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Local experimental growth rates respond to macroclimate for the lichen epiphyte *Lobaria pulmonaria*

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Background: Bioclimatic models are widely applied in biogeography and conservation biology; however, the functional relevance of macroclimate as an explanation for species performance (e.g. establishment, growth and survival, fecundity) has been challenged.

Aims: In this study, we aimed to determine whether the ecological performance of an epiphytic lichen is related to coarse-grained macroclimate.

Methods: A meta-analysis was carried out to compare local growth rates for a lichen epiphyte, *Lobaria pulmonaria*, to coarse-grained interpolated climate surfaces. Growth rates were sampled from small-scale experiments conducted within different forest settings and for different regions of the world. Generalised linear mixed models were used to compare thallus growth (response) to a suite of climatic variables derived from the WorldClim dataset.

Results: A significant relationship between thallus growth measured for experimental forest microhabitats and macroclimatic variables (total precipitation and annual mean temperature) was found. This relationship was validated through a comparison with *L. pulmonaria*'s North American range for which projected growth rates were higher and lower where the species tended to be present and absent, respectively.

Conclusions: The ecological relevance of coarse-grained macroclimate applied in bioclimatic modelling has been challenged. We show that the use of macroclimatic data may be functionally defensible where correlated with independent measures of local ecological success.

Keywords: bioclimatic modelling; epiphyte; growth rates; *Lobaria pulmonaria*; macroclimate; North America

Introduction

Bioclimatic models are widely applied in biogeography and conservation biology. They compare large-scale species distributions to present-day climate in order to generate and test predictive statistical models, projecting successful models using climate change scenarios (Pearson and Dawson 2003; Wiens et al. 2009). This procedure is used to assess the theoretical loss or gain in a species' bioclimatic space, quantify potential range shifts (Berry et al. 2002; Thuiller et al. 2005) and estimate threat (Thomas et al. 2004, 2011). Bioclimatic models are a correlative (phenomenological) tool used when a species' distribution (e.g. presence-only or presence–absence data) is compared to macroclimate based on an underlying assumption that the species' range is controlled by, and is in equilibrium with, the present-day climatic setting. This might be considered a robust assumption given evidence that climatic responses compared amongst species may be explained by morphological or physiological adaptation (Schimper 1903; Díaz et al. 1998; Harrison et al. 2010); however, there are two significant challenges to the generality of climatic control and equilibrium.

The first challenge relates to the statistical robustness of the bioclimatic approach. Species could be considered functionally neutral (e.g. Hubbell 2001; Etienne and Alonso 2007) and because of features such as dispersal-limitation leading to spatial aggregation, combined with spatially autocorrelated climatic trends, apparently robust, although entirely spurious bioclimatic models may emerge (Beale et al. 2010). On this basis, bioclimatic models have been negated when compared to statistically appropriate null tests (Beale et al. 2008; Chapman 2010: although see the counterpoint by Araújo et al. 2009).

The second challenge acknowledges a functional species response to environmental drivers, but raises concerns with bioclimatic modelling on two counts. Firstly, there is evidence to demonstrate that species' larger-scale distributions may be subject to historical contingency, failing to meet an underlying assumption of equilibrium with the present-day climate (Svenning and Skov 2004; Araújo and Pearson 2005). Secondly, there are concerns about the ecological relevance of coarse-grained macroclimatic surfaces, such as those derived from spatial interpolation and/or general circulation models (Kennedy 1997). A number of studies have demonstrated weak or inverse relationships between a species' ecological performance and its position in bioclimatic space (Gilman 2006; Monahan 2009), contrasting therefore with experimental evidence for sensitivity to simulated climate change (Hollister et al. 2005; Wahren et al. 2005; Yang et al. 2011) within the context of small-scale field trials (e.g. Marion et al. 1997; Godfree et al. 2011). Smaller-scale experiments also

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emphasise the important effect of local ecological processes in regulating direct climatic sensitivity (Davies et al. 1998; Suttle et al. 2007).

