

7-2016

Bayesian Methods for Comparing Species Physiological and Ecological Response Curves

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Citation Details

Ashcroft, M. B., Casanova-Katny, A., Mengersen, K., Rosenstiel, T. N., Turnbull, J. D., Wasley, J., Waterman, M. J., Zuniga, G. E. & Robinson, S. A. (2016). Bayesian methods for comparing species physiological and ecological response curves. *Ecological Informatics*, 34 35-43

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1 **Bayesian methods for comparing species physiological and ecological response curves**

2 Running title: Comparing species response curves

3 Word count: 6367

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28 Abstract

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

53 uncertainty in attributes when comparing the curves for different species. The model
54 introduced here could increase the robustness of research on niche partitioning, species
55 coexistence and niche conservatism.

56 **Keywords:** Antarctic moss; community ecology; niche partitioning; photosynthesis;
57 physiological response; uncertainty

58 **1. Introduction**

59 How species respond to environmental gradients is a fundamentally important topic in
60 ecology, biogeography and evolution (Quintero & Wiens 2013). These responses, known as
61 species response curves, are at the foundation of species distribution models (Guisan &
62 Zimmermann 2000; Elith & Leathwick 2009), which have been increasingly used over the
63 last 15 years to make ecological inferences based on species environmental niches. Recent
64 machine-learning approaches are in widespread use because of their perceived superior
65 performance in predicting species distributions (Elith *et al.* 2006), but the actual response
66 curves in these complex models can often be difficult to visualise and interpret ecologically
67 (Elith *et al.* 2005) and it can be challenging to estimate uncertainty when there is no
68 underlying parametric model. These issues are problematic as evaluating species response
69 curves is an integral part of interpreting species distribution models and assessing their
70 ecological validity (Austin 2002, 2007).

71 However, despite their fundamental role in species distribution models, interest in
72 species response curves extends far beyond this specific application. Quantifying the
73 attributes of species response curves, such as the optima, niche breadth or limits where the
74 response is above a certain threshold (Fig. 1a), is crucial for answering many physiological,
75 ecological and evolutionary questions even if the objective is not to predict or explain species
76 distributions *per se*. For example, scientists are often interested in species coexistence, niche
77 separation or overlap (Silvertown 2004); the relative position or critical limits of species'
78 niches on environmental gradients (Hernandez & Mulla 2008; Sinervo *et al.* 2010); niche
79 conservatism over space and time (Peterson *et al.* 2009; Pellissier *et al.* 2013); or niche shifts
80 of invasive species in new environments (Hill *et al.* 2013). For these topics, the shape and
81 attributes of species response curves are the focus of the research, and it is often necessary to

82 compare and test for differences between different curves (e.g. niche conservatism, niche
83 shifts of invasive species, niche separation and overlap).

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

94 There are existing methods that can quantify the uncertainty in the optima of a
95 response curve, but these generally need to make assumptions about the shape of the response
96 curve and focus only on the attribute of interest (Vetaas 2000; Björnsson *et al.* 2001; Dreyer
97 *et al.* 2001; Hernandez & Mulla 2008). For example, some methods rely on the assumption
98 that there are Gaussian responses to environmental gradients, even though evidence suggests
99 skewed or non-normal response curves are common, and even more complex shapes such as
100 multi-modal curves are possible when dealing with realised rather than fundamental niches
101 (Austin 2002, 2007; Oksanen & Minchin 2002). Other methods allow skewed responses by
102 fitting parametric functions (e.g. Higgins *et al.* 2014), and this also allows scope for the
103 uncertainty in some attributes of response curves to be quantified. However, there is still
104 scope to estimate the uncertainty in the optima and other attributes of species response curves
105 using a semi-parametric method that does not make *a priori* assumptions about the shape of a
106 given response.

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

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

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

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

147

148 **2. Materials and methods**

149 2.1 MODEL DEVELOPMENT

150 The Bayesian models were developed in R (R Core Team 2014) using the R2OpenBUGS
151 package. This requires the OpenBUGS software application to be installed, which is a newer
152 open-source version of WinBUGS. All software is freely available for download. The models
153 require a data file (cwc2003data.csv, etrdatahigh.csv or etrdatalow.csv in Supplementary
154 Material), a file which implements the OpenBUGS model (SplineModels.txt or
155 SplineModelsLogit.txt in Supplementary Material) and a set of R commands to specify model

156 parameters, run the model and display results (Rcommands.txt in Supplementary Material).
157 The analyses in this article can be repeated by downloading the files in the Supplementary
158 Material, updating the 4th line of Rcommands.txt to point to the directory where the files are
159 located, and adjusting lines 6–10 to select the desired case study. As the models are
160 stochastic, results will not necessarily be identical every time the models are run.

