I habitats comprising the EC Habitats Directive (McLeod *et al.* 2005).

This paper adopts *V. pinastri* as a case-study species. It represents a wider suite of boreal-montane lichens, which reach an oceanic-temperate range boundary in Britain (Fryday 2006), are expected to respond to rapid climate warming (van Herk *et al.* 2002) and which are simultaneously threatened by the historic and recurrent loss of local habitat (Gilbert 1977; Coppins *et al.* 2001). Accordingly, we ask questions targeted at two scales:

1. How might *V. pinastri* respond to changing climate, and how might this response be modified by an apparent dependence upon the occurrence of juniper?
2. How can stands of juniper be managed effectively to provide an appropriate habitat at sites where populations of *V. pinastri* may be most resistant to climate change?

Materials and Methods

Distribution maps

Modern records (post-1960) were derived from the British Lichen Society mapping scheme, from unpublished records entered into the SNH-funded Scottish

Lichen Database (B. J. Coppins, pers. comm.) and from personal communication with expert field operatives (e.g. A. Britton, MLURI; B. J. Coppins, RBGE; J. Douglass, independent consultant; S. Taylor, RSPB). Records were plotted as the confirmed presence of *V. pinastri* within a 10 km grid-square.

Modelled response to pollution and climate

We first tested for autocorrelation in the spatial distribution of *V. pinastri* (number of independent records per 10 km square) using a weighted Moran's I statistic (Moran 1950), implemented using the program Crimestat v. III (Levine & Associates 2004). Significance of spatial autocorrelation was assessed against a Monte Carlo simulation with 1000 runs to calculate confidence intervals.

Second, the confirmed presence of *V. pinastri* in 10 km grid-squares ($n=17$) was matched by pseudo-absences (*cf.* Zaniewski *et al.* 2002) randomly generated for an equivalent number of grid-squares ($n=34$). The climatic response of *V. pinastri* was examined by comparing presence and pseudo-absences to climate data provided as UK Meteorological Office gridded datasets (Perry & Hollis 2005): estimated monthly averages for (i) temperature (°C) and (ii) precipitation (mm). These estimated climate data are the verified averages derived for 5 km grid-squares, based on point records for the period 1961–2000 at 540 and 4400 monitoring stations across the British Isles (temperature and precipitation, respectively). Base-line data were used in an unmodified form to construct a suite of 13 climatic variables, 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. Distribution data plotted at a 10 km scale (mapping squares) were matched to climatic data for 5 km grid-squares which occurred centrally within their equivalent 10 km mapping square. The response of *V. pinastri* to pollutant loads was examined by comparing presence and pseudo-absences to mean values of wet deposited SO_4^{2-}, NO_3^{-} and NH_4^{+} (1997 modelled values derived from maps at a 10 km grid-square scale produced by NEGTAP 2001). Values for individual pollutants were compared between grid-squares with confirmed presences of *V. pinastri* versus randomly generated pseudo-absences, using a Mann-Whitney U-test (Genstat v. 7.1 2003: VSN International Ltd., Oxford, UK).

The response of *V. pinastri* (confirmed presences and randomly generate pseudo-absences) was compared to a matrix of explanatory variables (climatic variables and pollutant loads together), using the program Hyperniche v. 1beta (McCune & Mefford 2004) to implement nonparametric multiplicative regression (McCune 2006). Predictive response models were constructed using a local mean with Gaussian weighting (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. Model quality was assessed as the Bayes factor (logB), used to express model improvement over a 'naïve' model, and using a 'leave-one-out' strategy of cross-validation to prevent over-fitting (McCune & Mefford 2004; McCune 2006). The optimum selected model was assessed using a Monte Carlo randomization test, with 1000 runs to evaluate model fit, and assuming an equivalent number of explanatory variables.

The utility of the optimum model was assessed by comparing presence or pseudo-absence to the predicted likelihood of occurrence of *V. pinastri* calculated for a given grid-square (x), though based on an estimated likelihood value using $N-x$ grid-squares as model input. Predicted likelihood values (based on $N-x$) were compared to the 'independent observed values' (confirmed presence or pseudo-absence in x) as the area under the receiver operating curve (abbreviated to AUC: Swets 1988; Pearce & Ferrier 2000). This measure assesses model utility by comparing predicted and observed values, is independent of species prevalence within a sample (Pearce & Ferrier 2000) and is widely accepted as an appropriate diagnostic measure for the discrimination ability of predictive models, though subject to caveats outlined by Araújo *et al.* (2005).

Projected distribution

The climate-response model was used to predict the likelihood of occurrence of *V. pinastri* (Lv) for 10 km grid-squares across the British Isles. However, model application was limited to grid-squares whose input data satisfied the minimum threshold for an acceptable model ($=n^{*}0{\cdot}05$; McCune 2006). The projection of species data was therefore constrained to grid-squares whose climate was within a limit set by the data-range used to generate the predictive model, preventing erroneous application of the model beyond the boundaries of the calibration dataset. This is particularly important since the model was constructed using data restricted to the species' known extent in Britain, which represents a sub-set of *V. pinastri*'s world-wide range (*cf.* Thuiller *et al.* 2004; Randin *et al.* 2006).

A threshold value in likelihood of occurrence (Lv_{thr}), above which *V. pinastri* is more likely to be present than absent (and below which it is more likely to be absent than present), was identified by maximizing the sum of model sensitivity and specificity (Manel *et al.* 2001). Projected distribution of *V. pinastri* was plotted as presence in grid-squares with likelihood values $>Lv_{thr}$. An additional higher threshold was adopted (Lv_{high}), to identify areas of greater climatic suitability and thereby minimize the occurrence of 'false positives'. The projected present-day distribution of *V. pinastri* was overlaid with a 'habitat mask' equivalent to the distribution of juniper (Preston *et al.* 2002). Projected presence of *V. pinastri* was removed from grid-squares where juniper was absent, thus providing likelihood estimates based on both the suitability of climate and the occurrence of juniper habitat (*cf.* Pearson *et al.* 2004).

Future modelled likelihoods were generated based on standard climate change scenarios (Hulme *et al.* 2002): combining a single period (2050s) and two greenhouse gas emission levels (low and high emissions) corresponding to the Intergovernmental Panel on Climate Change (IPCC) B2 and A1F1 SRES scenarios respectively (Nakicenovic 2000; Hulme *et al.* 2002). These scenarios represent the best available dataset with which to examine projected climate change in the UK (Hulme *et al.* 2002), and provide a common framework for comparing the projected response of *V. pinastri* to a range of rare and threatened British species (Berry *et al.* 2005, 2007).

