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Bayesian Methods for Comparing Species Physiological and Ecological Response Curves

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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

1. Introduction

How species respond to environmental gradients is a fundamentally important topic in ecology, biogeography and evolution (Quintero & Wiens 2013). These responses, known as species response curves, are at the foundation of species distribution models (Guisan & Zimmermann 2000; Elith & Leathwick 2009), 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 curves 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 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 & Mulla 2008; Sinervo *et al.* 2010); niche conservatism over space and time (Peterson *et al*. 2009; Pellissier *et al*. 2013); 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

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—Olff—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 cm^2; 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 = ɸPSII × PAR × 0.5 ×

225   0.84 (Maxwell & Johnson 2000), where ɸPSII 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 μmol e m^{-2} 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   µmol e m^{-2} 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 ≤ 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

412   **Data accessibility**

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

414

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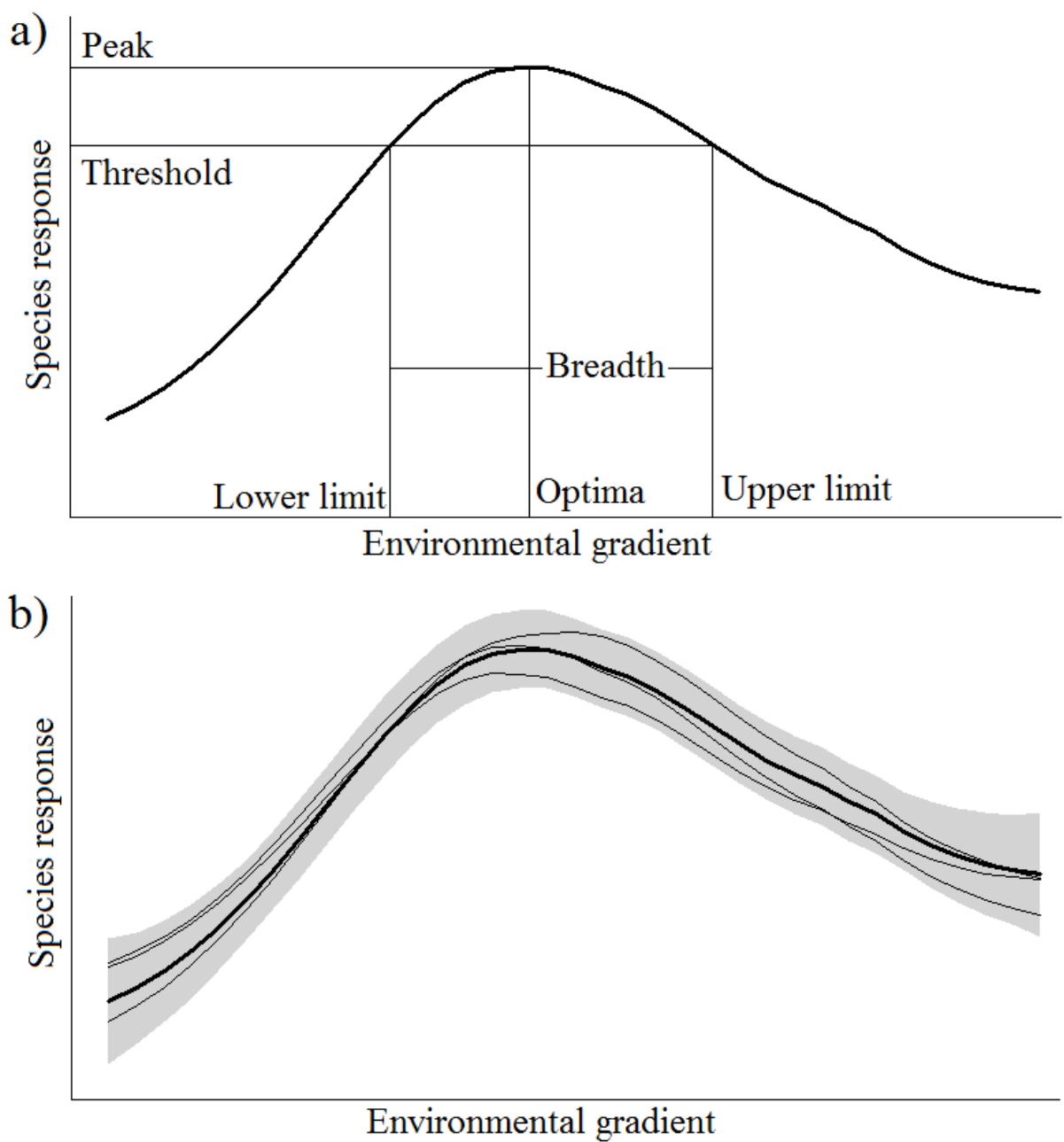
521   **Fig. 1** A species response to an environmental gradient (bold line) has attributes such as its

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.