We suggest that the null hypotheses of either functional neutrality or redundancy of coarse-grained macroclimate as an explanatory factor (relative to smaller-scale eco-logical processes) might be rejected if variability in a species' local performance was shown to be significantly related to macroclimatic variables. Such evidence would go some way to providing a functional basis for biogeographic distributions controlled by macroclimate. Additionally, evidence for stochasticity in the species' distribution would be weakened if the relationship between local ecological performance and macroclimate was consistent with a species' known biogeographic range.

We tested these null hypotheses for the lichen epiphyte *Lobaria pulmonaria* (L.) Hoffm., a widely used model organism for studies in epiphyte ecology (Scheidegger and Werth 2009). First, we compared *L. pulmonaria*'s local growth rate – compiled across independent experimental studies from the northern hemisphere – to coarse-grained macroclimate. Second, we tested to see whether this relationship was compatible with the species' continental-scale distribution in North America. Consistent with mainstream bioclimatic modelling, previous studies have assumed that lichen distributions may be controlled by macroclimate (Ellis et al. 2007); however, lichen epiphytes occur within and beneath the forest canopy and one might expect that the direct effect of macroclimate on ecological performance would be dampened by spatially-nested microhabitat factors (McCune et al. 2002; Lidén and Hilmo 2005). This makes *L. pulmonaria* an excellent model for testing the functional relevance of macroclimate.

Materials and methods

L. pulmonaria *growth rate model*

We carried out a systematic review of primary research papers downloaded from Web-of-Knowledge (2011) under the Boolean search term "(*Lobaria pulmonaria* OR *L. pulmonaria*) AND growth". One-hundred-and-sixty-one abstracts were critically examined to determine if the papers presented novel growth rate data on *L. pulmonaria*. Papers were rejected if (1) they did not report on growth rates in *Lobaria pulmonaria;* (2) they reported previously published results; (3) data were incomplete, lacking start weight or subsequent growth over a known time-period; (4) growth rates were derived from experimental manip-ulations, e.g. nutrient additions, temperature/humidity adjusted laboratory conditions; and (5) if the period of measured growth < 1 year. All the papers used in the study presented the mean start weight of thalli as well as the maximum average growth rate for a site. Any negative growth rates were omitted from analysis because these can be attributed to translocation adjustments (e.g. thallus frag-mentation) rather than negative carbon balance (Palmqvist and Sundberg 2000). To account for size dependency in the growth rates presented (Gauslaa et al. 2009), we calculated the relative growth rate i.e. grams per gram initial start weight, per year (Woolhouse 1968; Farrar 1974).

The growth rate of *L. pulmonaria* is known to be most rapid in small non-reproductive thalli (Gauslaa et al. 2006; Larsson and Gauslaa 2011), and it was expected – a priori – that the growth rate (g g^{-1} $year^{-1}$) declined logarith-mically as a function of thallus start weight (Woolhouse 1968). In a preliminary data analysis, growth rate was plotted against experimental start weight and fitted with a log-regression model. Residuals from the regression were large and normally distributed at low thallus start weights (<1 g), and low at high thallus start weights (see Figure 1). We therefore used the highly variable growth rates for thalli with an experimental start weight <1 g as the response. Residual values were strongly correlated with the growth rate ($r = 0.993$, $P < 0.0001$ with 18 d.f.) and we were therefore able to use growth rate values directly, rather than residuals.