Six future projected distributions were plotted for *V. pinastri* based on the two contrasting climatic scenarios—2050s low and high emissions:

- two projected distributions were based on climate suitability alone (≈'bioclimatic space'),
- the projected distributions of bioclimatic space were overlaid with the juniper habitat mask, equivalent to the present-day distribution of juniper (Preston *et al.* 2002),
- the projected distributions of bioclimatic space were overlaid with a juniper habitat mask, equivalent to the present-day distribution of juniper (Preston *et al.* 2002) minus a given number of juniper sites equivalent to the observed rate of loss in juniper habitat between 1987 and 2004 (Braithwaite *et al.* 2006): i.e. −0·47% per year, or −22·6% for the period 2007 to 2055. These lost sites were randomly selected from the available 'present-day' sites.

The present-day and future projected distributions of *V. pinastri* were plotted as maps using ArcGIS v. 9 (ESRI 1999–2005). The modelled present-day distribution was compared to projected future distribution as proportional change in the number of 10 km grid-squares for which climate and habitat are hypothetically suitable for *V. pinastri*.

Stand-scale dynamics

We examined the response of *V. pinastri* to stand-scale effects for two of its largest known populations in the British Isles, growing epiphytically on juniper at Glen Fenzie (NJ 3102; 430 m asl.) and Meikle Cairn (NJ 4125; 440 m asl.): Fig. 1. Both sites are located in the Grampian Region of the Scottish Highlands, within the biogeographic zone 'eastern Highland, low-plateau' (i.e. Group 7 of Brown *et al.* 1993). The area of juniper at Glen Fenzie was extensive and divided therefore into three discrete sub-sites, noted as GF-1, GF North and GF South (each separated by an open area with distance >100 m). The juniper at GF-1 and GF North comprised dispersed aggregations of juniper shrubs, probably representing clonal patches formed by layering, as well as scattered isolated individuals. In contrast, GF South comprised relatively fewer though more extensive layered thickets. The juniper at Meikle Cairn comprised mostly individual shrubs separated by varying distances. Both Glen Fenzie and Meikle Cairn appeared to be heavily grazed (by rabbits, sheep and deer), with no evidence of juniper regeneration. At Meikle Cairn approximately half of the juniper shrubs showed signs of accidental fire damage, caused by muirburn of the surrounding heathland during 1998 and 2002.

A central position was identified at each of the four sites, and geo-located (Garmin GPS 12). This formed the starting node for a 'random-walk' throughout each juniper habitat. A linear direction was selected using a random pointer, and followed until an individual juniper shrub was encountered, noting the distance and direction travelled. The process was repeated, travelling from individual shrub to shrub, until a total of 50 individuals had been recorded from each of the four sites ($n=200$). Each juniper shrub encountered was qualitatively scored into five life-stage categories and five structural categories, according to definitions previously adopted by Scottish Natural Heritage (Sullivan 2003): Table 1. The same shrubs were examined for the presence or absence of *V. pinastri* and the commonly co-occurring species *Cetraria sepincola* (Ehrh.) Ach. Including *C. sepincola* (an abundantly fertile and spore-producing species) provided an ecological comparison with *V. pinastri*, which reproduces asexually via soredia. Where it occurred, the abundance of *V. pinastri* on each of the juniper shrubs was estimated as the number of individual thalli counted per unit sampling effort. Sampling effort was standardized as 60 seconds examining each shrub by the same individual field worker (the first author). Differences in the abundance of *V. pinastri* were examined between juniper shrubs of different life-stage and structure, using a Kruskal-Wallis test to implement a nonparametric one-way analysis of variance (Genstat v. 7.1 2003).

The randomly-sampled spatial distribution of juniper and associated lichen epiphytes, *V. pinastri* and *C. sepincola*, were plotted as Euclidean co-ordinates and the spatial pattern of the species examined using Ripley's second-order statistic '*K*' (Dale 2002), implemented using the freeware program Crimestat v. III (Levine & Associates 2004). A default border correction was defined using a rectangle with dimensions equivalent to the minimum and maximum x/y co-ordinates. The significance of the measured distribution was compared to the 5% and 95% confidence intervals, using a Monte Carlo test based on 1000 randomized distributions.

Results

Modelled response to climate and pollutant loads

Analysis using Moran's *I* suggests the reconstructed British distribution of *V. pinastri* (Fig. 1) is not spatially auto-correlated (i.e. values of *I* did not exceed the 99·5 and 0·5% confidence intervals based on Monte Carlo randomization): assuming sampling for