Fig. 2 The open turf structure of *Polytrichastrum alpinum* (top), with gametophytes more

widely spaced from one another, contrasts with the densely packed *Chorisodontium*

aciphyllum (bottom) illustrated in cross section as well as from above. We hypothesised that

the different turf structures could influence the photosynthetic temperature response curves of

the two species (Fig. 3). Photographs taken on King George Island by SR and MW.

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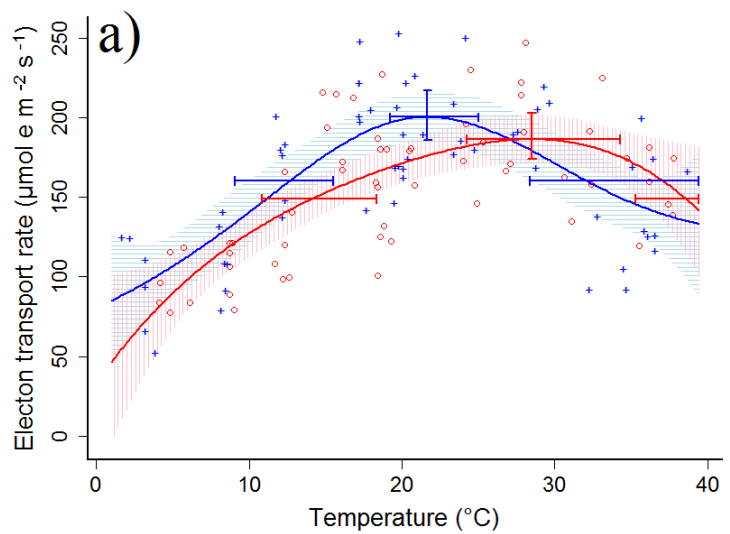
	P.alpinum	(blue)	C.aciphyllum	(red)	P-Value
	mean	CI	mean	CI	
Peak	200.2	185.7-216.9	186.2	173.6-202.9	0.096
Optima	21.7	19.2-25	28.5	24.2-34.3	0.012
Upper X limit	32.9	28.4-39.4	38.2	35.3-39.4	0.122
Lower X Limit	12.7	9.1-15.5	14.4	10.9-18.3	0.266
Breadth	20.2	14.5-27.9	23.8	18.3-28.2	0.221

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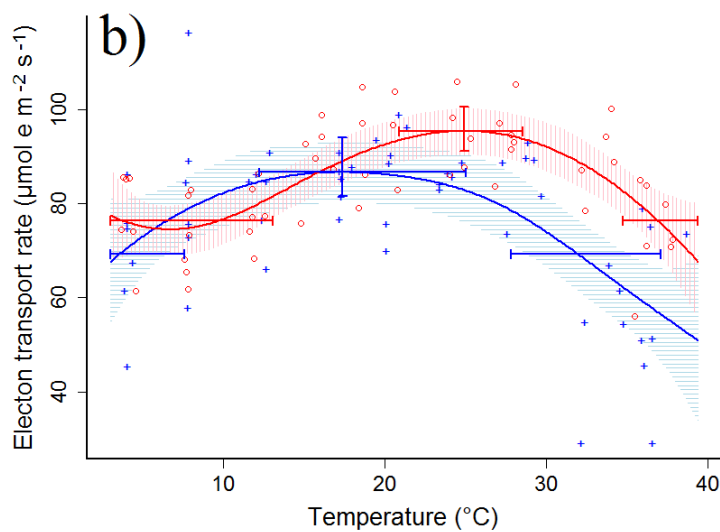
	P.alpinum	(blue)	C.aciphyllum	(red)	P-Value
	mean	CI	mean	CI	
Peak	86.6	81.6-94	95.4	91.1-100.4	0.022
Optima	17.4	12.3-25	24.9	20.9-28.6	0.055
Upper X limit	31.8	27.8-37.1	36.9	34.8-39.4	0.031
Lower X Limit	4.3	3-7.6	5.8	3-13.1	0.588
Breadth	27.5	21.5-33.5	31.1	22.5-36.4	0.247