161 Bayesian penalised splines are semiparametric models that had already been
162 implemented in a model for WinBUGS in R by Crainiceanu *et al.* (2005), and this formed the
163 basis for the model included here. Spline models are developed by fitting a number of
164 polynomial segments that are joined together at knot points spread evenly along the
165 environmental gradient. With four knots there is one polynomial from 0% to 20%, another
166 from 20% to 40%, and so on. The polynomials join together to form a continuous smooth
167 curve (spline) that has flexibility in its shape. More knots allow more complex shapes to be
168 fitted, but more data is needed to reduce the potential for overfitting. The original model used
169 20 knots, although this was reduced to four in our model. Having too many knots allows
170 complex responses that may be difficult to explain, and increases the uncertainty in the
171 attributes of response curves as they can take more varied forms (see Results section).

172 The original model of Crainiceanu *et al.* (2005) fitted one spline based on a dataset
173 containing a single response and covariate, but was modified to produce two splines for two
174 different datasets. The model initially only predicted the response for the environmental
175 conditions in the samples. To ensure complete response curves were produced for both
176 species the model was modified to accept three sets of environmental samples: *X1* for the
177 samples for the first response, *X2* for the samples for the second response, and *X* for the
178 complete gradient. The complete gradient was chosen such that it extended 2% past the
179 minimum and maximum environmental values from both data sets and was broken up into
180 300 samples to increase the precision with which the attributes could be estimated.

181 In each iteration of the MCMC algorithm, the two response curves were produced,
182 and the peak, optima, niche limits and breadth were then calculated deterministically from the
183 curves. A posterior mean and associated percentiles for these attributes were then calculated
184 based on a large number of iterations. Similarly, the step function in OpenBUGS was used to
185 estimate the probability that the attribute of one curve was larger than that of the other. This
186 is referred to as a P-value in the remainder of this paper, although it is acknowledged that it
187 does not have the same interpretation as a P-value obtained under a frequentist paradigm. We
188 considered a result to be substantive if the P-value was less than 5%, which occurs if the
189 attribute for one curve was higher than the other in 95% of the iterations. We acknowledge
190 this is different to traditional frequentist P-values, where a P-value of 5% indicates that there
191 is only a 5% chance that the results could have been obtained if there was actually no
192 difference. As our model estimates a P-value, thresholds other than 5% could also be used.

193

194 2.2 CASE STUDY 1: CONTINUOUS DATA OF PHOTOSYNTHETIC RATE

195 The model was tested on an effectively unbounded continuous response variable
196 (photosynthetic rate) using two species of moss from Ardley Island in the maritime Antarctic
197 (62.2 °S, 58.9 °W), *Polytrichastrum alpinum* (Hedw.) G.L. Sm. and *Chorisodontium*
198 *aciphyllum* (Hook.f. & Wilson) Broth. These two species of moss coexist in some
199 communities and we were interested in comparing their photosynthetic responses to
200 temperature. The two species have similar habitats, but *C. aciphyllum* has a very compact turf
201 structure with its gametophytes densely packed together while the *P. alpinum* turf is more
202 open, resulting in more space between adjacent gametophytes (see Fig 2). Antarctic moss
203 turves can maintain temperatures well above air temperature, especially in sun-exposed but
204 wind-sheltered sites (Smith 1988; Bramley-Alves *et al.* 2014). As a more open structure
205 allows wind to penetrate into the moss beds and potentially keep temperatures lower, we

206 were interested in whether the optimal temperature for photosynthesis for *P. alpinum* was
207 lower than that for *C. aciphyllum*.

208 Samples of moss tissue were collected in January 2015 and maintained in plastic
209 containers under field conditions for up to 2 days prior to measurements being made in the
210 laboratory of the Chilean Escudero Base on King George Island. Photosynthetic activity was
211 measured for both species in a water bath with temperatures varying from 1 to 44 °C.
212 Hydrated moss plugs (1 cm²; n = 6) were contained in aluminium cups to allow heat transfer
213 within the water bath but prevent submergence and ensure the photosynthetic surface of the
214 moss remained exposed to air. Moss was induced prior to measurements using a Dracast
215 LED160a light source (Dracast, San Jose, CA, USA) which also provided the actinic light
216 during the experiment.

