1 # A flexible model for thermal performance

2 # curves

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Abstract

Temperature responses of many biological traits—including population growth, survival, and development—are described by thermal performance curves (TPCs) with phenomenological models like the Briere function or mechanistic models related to chemical kinetics. Existing TPC models are either simple but inflexible in shape, or flexible yet difficult to interpret in biological terms. Here we present flexTPC: a model that is parameterized exclusively in terms of biologically interpretable quantities, including the thermal minimum, optimum, and maximum, and the maximum trait value. FlexTPC can describe unimodal temperature responses of any skewness and thermal breadth, enabling direct comparisons across populations, traits, or taxa with a single model. We apply flexTPC to various microbial and entomological datasets, compare results with the Briere model, and find that flexTPC often has better predictive performance. The interpretability of flexTPC makes it ideal for modeling how thermal responses change with ecological stressors or evolve over time.

Introduction

A fundamental problem in ecology is to understand how the growth, physiology, and behavior of organisms depend on their environment. Temperature variation is an important environmental characteristic due to its multiple effects on the physiology (Knapp & Huang 2022) and behavior (Ito & Awasaki 2022) of organisms. Through these effects, changes in temperature impact the fitness of organisms (Amarasekare & Savage 2012) and ultimately the distribution of species across geographic space (Jeffree & Jeffree 1994). Understanding the effects of temperature in organisms is thus crucial to predict how climate change will modify the geographic distribution of species and their interactions, as well as its potential impacts on biodiversity (Nunez *et al.* 2019; Waldock *et al.* 2018), agriculture (Jägermeyr *et al.* 2021), the transmission of infectious disease (Rocklöv & Dubrow 2020), and other important ecosystem processes.

Many traits, including rates of metabolism (Schulte 2015), population growth (Savage *et al.* 2004), and development (Briere *et al.* 1999) vary continuously and nonlinearly with temperature. This dependence can be represented by a thermal performance curve (TPC) that describes the value or performance of the trait at different temperatures (Huey & Kingsolver 1989). Empirically, TPCs are often unimodal, reaching maximum performance at a single optimum temperature and decreasing to a thermal maximum and minimum where performance goes to zero (Angilletta Jr. 2009; Dell *et al.* 2011; Huey & Berrigan 2001).

Various mathematical models have been developed to describe TPCs quantitatively (Arroyo *et al.* 2022; Briere *et al.* 1999; Hultin *et al.* 1955; Johnson & Lewin 1946; Ratkowsky *et al.* 1983, 2005; Ritchie 2018; Schoolfield *et al.* 1981; Sharpe & DeMichele 1977; Shi & Ge 2010; Yin *et al.*

50   1995). These models make it possible to infer useful summaries of the temperature dependence

51   of a trait (such as the optimum, maximum, and minimum temperatures) from experimental data.

52   These summaries can then be compared between different populations of the same species,

53   across species, or across traits (Barton & Yvon-Durocher 2019; Bennett 1980; Buckley & Huey

54   2016; Couper *et al.* 2024; Gounot 1976; Knies *et al.* 2009; Shocket *et al.* 2020). Models of TPCs

55   are also used as building blocks in more complex mathematical models that describe population

56   dynamics and interactions between species. For instance, due to the sensitivity of ectotherm

57   physiology to environmental temperature, transmission dynamics of vector-borne diseases are

58   often highly sensitive to temperature. Mathematical models for the temperature-dependent

59   transmission of these diseases can be constructed using TPC models for traits of the vector, host,

60   and pathogen that affect disease transmission (Mordecai *et al.* 2013, 2017; Shocket *et al.* 2020).

61   Models of predator-prey dynamics that incorporate the effects of temperature are also based on

62   TPC models for traits of the prey and predator (Dell *et al.* 2014; Gilbert *et al.* 2014; Pepi *et al.*

63   2023).

64

65   Thermal performance models can broadly be classified into mechanistic models that derive from

66   an underlying theory (Arroyo *et al.* 2022; Hultin *et al.* 1955; Johnson & Lewin 1946; Ratkowsky

67   *et al.* 2005; Ritchie 2018; Schoolfield *et al.* 1981; Sharpe & DeMichele 1977) and

68   phenomenological models that fit empirical data without attempting to explain the underlying

69   mechanism that gives rise to the TPC (Briere *et al.* 1999; Logan *et al.* 1976; Ratkowsky *et al.*

70   1983; Yin *et al.* 1995). Mechanistic models have some advantages, as they can be used to link

71   TPCs to other biological traits, such as body size or metabolic rate through theoretical

72   frameworks like the metabolic theory of ecology (Kirk *et al.* 2018; Molnár *et al.* 2013, 2017;

73   Savage *et al.* 2004). However, mechanistic TPC models are often parametrized in terms of

74   quantities that can be difficult to interpret in ecological terms (e.g., the activation energy for a

75   potentially rate-limiting chemical reaction for the trait being measured). Because of this, many

76   ecological and epidemiological applications use phenomenological models that are parametrized

77   in terms of more interpretable quantities (such as maximum and minimum temperatures) while

78   still providing a good fit to experimental data, often with fewer parameters than mechanistic

79   models. Moreover, many phenomenological models have explicit thermal limits for trait

80   performance rather than an asymptotic decrease, which is desirable for modeling some traits

81   (e.g., probability of survival to adulthood).