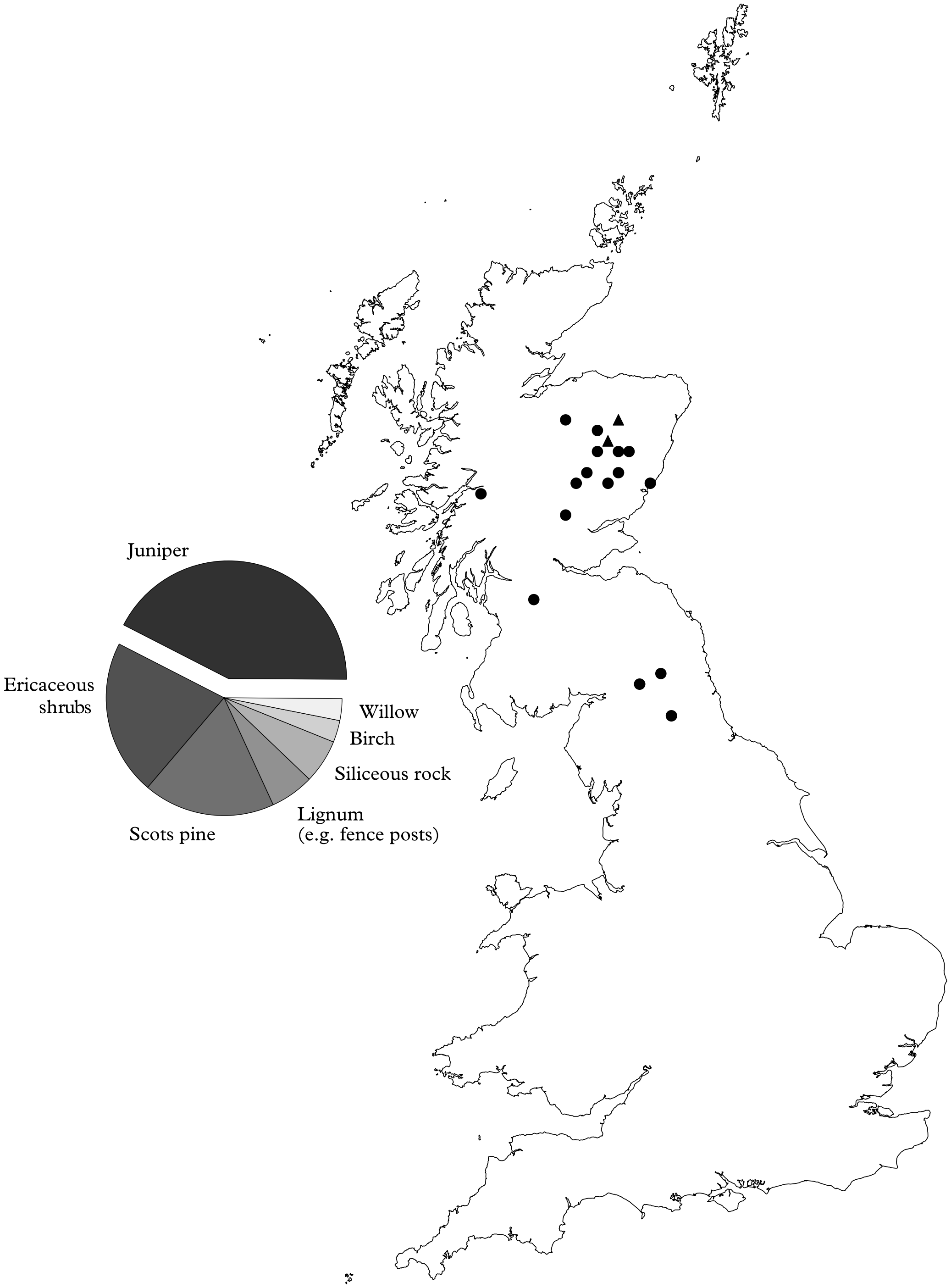

FIG. 1. The known British range of *Vulpicida pinastri*, based on records of confirmed presence for the period 1960–2007: the two study areas (Glen Fenzie and Meikle Cairn) are indicated separately as triangular symbols. The pie chart shows variation in the substrata from which the species has been recorded.

TABLE 1. *Classification of juniper life stage and structure, adapted from Sullivan (2003):* Extent and Condition of Juniper Scrub in Scotland, *unpublished report to Scottish Natural Heritage*

Life Stage	
Pioneer	Seedling or sapling stage. Small bushes usually growing vigorously, often with an open structure.
Building	Moderately sized, vigorous, well-branched bushes, with a full, dense canopy.
Mature	Bushes with canopy beginning to thin, but without dead or collapsed branches. Growth rate decreasing. Branches of prostrate bushes have not lost bark cover.
Old	Fully grown bushes but canopy thin, with dead branches and slow growth. May have collapsed branches. Branches of prostrate bushes may have lost some bark.
Dead*	Canopy mostly absent, with many dead branches and no growth. Often has collapsed branches. Many branches without bark.
Structure	
Columnar	Taller than broad and of relatively even width for most of its height, may taper towards apex or base.
Pyramidal	Triangular shape, wider at base than the apex, which may not be distinctly pointed.
Inverted pyramidal	Triangular shape, narrower at the base than the top, which may not be completely flat.
Low spreading	Broader than tall, with the most visible branches growing at an angle of less than 20° to the ground but not prostrately.
Low upright	Broader than tall, of relatively even width for most of its height, with most visible branches growing at an angle of 20° or greater to the ground. May be some layering, or stems buried in litter.

*Additional category not used by Sullivan (2003).

Moran's I follows a standard normal distribution (mean=0, variance=1) then $Z(I) = -1{\cdot}236$, and $P = 0{\cdot}39$. The use of randomly placed pseudo-absences is therefore appropriate to the modelled response (Zaniewski *et al.* 2002). Accordingly, an optimum non-parametric multiplicative model (logB= 4·39) was selected from 995 competing models generated in a stepwise free search. The model identified mean winter temperature and annual temperature range as optimum explanatory variables (Fig. 2): cross-validated $R^2 = 0{\cdot}497$, $P = 0{\cdot}007$. Comparison of projected likelihoods based on $n - x$, with the set of 'independent observed values' (values of x), suggests the variables selected as model predictors have strong predictive ability: AUC (±1 SE)=0·91± 0·027.

Pollutant loads were not selected as explanatory variables, and differences between measured pollutants were non-significant when compared between 10 km grid-squares with confirmed presences versus pseudo-absences: for NH_4^+, U=142, $P = 0{\cdot}946$; for NO_3^- U=114·5, $P = 0{\cdot}306$; for SO_4^{2-} U=116·5, $P = 0{\cdot}339$.

Projected response to climate change and juniper habitat distribution

The optimum predictive model (Fig. 2) was used to project the bioclimatic range of *V. pinastri* at 5 km resolution using present-day climatic values (Perry & Hollis 2005). An AUC determined threshold (Lv_{thr}= 0·53) was used to delimit modelled presences and absences (Manel *et al.* 2001). This value corresponded closely to the kappa determined threshold (Lv=0·52), which has sometimes been used as an alternative to the AUC threshold in comparable studies (e.g. Thuiller 2003, 2004). A second, higher threshold value (Lv_{high}=0·9) was used to identify areas of greater climatic suitability and thereby minimize 'false positives'. The model failed to predict likelihood values over *c.* 9% of the study area. Grid-squares outwith the data range used to calibrate the model occurred mostly along the oceanic west coast of Britain, though less frequently along the north and east Scottish coast and the south coast of England (Fig. 3). The projected response indicates broad climatic suitability for *V. pinastri* (Lv>0·53) in the uplands of northern and eastern Scotland, northern England and eastern Wales. However, areas of high bioclimatic suitability (Lv>0·9) are restricted to the central uplands of northern England and north-east Scotland (Fig. 3). Application of the juniper 'habitat mask', which selectively removed areas of bioclimatic suitability from which juniper is absent, significantly reduced *V. pinastri*'s projected extent (from *c.* 22% of geographic space, to just 1·4% of geographic space) and resulted in a more scattered distribution (Fig. 3).