217 Measurements were made under both low (non-saturating; 400 μmol photons m⁻² s⁻¹)
218 and high (saturating; 1000 μmol photons m⁻² s⁻¹) light. Surface photosynthetically active
219 radiation (PAR) was measured using an Apogee mq-200 quantum light sensor (Apogee
220 Instruments, Logan UT, USA). Thermocouples were used to measure temperature of the
221 photosynthetic tissue at the time of each photosynthetic rate measurement. Photosynthetic
222 rates were quantified using chlorophyll fluorescence (measured as Electron Transport Rate;
223 ETR; μmol e m⁻² s⁻¹) with a Walz MINI-PAM Photosynthesis Yield Analyser (Walz,
224 Effeltrich, Germany). ETR was calculated using the equation $ETR = \phi_{PSII} \times PAR \times 0.5 \times$
225 0.84 (Maxwell & Johnson 2000), where ϕ_{PSII} is the quantum yield of photosystem II,
226 estimated using chlorophyll fluorescence and PAR is the photosynthetically active radiation.
227 This widely used equation makes the assumption that the leaf, or gametophyte, absorbs 84%
228 of the incident light and that this light is shared equally between the two photosystems.

229 The Bayesian model was used to estimate the peak ETR, the optimal temperature, the
230 temperature limits corresponding to a threshold of 80% of the maximum ETR, and the

231 breadth of the response curve between these limits. The model also tested if the two species
232 were significantly different in any of these attributes. The model was repeated using the two
233 response curves for each species to test whether the attributes for either species were
234 substantively different under low and high light.

235

236 2.3 CASE STUDY 2: PROBABILITY OF PRESENCE ALONG MOISTURE GRADIENT

237 Sixty quadrats were surveyed in January and February 2003 across two long-term monitoring
238 sites near the Australian Casey station (66.28 °S, 110.53 °E) in the Windmill Islands, East
239 Antarctica (detailed site descriptions in Wasley *et al.* 2012 and Bramley-Alves *et al.* 2015).
240 The monitoring of these sites forms Australia's State of the Environment Indicator 72
241 (<https://data.aad.gov.au/aadc/soe/>). Each site contained 10 transects along a moisture
242 gradient, with three quadrats (25 × 25 cm) per transect. Quadrats were positioned in three
243 distinct vegetation communities; bryophyte dominated, lichen dominated, and a transitional
244 community in between (mix of moribund moss and encrusting lichens). In each quadrat, nine
245 small samples (tweezer pinches of vegetation) were taken and scored for presence or absence
246 of bryophyte and lichen species. These data were linearly scaled to a range of zero (not found
247 in any of the nine samples) to one (found in all nine samples). In this analysis, we focus on
248 how two of the dominant moss species (*Schistidium antarctici* (Card.) L. Savic. & Smirn.
249 (syn. *Grimmia antarctici* (Card.)) and *Ceratodon purpureus* (Hedw.) Brid.) respond to a
250 water availability gradient, and test the hypothesis that there is niche separation along this
251 gradient.

252 Community water content (CWC) was estimated by inserting a sponge into the
253 vegetation layer adjacent to each quadrat and measuring the amount of water it absorbed over
254 24 h (as described in Lucieer *et al.* 2014). This one-off measurement of water content may
255 not represent the long-term water availability in any quadrat, but does serve to differentiate

256 the moistest and driest quadrats and is a relative estimate of water availability in the
257 vegetation where the sponge was placed.

258 To model the proportion of samples where the species was present some minor
259 changes were needed in the model. Namely, as the response variable was constrained to a
260 range of zero to one a logit transform was added to four lines in SplineModelsLogit.txt (see
261 Supplementary Material) to replace the corresponding lines in SplineModels.txt. These
262 changes ensured the predicted response was not outside the range of zero to one after back
263 transformation. The data file was replaced (cwc2003data.csv in Supplementary Material) and
264 Rcommands.txt was modified to refer to the new data and model. The modified
265 SplineModelsLogit.txt model would be suitable for analysing a range of presence-absence
266 data where the response is constrained to zero to one, or percentage data, such as humidity,
267 where the response is constrained to 0–100% (e.g. Ashcroft & Gollan, 2012).

268

269 **3. Results**

270 3.1 PHOTOSYNTHETIC TEMPERATURE RESPONSE CURVES

271 The ETR data for both species under both high and low light conditions contained a high
272 degree of scatter, and there was considerable uncertainty in all the attributes for each of the
273 photosynthetic temperature response curves (Fig. 3, S1). The curves were somewhat skewed
274 and contained additional points of inflection that were not consistent with Gaussian response
275 curves. With 20 knots the response curves contained additional complexity, and this
276 increased the uncertainty in where the optima were located (Fig. S2). We therefore focus on
277 results from models with four knots in this paper, although the method itself is equally valid
278 with 20 knots and could be useful if there is sufficient data with less noise.