We compared *L. pulmonaria* growth rate (response) to macroclimate as our explanatory variable. The locations of experimental growth rate studies were overlaid in ArcMap v. 9.2 (ESRI 2006: Redlands, California) onto interpolated climate surfaces plotted at a spatial resolution of 2.5 arc-minutes (Hijmans et al. 2005 – available as a component of the WorldClim resource (www.worldclim.org/bioclim)); however, with only 20 growth rate data points available, we had to carefully control the number of explanatory vari-ables. We examined pair-wise product-moment correlation coefficients among six generic macroclimatic variables: (1) mean annual temperature; (2) mean annual tempera-ture of the coldest month; (3) mean annual temperature of the warmest month; (4) annual temperature range; (5) total annual precipitation; and (6) a coefficient of variation for annual precipitation expressed as the proportional rain-fall in the driest month with respect to the wettest month.
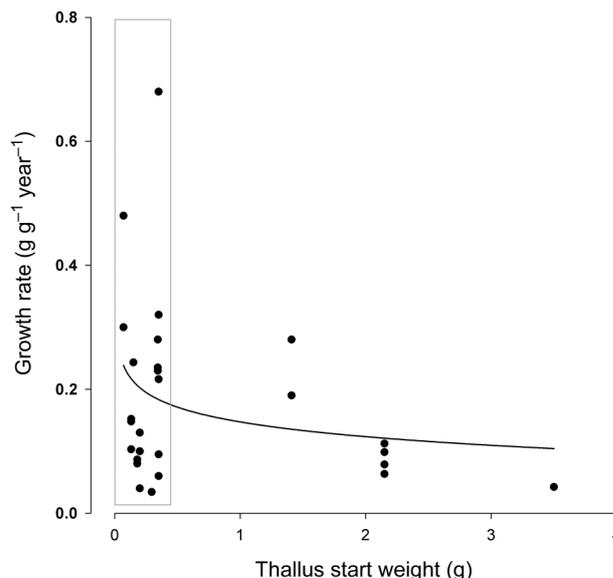

Figure 1.   Plot of thallus relative growth rate against thallus start weight, with logarithmic growth curve fitted to the data.

Note: The grey box delimits a region of high variability with normally distributed residuals (thalli <1 g).

We selected two variables representing a precipitation and temperature factor, and which were the least correlated.

We used a generalised linear mixed model (GLMM), with maximum likelihood estimation (ML) and Gaussian error structure, with four discrete geographic clusters amongst the experimental sites treated as a random effect. Starting from a full model with the two climate variables as fixed effects, and including their interaction, we used log-likelihood tests to make sequential comparisons (Crawley 2007; Zuur et al. 2009), aiming to minimise Akaike's Information Criterion for significant fixed effects. Analysis was performed in R v. 2.12.1 (2010), using the 'lme' function in the package 'nlme' (Pinheiro and Bates 2000; Venables and Ripley 2002).

Growth rate comparison with North American distribution

The spatial distribution of *L. pulmonaria* was reconstructed using the range map for continental North America presented by Brodo et al. (2001). The species' range was delimited using a combination of monographic work, herbarium specimens, confirmed literature records and primary field notes (I. Brodo, personal communication). This represents the best available published information on the species' distribution for North America. The published map for *L. pulmonaria* was scanned at 600 pixels per inch and rescaled by 650%. The large-format facsimile was then overlaid with an acetate sheet that contained 1752 equally spaced grid cells, projected using a latitude–longitude scale derived from the Chamberlin trimetric projection. Latitude and longitude co-ordinates were calculated for the centre of

each grid cell, and a presence was scored where this point was concurrent with the species' range.

Using the WorldClim resource, we extracted values for the precipitation and temperature factors that had been included as fixed effects in the optimised *L. pulmonaria* growth rate model, at a resolution of 2.5 arc-minutes across continental North America. These data were used to project the species' growth rate for the 1752 grid cells encompassing the species' range. We thus compared *L. pulmonaria* modelled response (growth rate) to an overlay for the species' presence (within its range) and absence (outside its range). We used a *t*-test to apply the null hypothesis of no difference in modelled growth rate for grid cells in which the species was present and absent. If a significant difference was detected in favour of higher growth rates where the species occurs, this would lend validity to the growth rate model by suggesting that a local sensitivity to macroclimate structures the species' biogeographic distribution.

Results

Focussing on normally distributed and highly variable growth for *L. pulmonaria* thalli with an experimental start weight <1 g dry weight (see Figure 1), eight papers provided the growth rate data used to model the species' performance (see Table 1). The mean time period over which an experiment was run was 517 ± 54 days. Experiments were confined to the northern hemisphere, although were widely distributed longitudinally, with four discrete geographic regions treated as random effects (see Figure 2). The pre-selection of climatic variables identified annual

Table 1. List of published papers used as a source of *Lobaria pulmonaria* growth rate data for thalli with a start weight <1g.