The extent of grid-squares outwith the data range used to calibrate the model increased under projections based on IPCC climate change scenarios (UKCIP02; Hulme *et al.* 2002), Fig. 4. This 'unmodelled' range increases from the south and east of Britain, consistent with a predicted warmer and drier climate for south-east England, that is, with winter temperatures exceeding the climatic range included in our calibrated model (Fig. 2). For the geographic range over which the model can be reasonably applied, the climate change scenarios tentatively indicate a loss of suitable bioclimatic space for *V. pinastri* in Britain (Fig. 4): proportional loss of space is 0·51 and 0·76 under low and high emissions scenarios, respectively (Fig. 5). The proportional loss of space is less when compared between scenarios including the juniper habitat mask (i.e. 0·32 and 0·63, for low and high emissions scenarios: Fig. 5) though the consequences of this change are greater (i.e. the proportional losses are from a reduced number of projected sites compared to bioclimatic space without the habitat mask: Fig. 4). Incorporating loss of juniper habitat at a rate consistent with observed loss for the period 1987–2004 (Braithwaite *et al.* 2006) increases proportional losses from 0·32 to 0·44 and 0·63 to 0·71, for the low and high emissions scenarios, respectively (Fig. 5).

Response to local stand structure

There were significant differences in the abundance of *V. pinastri* measured between shrubs of contrasting life-stage and structure (Fig. 6), tested using a Kruskal-Wallis test, for life-stage H=14·93, *P*=0·002 (3 d.f.), and for structure H=17·17, *P*=< 0·001 (2 d.f.). We believe these measured differences are accurate and far exceed any potential sampling error incurred by the contrasting ease or difficulty in counting lichen thalli on shrubs of a particular physiognomy. Accordingly, *V. pinastri* appears to be most abundant on juniper shrubs conforming to the 'low upright' structure, with fewer thalli typically occurring on 'low spreading' and still fewer on 'inverted pyramid' shrubs (Fig. 6). No 'columnar' or 'pyramidal' shrubs were encountered (Table 1). Similarly, significantly more *V. pinastri* thalli were recorded on 'old' as opposed to 'building', 'mature' or 'dead' shrubs (Fig. 6). No 'pioneer' shrubs were encountered (Table 1).

Spatial pattern analysis indicated the significant aggregation of juniper shrubs at GF-1, GF North and Meikle Cairn at distances >*c.* 5 metres (Fig. 7). At sites where the juniper is spatially aggregated it is closely matched by the spatial pattern of the lichen *C. sepincola* (i.e. at GF-1 and GF North, *C. sepincola* was absent from sampled shrubs at Meikle Cairn). Spatial distribution of *V. pinastri* is consistently more aggregated than that of the juniper across all three sites. However, at GF South the spatial structure of juniper is measured at a smaller spatial scale (up to a minimum of 12 metres for the 50 shrubs, Fig. 7), and the shrubs appear to be randomly distributed; both *V. pinastri* and *C. sepincola* follow this random pattern.

Discussion

This study provides an examination of projected climate change impact for a rare lichen

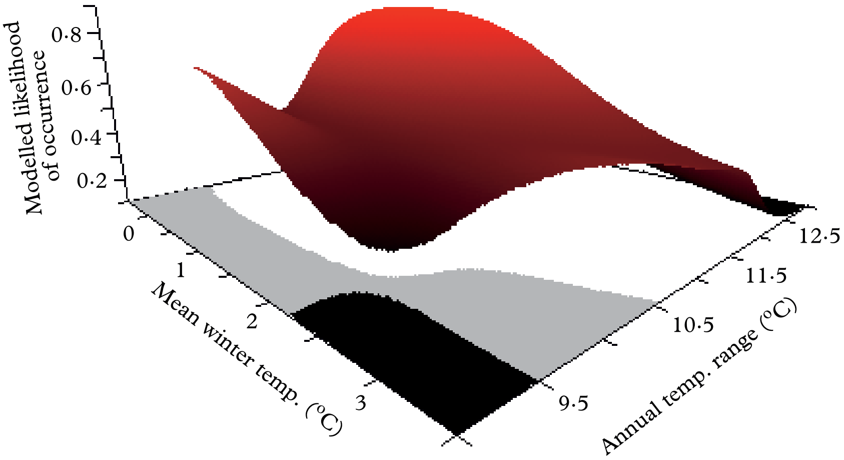

FIG. 2. Two-dimensional response surface generated for *Vulpicida pinastri* using nonparametric multiplicative regression (McCune 2006). Two optimum explanatory variables were selected: mean winter temperature (tolerance=1·298, sensitivity=0·07) and annual temperature range (tolerance=0·383, sensitivity=0·015); logB=4·39.