279 Under high light conditions, the peak ETR for *P. alpinum* was higher than that for *C.*
280 *aciphyllum*, but not significantly so (mean peaks of 200.2 and 186.2 $\mu\text{mol e m}^{-2} \text{ s}^{-1}$; $P =$

281 0.096; Fig. 3a). The optimal temperature for photosynthesis in *P. alpinum* was significantly
282 lower than for *C. aciphyllum* (mean optima of 21.7 °C and 28.5 °C; $P = 0.012$), but there
283 were no significant differences in the limits ($P = 0.122, 0.266$) or the breadth of the curves (P
284 $= 0.221$; Fig. 3a).

285 Under low light conditions the peaks were reversed, with the peak for photosynthesis
286 in *P. alpinum* significantly lower than that for *C. aciphyllum* (mean peaks of 86.6 and 95.4
287 $\mu\text{mol e m}^{-2} \text{ s}^{-1}$; $P = 0.022$; Fig. 3b). The optima were not significantly different (mean optima
288 of 17.4 °C and 24.9 °C; $P = 0.055$) but there was a difference in the upper limits (mean upper
289 limits of 31.8 °C and 36.9 °C; $P = 0.031$). The differences in lower limits and breadths were
290 not significantly different ($P = 0.588, 0.247$; Fig. 3b). The hypothesis that the temperature
291 optima of *P. alpinum* would be lower than that of *C. aciphyllum* was supported by both data
292 sets, but it was only significant under high light conditions (low light 95% CI 12.3–25.0 °C,
293 20.9–28.6 °C, $P = 0.055$; high light 95% CI 19.2–25.0 °C, 24.2–34.3 °C, $P = 0.012$; Fig. 3).

294 When the same data were analysed to compare the low and high light photosynthetic
295 temperature responses for each species (Fig. S1), the peaks and lower limits were
296 significantly higher under high light conditions ($P < 0.05$). The temperature optima were also
297 higher under high light conditions for both species, but these differences were not significant
298 ($P = 0.121, 0.074$; Fig. S1). Both curves were noticeably flatter under low light conditions.

299

300 3.2 PRESENCE-ABSENCE ALONG A MOISTURE GRADIENT

301 The response curves for the presence of *C. purpureus* and *S. antarctici* along a moisture
302 gradient were significantly different in terms of optima, peak, limits and breadth ($P \leq 0.002$;
303 Fig. 4). *Ceratodon purpureus* presence had an optima at relatively low water availability and
304 was absent from the moister quadrats, while *S. antarctici* was much more prevalent in the
305 moister quadrats. Once again the response curves were noticeably skewed indicating that

306 Gaussian responses would not be a good fit. In terms of the niche separation hypothesis, *S.*
307 *antarctici* inhabited significantly wetter microhabitats than *C. purpureus* (95% CI 0.27–0.57,
308 >1.28, $P < 0.001$, Fig. 4). This finding is in keeping with previous physiological studies
309 indicating that *C. purpureus* is more desiccation tolerant than *S. antarctici* (Robinson *et al.*
310 2000) but less tolerant of submergence (Wasley *et al.* 2006).

311

312 **4. Discussion**

313 A flexible and robust model has been successfully developed as a reliable strategy to compare
314 species response curves whilst also incorporating uncertainties in the data sets. Ecological
315 data from two case studies on Antarctic moss was visualised and interpreted using this model
316 allowing certain ecological niches to be identified.

317 The data used in this study had a high degree of scatter, which is typical of many
318 ecological studies. The models identified large differences in the attributes of the species
319 response curves, but not all of these differences were significant given the uncertainty in the
320 data and the semiparametric nature of the fitted model. For example, the mean low light
321 optima for *P. alpinum* (17.4 °C; Fig. 3b) was 7.5 °C lower than that for *C. aciphyllum* (24.9
322 °C), but the models suggested this difference was marginally non-substantive using a
323 traditional threshold of $\alpha = 0.05$ ($P = 0.055$) and there was overlap in the 95% credible
324 intervals (12.3–25.0 and 20.9–28.6 respectively). This example highlights the importance of
325 considering uncertainty in the optima and other attributes of species response curves. Our
326 models produce a P-value for the probability the two optima are different, and with minor
327 modifications could produce a 95% credible interval for what the difference is. This is much
328 more informative than taking no account of the uncertainty and simply comparing the
329 estimates of optima, and asserting a difference of 7.5 °C. Our P-values highlight it would be
330 premature to make this conclusion with the given data. A larger sample size or broader

331 temperature range would be needed to reduce uncertainty and prove that differences between
332 the curves are substantive.

