Research article

Lichen epiphyte response to non-analogue monthly climates: A critique of bioclimatic models

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ABSTRACT

There has been extensive effort to quantify the biodiversity response to climate change. Bioclimatic models are widely used to correlate species landscape distributions with macroclimate, projecting and then comparing suitable climate space at a baseline and for future climate change scenarios. This bioclimatic approach has two assumptions: 1. Species distributions are at equilibrium with, and represent direct sensitivity, to macroclimate; 2. Relationships among climate predictors remain comparable when extrapolating from baseline to climate change scenarios. In contrast, species distributions have multiple drivers and may fail to reflect direct climate sensitivity. Furthermore, future climate change – especially at weekly or monthly timescales – may include novel combinations of temperature, moisture, and solar irradiance, without present-day analogues. Bioclimatic assumptions are especially problematic for subdominant guilds such as epiphytes. Controlled growth experiments were conducted over 25 months, for three ecologically different lichen epiphyte species, across three climatically contrasting botanic garden sites. There was correspondence between the response to climate (growth rate) and landscape distribution for two out of the three species, in support of bioclimatic modelling at the baseline. In addition, statistical growth models at monthly resolution were used to understand how projected outcome (increased or decreased growth comparing baseline with 2080s climate) might be sensitive to choice of model predictors. Model projections were highly sensitive to non-analogue future climates, including novel monthly combinations of moisture and irradiance. These discrepancies in a species projected outcome: 1. Send a caveat to the interpretation of coarser-grained bioclimatic models, e.g. those based on annual climate averages at kilometre grid-scales; 2. Identify irradiance as a necessary covariable in bioclimatic models. Statistical partitioning of contrasting species response – focussed on species identify, choice of model predictors and location – provides structured recommendations for the future development of biologically-realistic and downscaled growth models.

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1. Introduction

Rapid human-induced climate change presents a major challenge to species conservation (Thuiller et al., 2005; Araújo et al., 2011). Fundamental questions in climate change biology relate to the perennial problem of scale: how will species respond to climate change in terms of their ecological performance at a local scale, or in terms of distributional change at a larger scale, and how are responses at these two contrasting scales linked? Studies at the larger scale compare species landscape distribution to baseline cli-

mate variables, in order to quantify a species suitable bioclimatic space (Pearson and Dawson, 2003; Peterson et al., 2011). These 'bioclimatic models' can then be projected for baseline and future climate change scenarios, to explore a species risk as the loss or spatial shift in availability of suitable climate (Araújo et al., 2004; Thomas et al., 2004). Although widely applied, there are two general criticisms to this bioclimatic modelling, which are explored and tested in this study.