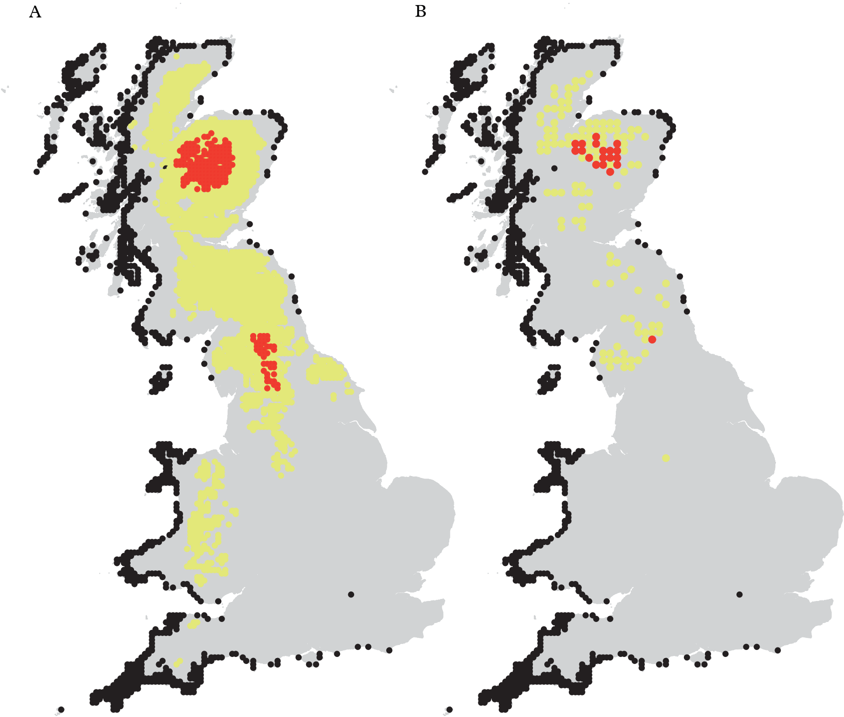

FIG. 3. Projected bioclimatic space for *Vulpicida pinastri* in Britain based on the response to mean winter temperature and annual temperature range (*cf*. Fig. 2) and using the present-day climate scenario. Two thresholds of suitability are projected: Lv=0·53–0·9 and >0·9. A, present-day projected distribution; B, distribution reduced by the application of a habitat mask equivalent to the present-day distribution of juniper. ●=unmodelled range; ● Lv=0·53–0·9; ● Lv=>0·9.

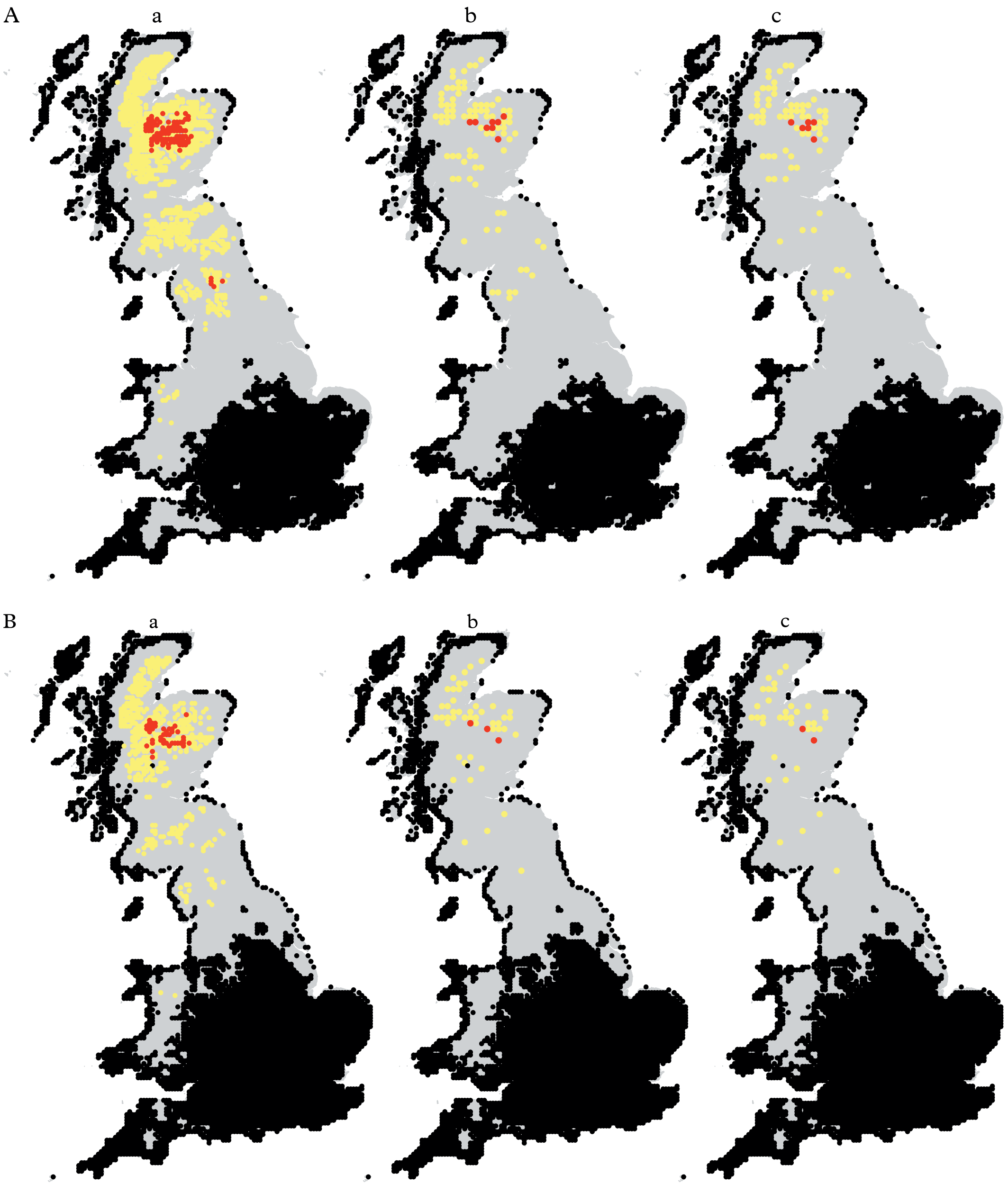

FIG. 4. Projected bioclimatic space for *Vulpicida pinastri* in Britain based on the response to mean winter temperature and annual temperature range (*cf.* Fig. 2). A, IPCC low emissions scenario for the 2050s; B, IPCC high emissions scenario for the 2050s (UKCIP02: Hulme *et al.* 2002). Two thresholds of suitability are projected: Lv=0·53–0·9 and >0·9. Individual maps show: a, 2050s projected distribution; b, projected distribution reduced by application of a habitat mask equivalent to the present-day distribution of juniper; c, theoretical future distribution by application of habitat mask derived by forecasting existing rates of decline of juniper (1987–2004: Braithwaite *et al.* 2006). ●=unmodelled range; 🟡 Lv=0·53–0·9; 🔴 Lv=>0·9.