333 The estimated uncertainty in optima is even higher if more complex response curves
334 are fitted, for example by using 20 knots instead of four (Fig. S2). The uncertainty is
335 especially high near the extremities of environmental gradients where it is uncertain if splines
336 may continue to increase or decrease. To reduce this uncertainty, data should be gathered
337 over as wide a range of environmental conditions as possible, however reducing the number
338 of knots also limits the amount of extrapolation that is possible.

339 Numerous other approaches have been used to estimate the attributes of species
340 response curves or compare them between different species. Some researchers have
341 compared response curves by classifying them into a limited number of predefined categories
342 based on the approximate position of the optima or the shape of the curve (Oksanen &
343 Minchin 2002; Horsák 2006). Others have estimated the uncertainty in the optima or
344 compared curves by assuming the shape of the response curve is known (Vetaas 2000;
345 Björnsson *et al.* 2001; Dreyer *et al.* 2001; Hernandez & Mulla 2008). Another approach is to
346 compare entire curves quantitatively but without considering uncertainty in the curves
347 (Warren *et al.* 2008; Hill *et al.* 2013). Similarly, thermal tolerance limits are often determined
348 from observational data without any estimate of uncertainty (Pellissier *et al.* 2013; Gouveia *et*
349 *al.* 2014). The Bayesian semi-parametric model used here is advantageous because it
350 quantifies the uncertainty in the attributes of species response curves without assuming a
351 rigorous (parametric) shape of the response. This will increase the robustness of ecological
352 studies on niche conservatism, niche partitioning and species coexistence. The method could
353 also be extended to quantify the uncertainty in other attributes of species response curves,
354 such as the probability the curve is above a certain threshold, determining the ranks of

355 multiple curves, or testing multiple curves for substantive differences if one species is used as
356 a reference class (McCarthy 2007).

357

358 4.1 LIMITATIONS AND FUTURE ENHANCEMENTS

359 The model as it is currently implemented is restricted to a single covariate. As our
360 photosynthesis results illustrate, the optima and limits on any gradient (e.g. temperature) may
361 be affected by other conditions (e.g. light). For example, the optima we observed under low
362 light were lower than the optima under high light (Fig. S1), even if these differences were
363 marginally non-substantive ($P = 0.074, 0.121$). The shapes of the curves were also different:
364 moss ETR did not change dramatically with temperature under low light conditions (flat red
365 curves in Fig. S1) but did increase notably near the optimal temperature under high light
366 conditions. It is possible to examine the optima along a single environmental gradient if other
367 factors are held constant, but if multiple environmental factors are varied then the position of
368 the optima may not be constant on any individual gradient.

369 Similarly, the current implementation only caters for a single pair of species.
370 However, if one species is used as a reference then multiple species can be included in a
371 Bayesian ANOVA analysis with each tested for substantive differences against the reference
372 species (McCarthy 2007). This is not implemented in the current script but would be a
373 relatively straight forward extension.

374 As noted in the methods section the ETR calculations were based on an assumption
375 that turf absorbance was 0.84 for both species. This may not be the case. While this is not
376 important for the methodology introduced in this paper, it may affect the comparisons of the
377 peak in the first case study. If the actual absorbance has not been measured then it would be
378 more correct to compare different species on the basis of relative ETR (scaled to % maximum
379 ETR). This could easily be accommodated by applying the techniques used in the

380 presence/absence example where data are scaled to a range of zero to one, or by placing a
381 prior distribution on the value to represent this uncertainty. This prior will then induce
382 associated uncertainty in the posterior estimates and associated comparisons and inferences.

383 Another limitation is that the model does not predict optima that are outside the range
384 of the environmental gradient examined. For example, it appears that the peak for
385 *S. antarctici* occurred at a log(CWC) higher than 1.28 (Fig. 4). It is relatively simple to
386 extend the range of the environmental gradient in the model to make predictions at higher
387 values but this would be highly uncertain, especially given the semiparametric setup of the
388 model, and was deliberately avoided. In our study it is not clear if the curve would begin to
389 fall at higher water contents, or whether it becomes limited by water depth, substrate
390 availability or flow rate once the moss is completely saturated. To accurately predict optima
391 or limits that are outside the range of observations it would be better to collect data over a
392 broader range of conditions. Any 95% credible intervals that include either of the extremities
393 on the environmental gradient may not be accurate and should be interpreted cautiously.