Code	Citation	Location	Broad micro-habitat
A	McCune et al. (1996)	Oregon, U.S.A.	Deciduous forest (*Quercus*, *Fraxinus*)
B	Muir et al. (1997)	Oregon, U.S.A.	Deciduous forest (*Fraxinus*)
C	Renhorn et al. (1997)	Sweden	Norway spruce forest (*Picea abies*)
D	Denison (1998)	Oregon, U.S.A.	Woodland fragments
E	Sillett et al. (2000)	Oregon, U.S.A.	Douglas fir forest (*Pseudotsuga menziesii*)
F	Antoine and McCune (2004)	Washington, U.S.A.	Douglas fir forest (*Pseudotsuga menziesii*)
G	Gaio-Oliveira et al. (2004)	Sweden and Portugal	Mixed broadleaf–Norway spruce (*Picea abies*)
H	Coxson and Stevenson (2007)	British Columbia, Canada	Western hemlock forest (*Tsuga heterophylla*)

Figure 2. Map showing the location of eight independent experimental studies used to compare *L. pulmonaria* growth to interpolated macroclimatic variables.

Note: Sites are labelled according to the study codes in Table 1, with the four discrete experimental regions treated as random effects in the growth model (cf. Table 3).

Table 2. Pair-wise product–moment correlation coefficients among five macroclimatic variables, extracted from the WorldClim database for sites in which *Lobaria pulmonaria* growth rate has been measured experimentally (cf. Table 1, Figure 1).

	[1]	[2]	[3]	[4]	[5]
[1] Precipitation	1				
[2] Precipitation variability	−0.667**	1			
[3] Mean temperature	0.373	−0.919***	1		
[4] Maximum temperature	0.528*	−0.949***	0.890***	1	
[5] Minimum temperature	0.444*	−0.948***	0.996***	0.905***	1

Note: $P < 0.05$; * < 0.01; ** < 0.001; *** with 18 d.f.

Table 3. Model diagnostics for an optimised GLMM comparing variation in thallus growth for *Lobaria pulmonaria* to the macroclimatic setting.

Fixed effects	Coefficient	t	P
Intercept	−0.5015540	−2.486992	0.0272
Annual precipitation	0.0009221	3.322082	0.0055
Mean annual temperature	0.0125327	4.400000	0.0007
Precipitation × temperature	−0.0000133	−3.838475	0.0021

Note: Fitted using restricted maximum likelihood, the variance for the random intercept <0.000001, compared to residual variance $= 0.1022017$; d.f.=13.

precipitation and mean annual temperature as the least correlated (see Table 2); these were subsequently included as fixed effects in a GLMM. Model optimisation indicated that precipitation, mean temperature and their interaction should be retained in the model (see Table 3).

Reconstruction of *L. pulmonaria*'s North American range generated 459 presences across 1752 grid-cells (see Figure 3, inset A). Projection of the growth model across continental North America resulted in areas of negative growth (Figure 3, inset B), which we interpret as unsuitable for survival, e.g. with respiration exceeding photosynthetic carbon gain. The known northern range limit for *L. pulmonaria* was congruent with an isocline for zero growth, though with sporadic northerly outliers predicted by the model, and with positive growth projected for central continental North America outside the species' known range (see Figure 3, inset B). Using a *t*-test to compare the modelled growth rate for grid cells in which the species was present and absent, there was a significant difference ($t = -7.164$, $P < 0.0001$ with 1293 d.f.) with a higher and positive mean growth rate (0.0346) within *L. pulmonaria's* known range, and a significantly lower and negative growth rate (−0.223) where the species is absent (see Figure 3).

Discussion

We tested the null hypothesis that local experimental growth rates for the lichen epiphyte *Lobaria pulmonaria* would be insensitive to large-scale macroclimate. The species was selected because (1) it is a widely used model organism for studies in epiphyte ecology (Scheidegger and Werth 2009); (2) there is evidence for wide variation in its growth rates (cf. Renhorn et al. 1997; Larsson and Gauslaa 2011); and (3) it is known to be sensitive to forest microhabitat conditions (Gauslaa et al. 2007), which brings into question a direct functional link between macroclimate and the organisms' ecological performance.