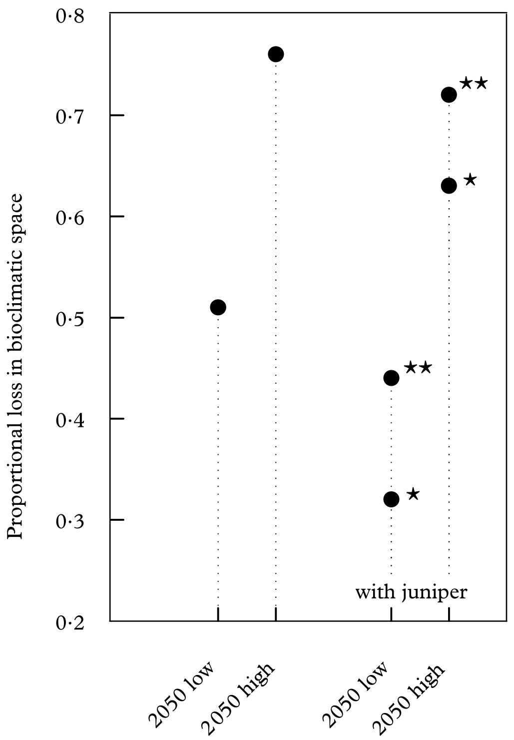

FIG. 5. Proportional loss of bioclimatic space for *Vulpicida pinastri*, calculated (i) between the present-day and 2050s low and high emissions scenarios [i.e. between Fig. 3A and Fig. 4A(a) & B (a)] between present-day projected range with application of the juniper habitat mask (Fig. 3B) and projected future range with a juniper habitat mask equivalent to the present-day distribution of juniper* [Fig. 4A(b) & B(b)] and based on forecasting the existing rates of juniper decline** [Fig. 4 A(c) & B(c)].

species, 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 an example of ecological niche-based modelling, which has been used to examine the conservation status of lichen species based on habitat requirements and availability (Martínez *et al.* 2006; Bolliger *et al.* 2007). The use of ecological niche-models is subject to a well-documented range of assumptions and caveats (e.g. Pearson & Dawson 2003; Hampe 2004; Araújo *et al.* 2005; Heikkinen *et al.* 2006; Botkin *et al.* 2007). However, previous studies have identified opportunities to reduce inherent uncertainties in predictive modelling and our analysis was based, therefore, on non-parametric regression (Segurado & Araújo 2004; Araújo *et al.* 2005) using a tested methodology (McCune 2006) with confirmed presences and pseudo-absences as input data (Zaniewski *et al.* 2002; Engler *et al.* 2004; Pearson *et al.* 2006). We selected nonparametric multiplicative regression based on 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)]; these tests included data specifically relevant to the environmental response of lichens (McCune 2006). Additionally, *V. pinastri* occurred at low-moderate prevalence within a reasonably well-defined range (Fig. 1), though abundances were not spatially autocorrelated, demonstrating species attributes that are thought to be appropriate to bioclimatic modelling (Brotons *et al.* 2004; Segurado & Araújo 2004; Luoto *et al.* 2005; Segurado *et al.* 2006). Many lichen epiphytes are highly sensitive to airborne pollutants, including the major wet deposited ions examined here, SO_4^{2-} (Hawksworth & Rose 1970), NH_4^+ and NO_3^- (van Herk *et al.* 2003), though the present-day distribution of *V. pinastri* did not appear to be confounded by air-borne pollutant loads. This is supported circumstantially by the poor correspondence between *V. pinastri* distribution and spatial trends in pollution; that is, *V. pinastri* is broadly restricted to north-east Scotland and northern England (Fig. 1), and therefore absent from many regions of Britain that are climatically different though which have similar pollution regimes (NEGTAP 2001). Accordingly, we believe the application of predictive modelling to project a response to climate change scenarios provides for *V. pinastri* a worthwhile though cautious indication of the possible direction and relative magnitude of change in the availability of bioclimatic space. The extension of model projections to include habitat effects (i.e. current and possible distribution of juniper) is predicated on observational evidence to suggest that the

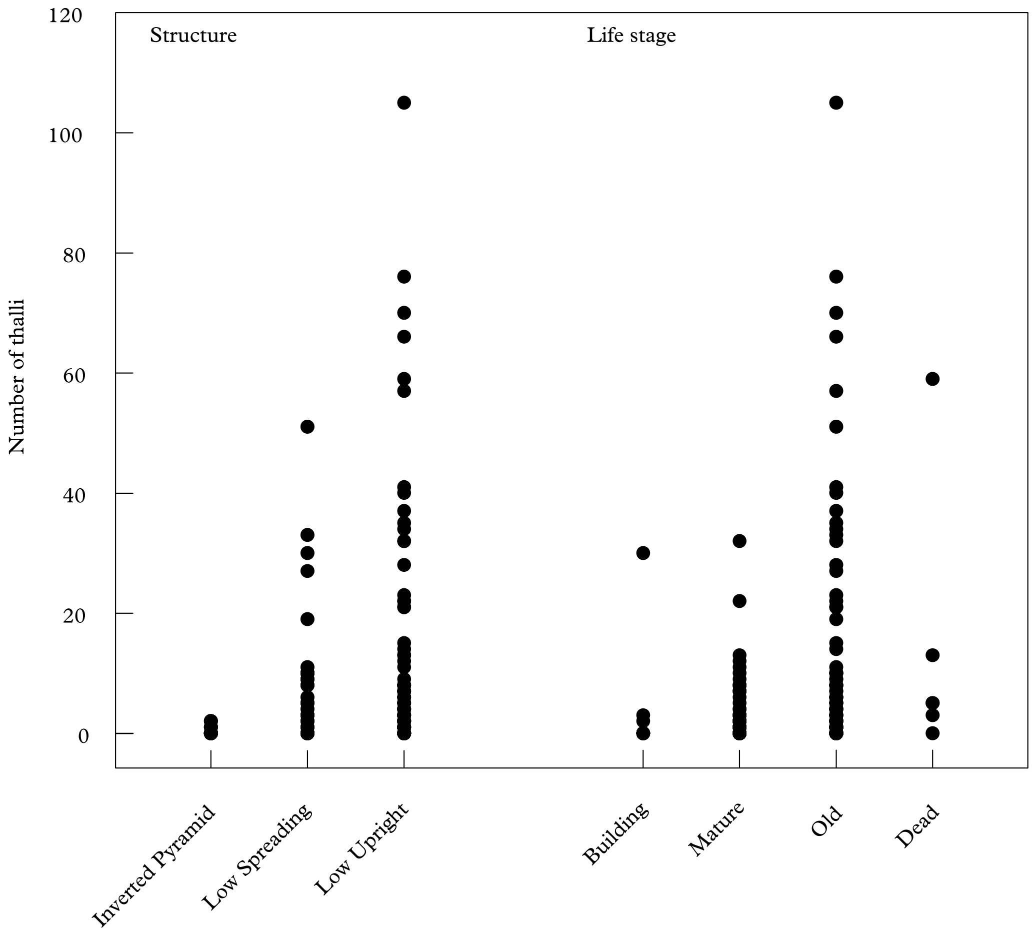

FIG. 6. Point plots showing the abundance (number of thalli) for *Vulpicida pinastri* on juniper shrubs with contrasting physiognomy, i.e. structure and life stage (*cf.* Table 1).

largest populations of *V. pinastri* in present-day Scotland are restricted to juniper. This represents therefore one of multiple hypothetical future possibilities (i.e. referring only to *V. pinastri* where it occurs on juniper). Our general conclusions regarding the conservation status of *V. pinastri* within the UK are based on the assumption that this substratum preference will remain static, including under a changed climate. We caution that such conclusions would thus be weakened if *V. pinastri* experienced a shift in local resource requirements in response to climate warming.