Fig. 3 Photosynthetic temperature response curves under high (a) and low (b) light. Data fitted with Bayesian models using splines with four knots. The responses are shown for *Polytrichastrum alpinum* (blue crosses, lines and horizontal shading) and *Chorisodontium aciphyllum* (red circles, lines and vertical shading). Shaded bands highlight the 95% credible intervals for the responses. Error bars highlight the 95% credible intervals for the peak and optima as well as the upper and lower limits based on a threshold of 80% of the peak. The posterior means and 95% credible intervals are provided in the tables underneath, with a P-value given for the probability that the two curves are different with respect to each attribute.
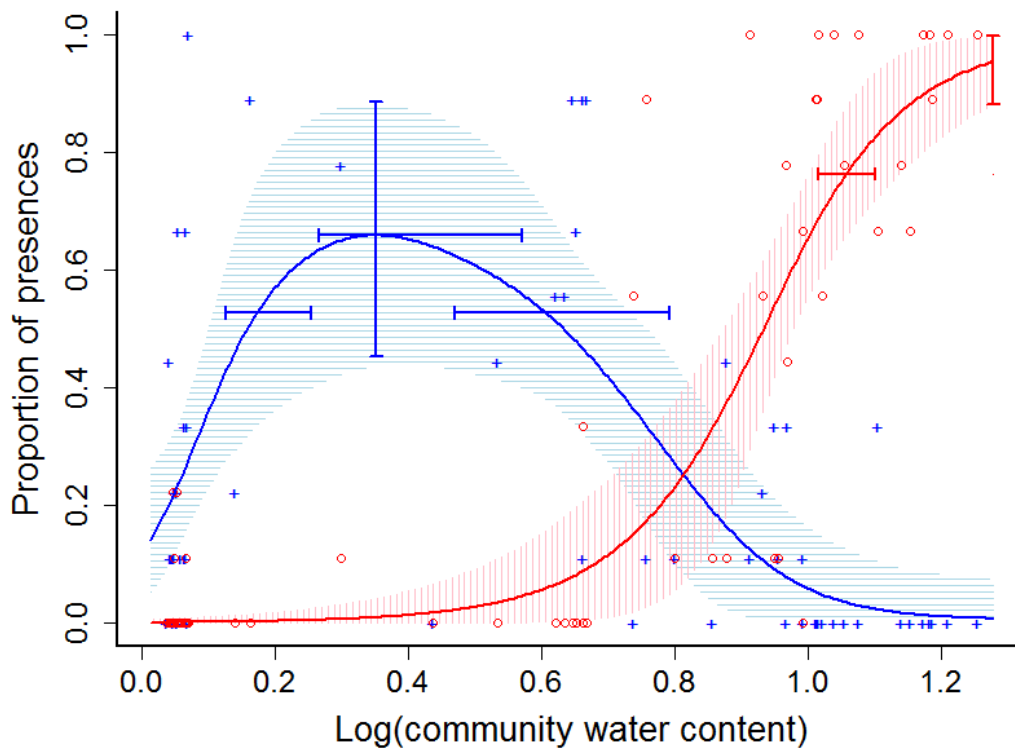
	C.purpureus	(blue)	S.antarctici	(red)	P-Value
	mean	CI	mean	CI	
Peak	0.66	0.45-0.89	0.95	0.88-1	0.002
Optima	0.35	0.27-0.57	1.28	1.28-1.28	<0.001
Upper X limit	0.61	0.47-0.79	1.28	1.28-1.28	<0.001
Lower X Limit	0.18	0.13-0.25	1.06	1.01-1.1	<0.001
Breadth	0.43	0.32-0.61	0.22	0.18-0.26	<0.001

Fig. 4 The proportion of presences in nine pinch samples in a quadrat that contained

Ceratodon purpureus (blue crosses, lines and horizontal shading) or *Schistidium antarctici*

(red circles, lines and vertical shading) from samples collected over a moisture gradient in

2003. Species response curves have been fitted with Bayesian models using splines with four

knots. See Fig. 3 for full explanation of error bars.