A first criticism has focussed on the concept of climatic equilibrium (Araújo and Pearson, 2005), which expects a species landscape distribution to reflect its climate sensitivity. A multitude of factors might determine a species distribution (e.g. Svenning and Skov, 2004; Svenning et al., 2008), and the under-pinning concept of climatic equilibrium is inadequately tested when comparing dis-
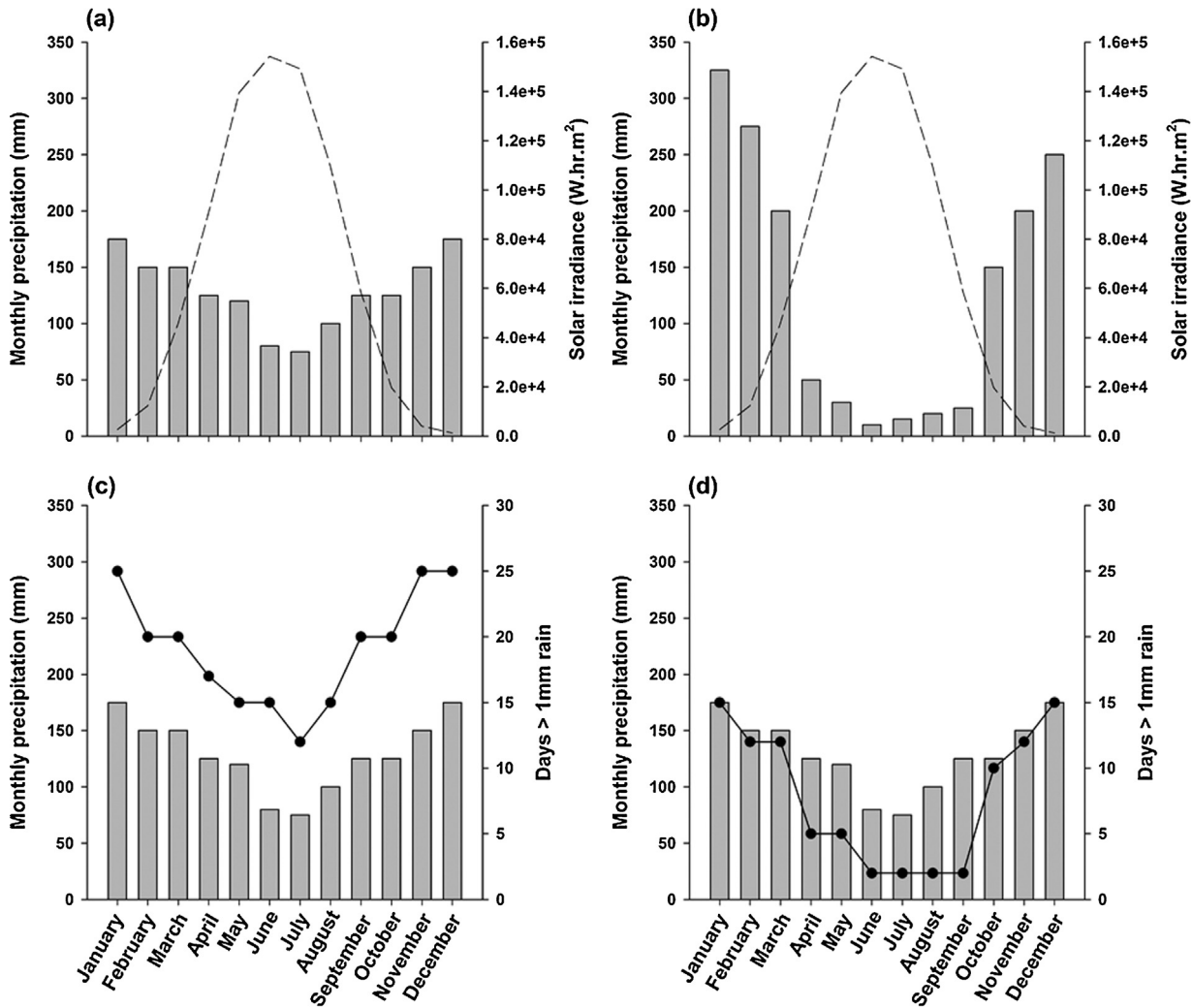
Fig. 1. Comparison between monthly precipitation (bars) that is distributed evenly across the year for the baseline climate (a), but which becomes more strongly seasonal for a climate change scenario (b), thus shifting trends in wetness with respect to values of irradiance (dashed lines) despite maintaining the same annual precipitation total of 1550 mm per year. Also considering a situation in which an alternative parameter for wetness (rain-days, as the number of days per month with ≥1 mm rainfall; closed circles with solid lines), may become decoupled from precipitation totals, for example if rainfall intensity increases between a baseline climate with many rain-days per month (c) and a climate change scenario with fewer rain-days per month (d).

tribution patterns to spatially correlated climate surfaces (Beale et al., 2008; Chapman, 2010), as is standard practice for bioclimatic models. Notwithstanding efforts to address statistical issues such as sample size and bias (Wisz et al., 2008; Boria et al., 2014), the comparison of distribution with climate surfaces implicitly assumes, rather than robustly tests for, climatic control. The problem of non-equilibrium distribution is potentially most serious for subdominant guilds such as epiphytes. These species are nested within and beneath the tree canopy, and are subject to important microclimatic effects (Campbell and Coxson, 2001; Coxson and Coyle, 2003) determined by forest/woodland stand age and structure (McCune and Antos, 1982; Peterson and McCune 2001). This influence of microhabitat may confound species response at scales typical of bioclimatic models (1–10 km²), i.e. landscape distributions might reflect the historical development and spatial pattern of forest/woodland structure, rather than macroclimate. Since they have been the subject of repeated bioclimatic modelling (Ellis et al., 2007a, 2007b, 2014), lichen epiphytes are adopted as an appropriate test-case for this study.

A second criticism relates to the forward projection of climate models, and in particular the extrapolation to future non-analogue climate space (Williams and Jackson, 2007; Fitzpatrick and

Hargrove, 2009). On the one hand, this is avoided by not projecting species response into climate space outside the baseline environment used to build and test bioclimatic models. However, adopting this cautious approach, potential errors arise if species ecological performance is sensitive to climate variability measured over short timescales, i.e. daily, weekly or monthly series (Jentsch et al., 2009; Levine et al., 2011), as opposed to long-term averaged conditions (seasonal or annual) that are often used as model predictors. For example, lichen epiphytes are poikilohydric, and respond to the ambient environment by being dormant when dry, becoming photosynthetically active when rehydrated, though with limited photosynthesis if supersaturated (Lange et al., 1986, 2001). Patterns of photosynthesis and respiration are also affected by temperature and light availability (Sundberg et al., 1997; Palmqvist and Sundberg, 2000). In response to this combination of factors lichen epiphyte growth varies over monthly timescales (Fisher and Procter, 1978; Armstrong, 1993). Physical climate models point to a potential for changed combinations in temperature and precipitation at sub-annual scales (Zeppel et al., 2014), which could therefore affect the weekly to monthly signature of lichen epiphyte growth. This brings into question the validity of seasonal or annual averaged climate predictors, such as the widely applied BIOCLIM