Projected response to climate change and juniper habitat

The selection of winter temperature and yearly temperature range as climatic variables best explaining the distribution of *V. pinastri* (Fig. 2) matches observed trends in the species' continental biogeography (i.e. increasing occurrence from temperate/lowland to boreal/montane regions: Mattsson 1993; Randlane & Saag 2005) and its distribution along regional climatic gradients, for example in North America its increasing occurrence towards cool interior forests

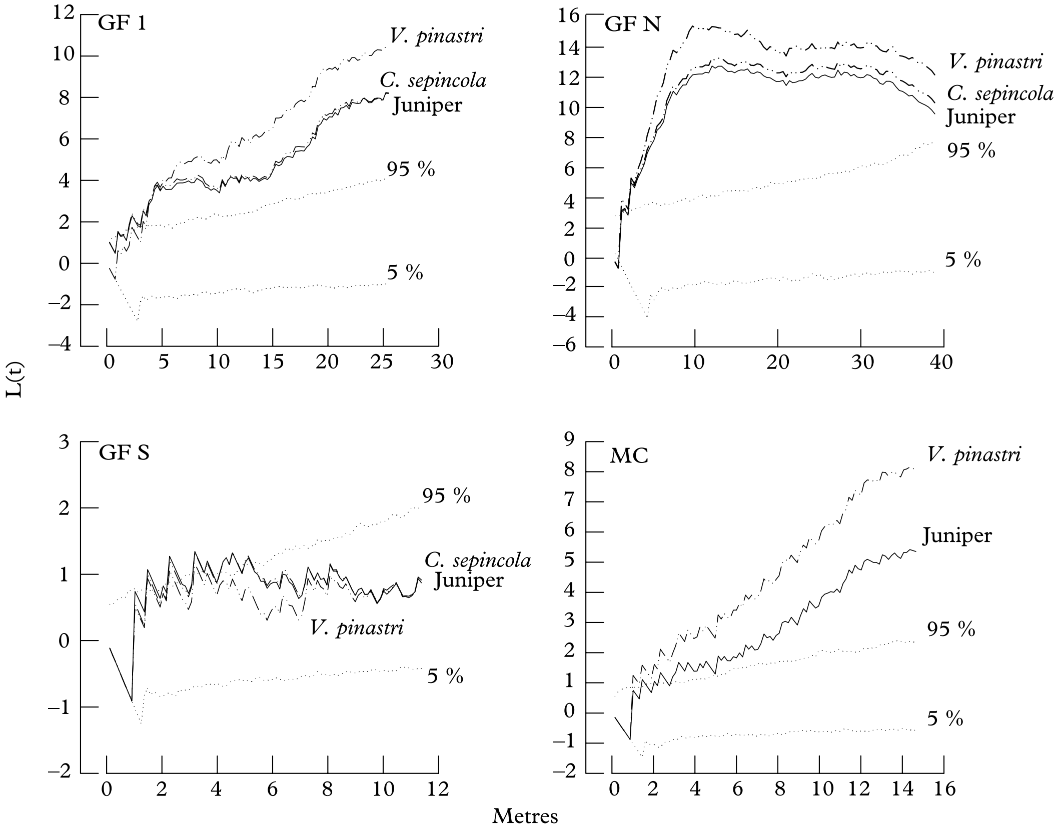

FIG. 7. Second-order analysis by Ripley's 'K' statistic [L(t)], comparing the spatial distribution of juniper and its lichen epiphytes *Vulpicida pinastri* and *Cetraria sepincola* at the four study sites. Confidence intervals (5th and 95th) indicate the limits of a spatially randomized distribution. Values of L(t) above the 95th confidence interval indicate statistically significant aggregation at the given scale of analysis (i.e. metres, x-axis).

with greater periods of snow-lie (McCune & Geiser 1997; Nash *et al.* 2002). Consequently, the projection of suitable bioclimatic space in Britain is limited along a steep climatic gradient, to northern and inland regions of Britain away from the oceanic western coast, i.e. eastern Wales, and north-eastern England and Scotland (Fig. 3). Greatest bioclimatic suitability is identified in the north-central Pennines and the north-eastern Scottish uplands (Fig. 3). The projection of IPCC climate change scenarios indicates potential loss of suitable bioclimatic space for *V. pinasti* ranging between 51% and 76% of climate space depending on greenhouse gas emissions scenarios (Fig. 5). These projected impacts are consistent with expectations for a weakening of winter severity with higher winter temperatures and increased winter rainfall (Hulme *et al.* 2002; Barnett *et al.* 2006). The geographic range of 'unmodelled' grid-squares increases in a region where the presence of *V. pinastri* is expected to be limited by increasing warmth (i.e. south-eastern England: Fig. 4), and we can reasonably assume that the species is unlikely to be abundant within this range, consistent therefore, with the projected loss of bioclimatic space.

Projected bioclimatic space for *V. pinastri* in Britain exceeds its actual distribution (*cf.* Figs 1 & 3), and a more appropriate estimate of a species' potential range may theoretically be gained by the hierarchical application of a ‘habitat mask’ (*cf.* Pearson *et al.* 2004). Consistent with our notion that juniper represents *V. pinastri*’s principal habitat in the British Isles, the application of a juniper habitat mask restricts the projected British range to a smaller number of localities which are broadly consistent with its known distribution (Figs 1 & 3). However, juniper in Britain continues to suffer a long-term decline (Preston *et al.* 2002; Braithwaite *et al.* 2006), attributed to poor management, that is, over-burning and grazing (Miles 1988). When the existing rate of juniper decline is included in projected potential range for the 2050s (Fig. 4), the loss of *V. pinastri* increases substantially as a consequence (Fig. 5). The projected rates of juniper decline up to the 2050s have been based on estimated change during the period 1987–2004, attributable to local management factors. Projected future decline of juniper is based therefore on the inferred impacts of past and present management only, and it is implicit in our analysis that the response of *V. pinastri* to changing climate will be more rapid than the climate-response of juniper. However, over the long-term, direct climate change effects on *V. pinastri* may be further exacerbated if the population viability of juniper is itself impacted by climate warming (García *et al.* 2000).