394 Despite these limitations the models developed in this study provide ecologists and
395 physiologists with a powerful tool for assessing species response curves along single
396 environmental gradients. The methods we present here allow quantification of attribute
397 uncertainty, which represents an important advance of studies that currently compare species
398 response curves qualitatively or subjectively without considering the uncertainties involved.

399

400 **Acknowledgements**

401 This research was primarily funded through Australian Research Council DP110101714 and
402 Australian Antarctic Science grants AAS1313 and AAS4046 with logistical support from the
403 Australian Antarctic Division for visits to Casey Station and Instituto Antártico Chileno
404 (INACH) for Julio Escudero Station. ACK was supported by the grant FONDECYT

405 1120895, and INACH FR 0112 and the VRIDEI, USACH; GEZ was supported by the grant
406 FONDECYT 1140189, CEDENNA and Proyectos Basales, VRIDEI, USACH. TNR was
407 supported by the U.S. National Science Foundation (grants 1341742 and 1258225). KM
408 acknowledges support from ARC DP and COE funding schemes and from the QUT Institute
409 for Future Environments. MW held Australian Postgraduate and AINSE Awards during the
410 time of the study. JW held an APA at the time of field data collection.

411

412 **Data accessibility**

413 The data and models used in this study are available in the Supplementary Material.

414

415 **References**

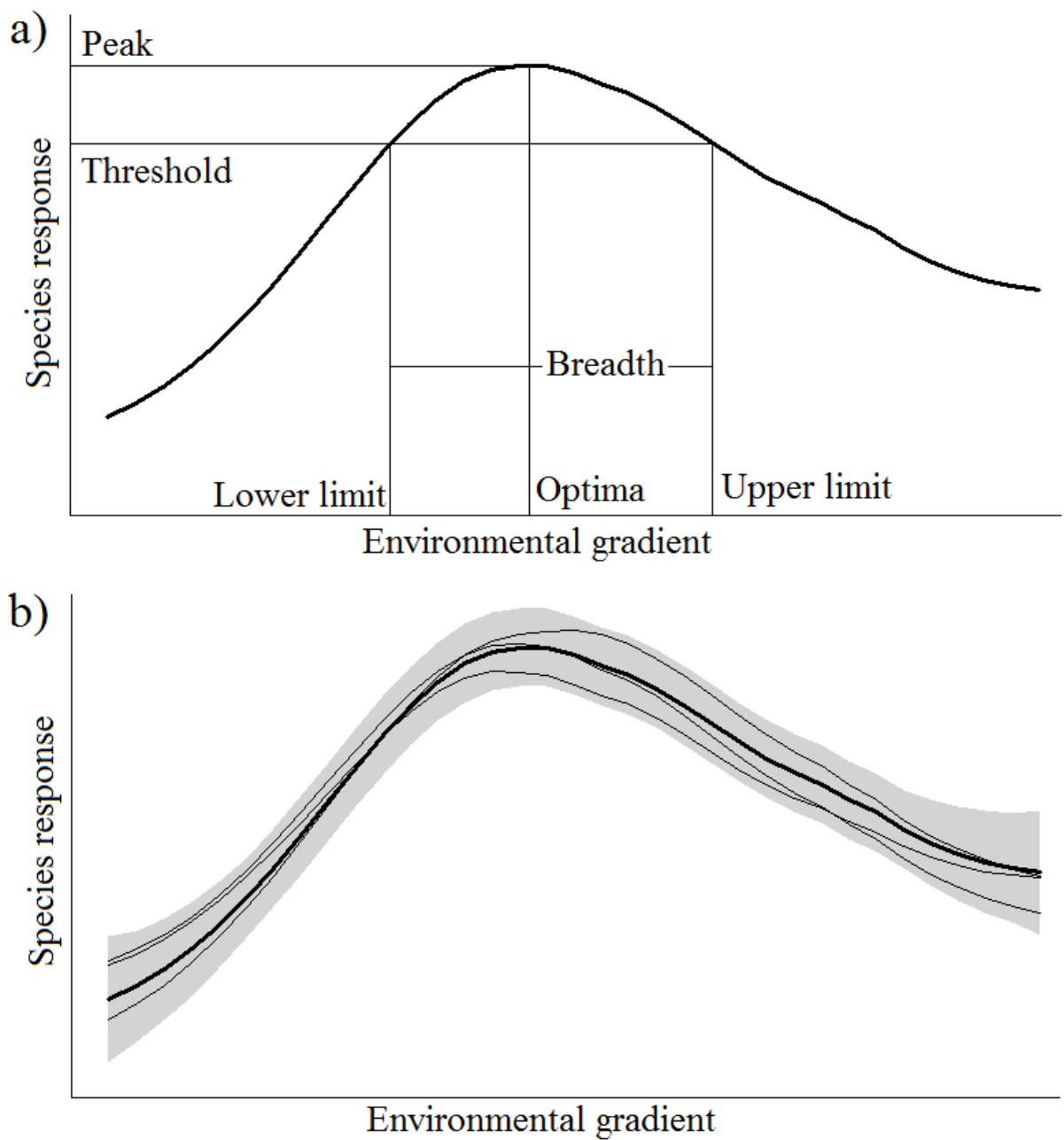
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520