Rejecting our null hypothesis, we demonstrate a statistical relationship between *L. pulmonaria* growth rate for small thalli (<1 g), and macroclimate: total precipitation and mean annual temperature. We caution that this result is circumspect, being limited to 20 data points, and with the significance of fixed effects assessed against 13 d.f. Additionally, the growth rate model over-fitted the species known range in North America. This may be because the growth rate data present an aspect of the species' fundamental niche, whilst the range reflects its realised niche (cf. Monahan 2009), i.e. the absence of suitable forest habitat in the 'prairie region' of central North America, and/or because the locations of the experimental studies capture only a portion of the species' realised bioclimatic space. The growth rate model cannot therefore be used to generate a bioclimatic envelope that reconstructs *L. pulmonaria*'s North American distribution.

Nevertheless, the growth rate model does tentatively point to macroclimatic sensitivity, and its validity is supported on three counts. First, when penalised for the small sample size, the model is successfully validated against standard model diagnostics (e.g. log-likelihood tests, AIC). Second, the model is consistent with evidence from the species' functional ecology. The coefficients for all non-interacting fixed effects were positive, suggesting that *L. pulmonaria* growth rate is higher in regions with higher precipitation and a warmer climate, although with a negative effect for the interaction term, indicating climatic constraints to growth (see Table 3). This matches with previously established physiological limits controlling *L. pulmonaria*'s ecological success. Dry matter gain in *L. pulmonaria* is sensitive to rainfall (Gauslaa et al. 2007) and there is evidence that seasonal growth patterns are limited by low precipitation during summer (Muir et al. 1997). Acknowledging other constraints (e.g. hydration, light conditions), *L. pulmonaria* growth is also limited at lower temperatures (Gaio-Oliviera et al. 2004; Larsson and Gauslaa 2011). Climatic effects may extend to include the role of N-fixation, e.g. there is a positive relationship between thallus hydration and temperature on N-fixation for the con-generic *L. oregana* (Tuck.) Müll.Arg. (Antoine 2004). Third, model projections confirm higher growth rates within the bounds of the species' known distribution and there are significantly lower growth rates outside the known range.

The growth rate model provides two further observations relevant to *L. pulmonaria*'s biology. First, the structure of the optimum GLMM was constrained by random effects (geographic location). Including four discrete
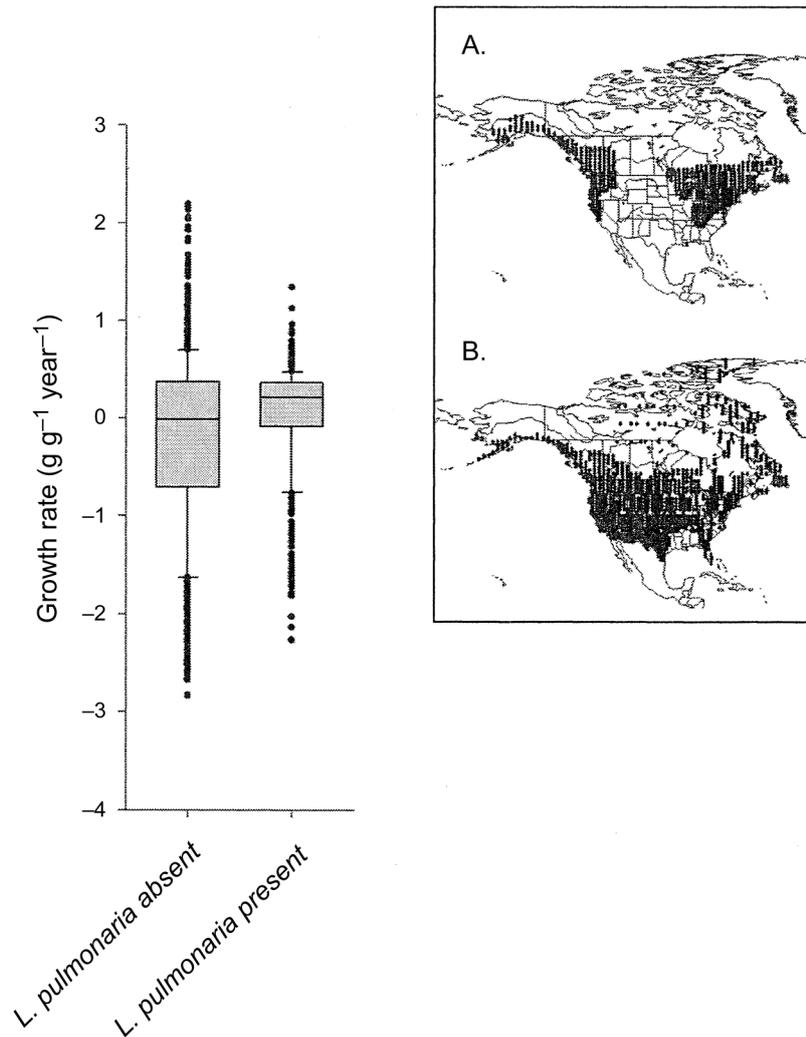
Figure 3. Box-plots showing the modelled growth rates in locations were *Lobaria pulmonaria* was expected to be present or absent. Inset A shows the species' expected distribution in North America (cf. Brodo et al. 2001); inset B highlights areas with predicted positive growth rate based on the macroclimate.