Vulpicida pinastri response to local stand structure

In addition to limits imposed by climate and juniper presence-absence there are clear limits to the local occurrence of *V. pinastri* within a juniper stand. The species occurs to a greater extent on old, low upright shrubs, and is relatively more aggregated at sites GF-1, GF North and Meikle Cairn than the spatial pattern of juniper (Figs 6 & 7). There was no apparent relationship between shrub physiognomy and spatial pattern (based on field observations) and degree of aggregation may therefore indicate possible limits to local dispersal. Pattern analysis indicates that *V. pinastri* becomes more aggregated than juniper at distances >5 metres (Fig. 7), tentatively suggesting *V. pinastri* might be easily dispersed between proximal shrubs within a group (i.e. ≤5 metres distance) but that effective local dispersal is limited as the distance between shrubs increases. These results are consistent with observations made between lichens with contrasting reproductive traits. Previous studies have indicated that asexually reproducing epiphytes (with larger diaspores) may be effectively dispersed at small local scales, though become dispersal limited at larger scales relative to sexually reproducing species with smaller spores (Hedenås *et al.* 2003; Löbel *et al.* 2006*a*, *b*). Similarly, the spatial pattern of *C. sepincola* appears to track closely the spatial pattern of juniper across all sampled distances (Fig. 7), suggesting the spores of this species (*c.* 11×5 µm) may be more easily dispersed within juniper stands than the larger asexual propagules of *V. pinastri* (*c.* 30 µm diameter).

In contrast, within GF South both the juniper and its epiphytes *V. pinastri* and *C. sepincola* are randomly distributed and we believe this reflects a different effective scale of analysis. Thus, while random sampling at GF-1, GF North and Meikle Cairn appears to have captured the spatial pattern between clumps of juniper, at GF-South the sampling occurred mostly within a single extensive thicket. The random pattern at GF South reflects therefore the random distribution of individual shrubs within a single clump, contrasting with the aggregated distribution measured between clumps at the other three sites.

The presence of *V. pinastri* on shrubs within a stand may be affected in part by the spatial distribution of juniper shrubs (Fig. 7), though abundance is related to shrub physiognomy (Fig. 6). *Vulpicida pinastri* was most abundant on old shrubs with a low upright structure (Fig. 6), characterized therefore by their relatively low height and thinning canopy with some collapsed branches (Table 1). This structure is likely to create local conditions within the shrub that are relatively exposed, with a higher light regime and more rapid drying (lower humidity) compared to juniper in the building phase, though with less severe exposure than within dead shrubs. This effect of shrub physiognomy is consistent with previous studies which have highlighted the importance of local environmental conditions controlling lichen position on a tree or within a forest canopy, for example differences in exposure relating to light/temperature regime and moisture (McCune & Antos 1982; Eversman *et al.* 1987; Campbell & Coxson 2001). It is possible also that the more open structure of old, low upright shrubs may facilitate the more effective capture of *V. pinastri* propagules, which may arrive more easily onto the open twigs and branches than during the compact building phase, and are perhaps less likely to be redeposited than within very exposed dead shrubs.

The observed local response of *V. pinastri* to the structure of a juniper stand may act to further limit the occurrence and abundance of this species within a landscape. High grazing pressures at many juniper sites result in the break-up of existing juniper stands and increasingly scattered bushes (Gilbert 1980; Clifton *et al.* 1997), possibly negating the local dispersal of *V. pinastri* within occupied sites. Additionally, there is a scarcity of regenerating shrubs to replace the cohort of old shrubs on which the species is most abundant at the study sites. The age structure of juniper shrubs at the sites examined indicates a peak in the occurrence of old shrubs (75% of individuals), an absence of pioneer shrubs and relatively few building or mature shrubs (1% and 18% of individual shrubs, respectively). The absence of pioneer shrubs at the sites examined (GF or Meikle Cairn) matches the trend towards an ageing population structure observed more widely for juniper in Britain (e.g. Sullivan 2003) and consistent with the widespread decline of juniper scrub (Preston *et al.* 2002; Braithwaite *et al.* 2006).

Opportunities for conservation

The dual impact of climate warming combined with further loss of primary habitat represents a clear threat to *V. pinastri* in the British Isles, and we suggest the species should be closely monitored as it may in the future require reclassification from IUCN category 'Near Threatened' (Woods & Coppins 2003) to 'Vulnerable'. However, large-scale monitoring should include an assessment of changing substratum requirements, i.e. the extent to which large populations of *V. pinastri* are restricted to juniper now and during a period of changing climate. Assuming that juniper is and will remain the most important habitat for *V. pinastri* in Britain, the disparity between the projected bioclimatic space (Fig. 3A) and the potential range limited by the presence of juniper (Fig. 3B) highlights the opportunity for conservation. Thus, the improvement or recreation of juniper scrub in those areas where the climate is predicted to remain suitable to *V. pinastri*, even under the more severe climate change scenario (i.e. the 2050s high emissions scenario, Fig. 4B), possibly combined with transplantation of thalli into this habitat, might offer the best solution for long-term conservation of *V. pinastri* in Britain. These actions need not entail great additional cost, and could take place as part of existing efforts to improve or recreate Britain's upland scrub habitat, including juniper (Mortimer *et al.* 2000). However, our results indicate that even within core areas of its British distribution not all juniper stands can be expected to support large and viable populations of *V. pinastri*. As a contribution to recommendations in juniper habitat management, *V. pinastri* appears to favour the presence of partially collapsed and degenerate old shrubs in scattered groups of closely associated clusters (Figs 6 & 7). Conservation efforts should thus aim for a mixed within-stand age structure, ensuring the continued recruitment of older cohorts into the juniper population and maximizing suitable local habitat for *V. pinastri*.

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