



Bayesian methods for comparing species physiological and ecological response curves



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ABSTRACT

Many ecological questions require information on species' optimal conditions or critical limits along environmental gradients. These attributes can be compared to answer questions on niche partitioning, species coexistence and niche conservatism. However, these comparisons are unconvincing when existing methods do not quantify the uncertainty in the attributes or rely on assumptions about the shape of species' responses to the environmental gradient. The aim of this study was to develop a model to quantify the uncertainty in the attributes of species response curves and allow them to be tested for substantive differences without making assumptions about the shape of the responses. We developed a model that used Bayesian penalised splines to produce and compare response curves for any two given species. These splines allow the data to determine the shape of the response curves rather than making a priori assumptions. The models were implemented using the R2OpenBUGS package for R, which uses Markov Chain Monte Carlo simulation to repetitively fit alternative response curves to the data. As each iteration produces a different curve that varies in optima, niche breadth and limits, the model estimates the uncertainty in each of these attributes and the probability that the two curves are different. The models were tested using two datasets of mosses from Antarctica. Both datasets had a high degree of scatter, which is typical of ecological research. This noise resulted in considerable uncertainty in the optima and limits of species response curves, but substantive differences were found. *Schistidium antarctici* was found to inhabit wetter habitats than *Ceratodon purpureus*, and *Polytrichastrum alpinum* had a lower optimal temperature for photosynthesis than *Chorisodontium aciphyllum* under high light conditions. Our study highlights the importance of considering uncertainty in physiological optima and other attributes of species response curves. We found that apparent differences in optima of 7.5 °C were not necessarily substantive when dealing with noisy ecological data, and it is necessary to consider the uncertainty in attributes when comparing the curves for different species. The model introduced here could increase the robustness of research on niche partitioning, species coexistence and niche conservatism.

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1. Introduction

How species respond to environmental gradients is a fundamentally important topic in ecology, biogeography and evolution (Quintero and Wiens, 2013). These responses, known as species response curves, are at the foundation of species distribution models (Elith and Leathwick, 2009; Guisan and Zimmermann, 2000), which have been increasingly used over the last 15 years to make ecological inferences based on species environmental niches. Recent machine-learning approaches are in

widespread use because of their perceived superior performance in predicting species distributions (Elith et al., 2006), but the actual response curves in these complex models can often be difficult to visualise and interpret ecologically (Elith et al., 2005) and it can be challenging to estimate uncertainty when there is no underlying parametric model. These issues are problematic as evaluating species response curve is an integral part of interpreting species distribution models and assessing their ecological validity (Austin, 2002, 2007).

However, despite their fundamental role in species distribution models, interest in species response curves extends far beyond this specific application. Quantifying the attributes of species response curves, such as the optima, niche breadth or limits where the response is above a certain threshold (Fig. 1a), is crucial for answering many

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physiological, ecological and evolutionary questions even if the objective is not to predict or explain species distributions per se. For example, scientists are often interested in species coexistence, niche separation or overlap (Silvertown, 2004); the relative position or critical limits of species' niches on environmental gradients (Hernandez and Mulla, 2008; Sinervo et al., 2010); niche conservatism over space and time (Pellissier et al., 2013; Peterson et al., 1999); or niche shifts of invasive species in new environments (Hill et al., 2013). For these topics, the shape and attributes of species response curves are the focus of the research, and it is often necessary to compare and test for differences between different curves (e.g. niche conservatism, niche shifts of invasive species, niche separation and overlap).

The attributes of species response curves are difficult to compare using many common statistical models. Response curves can be presented with 95% confidence intervals (e.g. Fig. 1b), but this only quantifies the uncertainty in the response at a given position on the environmental gradient. There is generally no indication of uncertainty for the optima, limits or breadth of the curve as a whole, and there are limitless response curves that fit within the 95% confidence intervals but vary in optima or other attributes (Fig. 1b). This is an important limitation because it is problematic to test if the optima of two curves are different if we have not estimated their uncertainty (Hernandez and Mulla, 2008). This would be analogous to directly comparing the absolute means of two data sets without considering the variances using Student's *t*-test or equivalent.

There are existing methods that can quantify the uncertainty in the optima of a response curve, but these generally need to make assumptions about the shape of the response curve and focus only on the attribute of interest (Björnsson et al., 2001; Dreyer et al., 2001; Hernandez and Mulla, 2008; Vetaas, 2000). For example, some methods rely on the assumption that there are Gaussian responses to environmental gradients, even though evidence suggests skewed or non-normal response curves are common, and even more complex shapes such as multi-

modal curves are possible when dealing with realised rather than fundamental niches (Austin, 2002, 2007; Oksanen and Minchin, 2002). Other methods allow skewed responses by fitting parametric functions (e.g. Higgins et al., 2014), and this also allows scope for the uncertainty in some attributes of response curves to be quantified. However, there is still scope to estimate the uncertainty in the optima and other attributes of species response curves using a semi-parametric method that does not make a priori assumptions about the shape of a given response.