experimental regions as random effects in a mixed model allowed for the possibility of autocorrelation in growth rates, which may emerge from genetic relatedness. For example, *L. pulmonaria* genetic structure is highly differentiated at a regional- to continental-scale (Walser et al. 2003, 2005), and genetic variation in lichens has been associated with evolutionary adaptation to contrasting climatic regimes (Murtagh et al. 2002); however, our results indicated low variability in growth rate structured by location at a global scale. Second, small thalli showed high variability in growth rates, pointing to environmental sensitivity among juvenile and early-mature thalli. The growth of *L. pulmonaria* shifts from apical to laminal growth as thalli mature and become reproductively active (Scheidegger et al. 1998; Giordani and Brunialti 2002), and our results point to macroclimatic sensitivity at the apical growth stage. This extends both experimental (Ott 1987; Hilmo et al. 2011) and molecular (Werth et al. 2006) evidence for environmental sensitivity during the early stages of thallus development.

The climatic response

Relatively early criticism of bioclimatic models focussed on the absence of ecological mechanisms underpinning model validity and subsequent projection (Woodward 1993; Woodward and Beerling 1997), and the reliability of bioclimatic models may be improved through synthesis with functional ecological processes (Mokany and Ferrier 2011). Accordingly, correlative bioclimatic models, coupled with a functional understanding of ecological performance, provide a more robust assessment of climatic sensitivity (Morin and Thuiller 2009; Buckley et al. 2010). Demonstrating the sensitivity of *L. pulmonaria*'s local growth to large-scale interpolated climate data (Hijmans et al. 2005) tentatively supports the macroclimatic response of lichen epiphytes, which is consistent with assumptions in bioclimatic modelling (Pearson and Dawson 2003; Ellis et al. 2007). Nevertheless, it is important to recognise that alongside a degree of macroclimatic sensitivity, the real world response of *L. pulmonaria* to climate change will be constrained by an amalgam of spatially nested

and interacting factors. Bioclimatic models may therefore be improved by considering the cross-scale interaction between local habitat quality and macroclimatic setting (Ellis et al. 2009; Lisewski and Ellis 2010). Additionally, climatic sensitivity will be modified by a capacity for in situ acclimation (MacKenzie et al. 2001, 2004; Schofield et al. 2003). For lichens, this includes a potential to switch and optimise amongst photobiont clades (Piercey-Normore 2006; Yahr et al. 2006), as well as the role of dispersal-limitation and gene flow in controlling opportunities to migrate across fragmented landscapes, and also the potential to undergo evolutionary adaptation to changed environments in situ (Scheidegger and Werth 2009; Ellis and Yahr 2011). Understanding climate sensitivity within this broader context of a species' evolutionary and ecological response remains a major challenge.

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Notes on contributors

Sally Eaton is a research assistant; she studies community structure in epiphytic lichens and bryophytes.

Christopher Ellis is an ecologist specialising in the study of lichens and bryophytes.

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