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

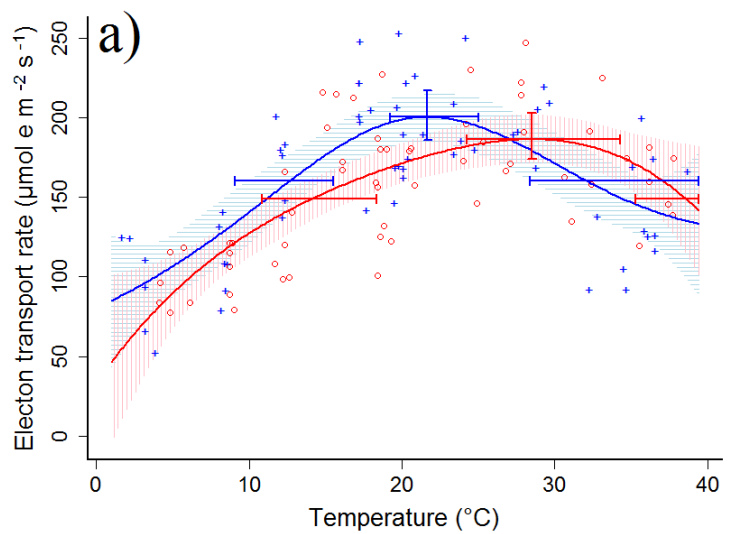


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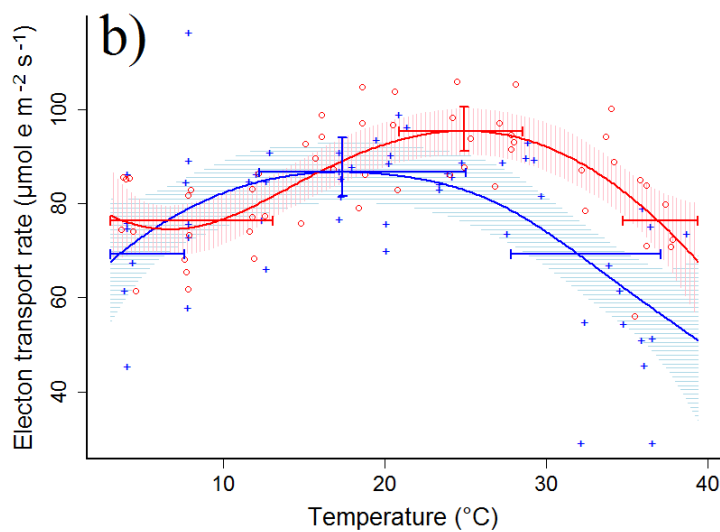
529 **Fig. 2** The open turf structure of *Polytrichastrum alpinum* (top), with gametophytes more
530 widely spaced from one another, contrasts with the densely packed *Chorisodontium*
531 *aciphyllum* (bottom) illustrated in cross section as well as from above. We hypothesised that
532 the different turf structures could influence the photosynthetic temperature response curves of
533 the two species (Fig. 3). Photographs taken on King George Island by SR and MW.