Bayesian models have the potential to address this deficiency. Bayesian models (McCarthy, 2007) can be fitted using Markov Chain Monte Carlo (MCMC) random sampling which iteratively fits alternative species response curves that can explain the observed data. It does this by simulating sets of parameter values from their Bayesian posterior distributions, then generating values from the resultant response curves. After repeating this thousands of times, the collection of simulated values can be used to estimate not just the mean and 95% credible intervals (the Bayesian equivalent of confidence intervals; McCarthy, 2007) for the species response curves (Fig. 1b), but also the mean and credible intervals for other attributes of the curve, such as the optima, niche breadth and limits.

In this paper we adapt the Bayesian penalised splines of Crainiceanu et al. (2005) to predict species response curves. Similarly to the Generalised Additive Models commonly used in ecological studies (GAMS; Hastie and Tibshirani, 1990; Guisan and Zimmermann, 2000; Austin, 2002; Elith et al., 2006), the shape of penalised splines is determined by the data, so the shape of the response curves can be skewed or even multi-modal. However, the curves are smooth unlike methods such as classification and regression trees (Elith et al., 2008) and Maxent (Phillips et al., 2006), which can have discrete steps. The advantage of the Bayesian implementation of penalised splines is that the iteration involved allows us greater flexibility to examine the uncertainty in many attributes of the fitted curves. Our model was designed to estimate the means and 95% credible intervals for the peak and optima, as well as the niche breadth and limits based on a threshold of 80% of the peak (Fig. 1a). The model could also be modified to examine other attributes of species response curves or to use predefined response shapes such as Gaussian, Beta distribution, Huisman–Olf–Fresco (HOF) models (Oksanen and Minchin, 2002) or the Arrhenius equation. If applied to parametric models it could be used to estimate the uncertainty in the parameter estimates.

The overall objective of this study was to develop a model that allowed users to quantify uncertainty in a wide range of attributes of species response curves and enable comparison with other curves. This represents an important advance from prior studies that primarily compare optima or limits of species response curves without considering the uncertainty in those estimates, or which estimate the uncertainty in a limited number of attributes by assuming, a priori, the shape of the response curve. Additionally, such a model also needs to be inherently flexible so that it can be applied to a wide variety of datasets or modified to address similar research questions.

The model is demonstrated here using two datasets of mosses in Antarctica. The first example uses an unrestricted continuous response variable, and examines whether the optimal temperature for photosynthesis varies between two species of moss from maritime Antarctica. The second uses a response variable that is constrained to a range of zero to one (proportion of presences in samples along a moisture gradient), and examines whether two species of moss from continental Antarctica have different moisture optima. The two examples illustrate how the model can be used to test for differences between the response curves of different species using contrasting types of response variables.

2. Materials and methods

2.1. Model development

The Bayesian models were developed in R (R Core Team, 2014) using the R2OpenBUGS package. This requires the OpenBUGS software application to be installed, which is a newer open-source version of WinBUGS.

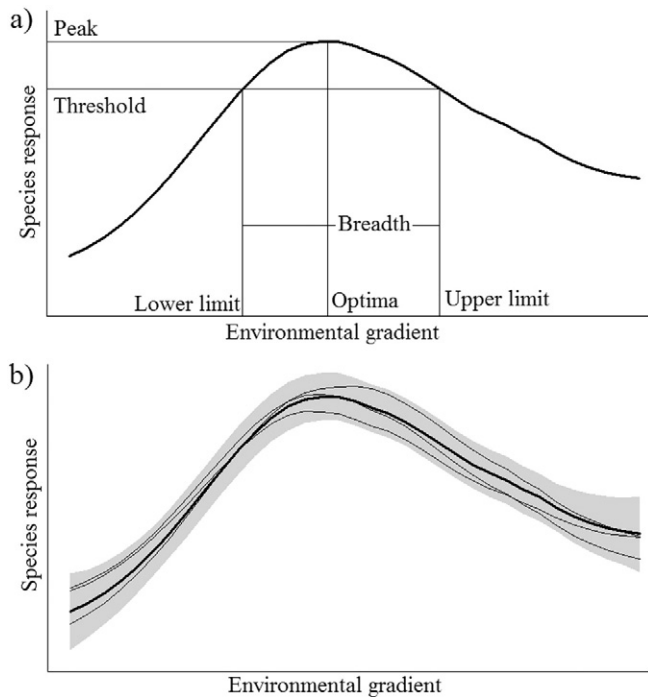


Fig. 1. A species response to an environmental gradient (bold line) has attributes such as its peak (maximum Y value), optima (corresponding X value), and for a given Y threshold, a niche breadth and upper and lower limit (a). Traditional statistical methods can capture the uncertainty in response for given environmental conditions (95% confidence interval – grey shading in (b)) but there are limitless alternative curves (e.g. thin lines in (b)) that fit within this zone of uncertainty and there is no estimate of uncertainty for the optima, peak or other attributes of the curves unless you make assumptions about the shape of the response.

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