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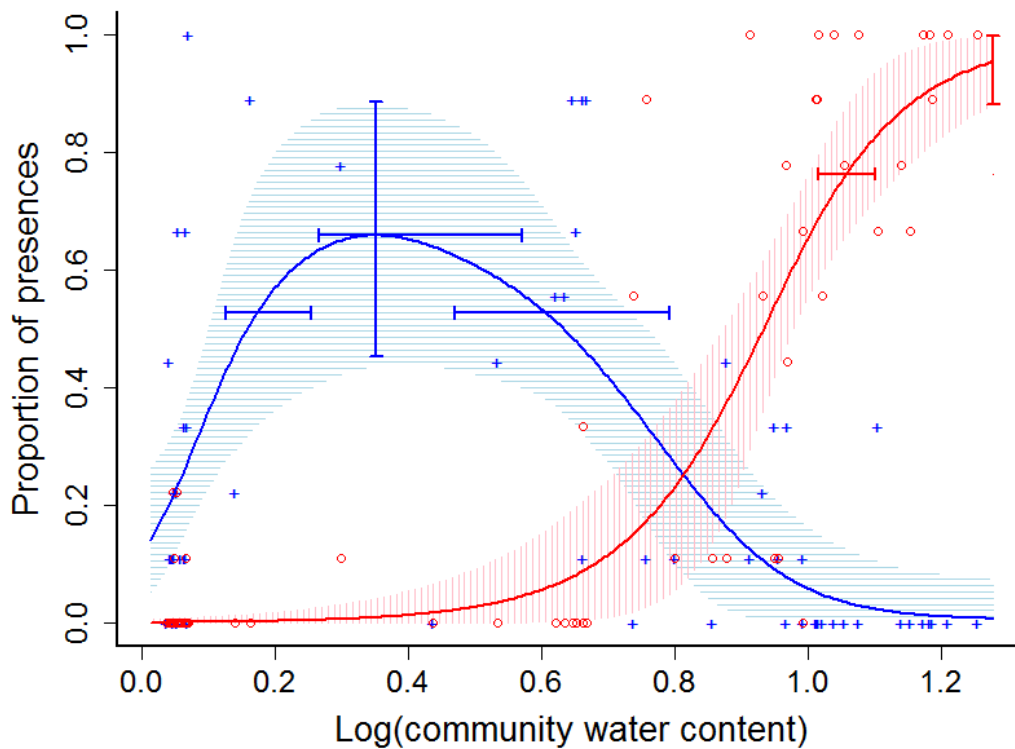
	P.alpinum mean	(blue) CI	C.aciphyllum mean	(red) CI	P-Value
Peak	200.2	185.7-216.9	186.2	173.6-202.9	0.096
Optima	21.7	19.2-25	28.5	24.2-34.3	0.012
Upper X limit	32.9	28.4-39.4	38.2	35.3-39.4	0.122
Lower X Limit	12.7	9.1-15.5	14.4	10.9-18.3	0.266
Breadth	20.2	14.5-27.9	23.8	18.3-28.2	0.221



	P.alpinum mean	(blue) CI	C.aciphyllum mean	(red) CI	P-Value
Peak	86.6	81.6-94	95.4	91.1-100.4	0.022
Optima	17.4	12.3-25	24.9	20.9-28.6	0.055
Upper X limit	31.8	27.8-37.1	36.9	34.8-39.4	0.031
Lower X Limit	4.3	3-7.6	5.8	3-13.1	0.588
Breadth	27.5	21.5-33.5	31.1	22.5-36.4	0.247

536

537 **Fig. 3** Photosynthetic temperature response curves under high (a) and low (b) light. Data
 538 fitted with Bayesian models using splines with four knots. The responses are shown for
 539 *Polytrichastrum alpinum* (blue crosses, lines and horizontal shading) and *Chorisodontium*
 540 *aciphyllum* (red circles, lines and vertical shading). Shaded bands highlight the 95% credible
 541 intervals for the responses. Error bars highlight the 95% credible intervals for the peak and
 542 optima as well as the upper and lower limits based on a threshold of 80% of the peak. The
 543 posterior means and 95% credible intervals are provided in the tables underneath, with a P-
 544 value given for the probability that the two curves are different with respect to each attribute.



	C.purpureus mean	(blue) CI	S.antarctici mean	(red) CI	P-Value
Peak	0.66	0.45-0.89	0.95	0.88-1	0.002
Optima	0.35	0.27-0.57	1.28	1.28-1.28	<0.001
Upper X limit	0.61	0.47-0.79	1.28	1.28-1.28	<0.001
Lower X Limit	0.18	0.13-0.25	1.06	1.01-1.1	<0.001
Breadth	0.43	0.32-0.61	0.22	0.18-0.26	<0.001

545
546

547 **Fig. 4** The proportion of presences in nine pinch samples in a quadrat that contained
 548 *Ceratodon purpureus* (blue crosses, lines and horizontal shading) or *Schistidium antarctici*
 549 (red circles, lines and vertical shading) from samples collected over a moisture gradient in
 550 2003. Species response curves have been fitted with Bayesian models using splines with four
 551 knots. See Fig. 3 for full explanation of error bars.