82

83   One popular set of phenomenological models—the Briere models—are commonly used to

84   describe the temperature dependence of insect developmental rates (Briere *et al.* 1999) and have

85   been widely adopted in the ectotherm thermal biology literature (Haye *et al.* 2014; Lachenicht *et*

86   *al.* 2010; Lemoine 2017; Mordecai *et al.* 2013, 2017; Paaijmans *et al.* 2009; Sentis *et al.* 2012;

87   Tochen *et al.* 2014). These models are based on the same mathematical equation (Equation 1),

88   differing only in the number of free parameters. The sparser three-parameter model—commonly

89   referred to as the Briere1 model (or just the Briere model)—is popular in applications due to its

90   parsimony, the biological interpretability of two of its parameters (the minimum and maximum

91   temperatures), and its ability to describe many left-skewed TPCs for biological rates (Briere *et*

92   *al.* 1999; Mordecai *et al.* 2013, 2017).

93

94   However, both Briere models have shortcomings that should be carefully considered before their

95   use. First, the Briere1 model makes a very strong implicit assumption about the relationship

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96   between the minimum, maximum, and optimum temperatures that does not have a biological

97   justification and that can potentially bias optimum temperature estimates. Second, due to their

98   mathematical structure, the Briere1 and Briere2 models cannot describe thermal performance

99   curves from psychrophilic organisms that can function below freezing temperatures. Lastly, the

100   Briere models can only describe thermal performance curves that are left-skewed but are unable

101   to describe TPCs with different shapes. This limitation is important when the goal is to compare

102   traits that differ in TPC shape, such as symmetric and asymmetric responses.

103

104   As an alternative to the Briere models we present a flexible model for thermal performance

105   curves that addresses these limitations, and can describe left-skewed, symmetric, and right-

106   skewed unimodal TPCs of varying thermal breadth. This model, which we call flexTPC, is

107   mathematically equivalent to the Beta model for crop development as originally presented by

108   (Yin *et al.* 1995), which has not been widely adopted ectotherm animal physiology and ecology

109   literature, but is reparametrized in terms of biologically interpretable quantities to make it more

110   suitable for applications in ecology and infectious disease modeling. A previous version of this

111   model was derived in (Cruz-Loya *et al.* 2021) by modifying the Briere2 model (Equation 1) with

112   the goal of describing TPCs of bacterial growth under antibiotics. However, this previous work

113   focused primarily on how antibiotics modify TPCs rather than on the much broader potential

114   applications of the mathematical model, and the model as presented previously had a remaining

115   parameter without a direct biological interpretation.

116

117   In this work, we provide a novel, fully biologically interpretable parametrization of the flexTPC

118   model and compare its predictive performance with that of the Briere1 and Briere2 models in

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119   real-world datasets. We find that flexTPC has similar or better performance than the Briere

120   models when describing insect development data, while performing much better when describing

121   thermal performance curves of psychrophilic organisms and TPCs that are symmetric or right-

122   skewed. Finally, we show that flexTPC can accurately describe many different mosquito life

123   history traits for which different functional forms (linear, quadratic, and Briere1) were used in

124   the past. Our results show that flexTPC is a flexible and interpretable descriptive model for

125   unimodal TPCs that has some important advantages compared to the Briere models, and that is

126   especially well-suited for applications where TPCs of different shapes need to be compared. Its

127   interpretability is well-suited for Bayesian approaches for parameter inference, enabling the use

128   of informative prior distributions based on biological knowledge such as the thermal range of the

129   species habitat and typical maximum trait values for the same trait in related species.

130   ## Methods
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132   ### The Briere models
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134   Thermal performance curve models describe trait performance r as a function of temperature T.

135   The Briere2 model is defined as follows:

136

137
$$r(T) = \begin{cases} cT(T - T_{min})(T_{max} - T)^{\frac{1}{m}} & T_{min} < T < T_{max} \\ 0 & otherwise \end{cases} \quad (1)$$

138

139   where T_{min} and T_{max} are the minimum and maximum temperatures for the trait, respectively,

140   and $c, m \geq 0$ are arbitrary constants. The Briere1 model is the special case of equation (1) where

141    $m = 2$. In general, $r(T)$ has three roots (values of T where $r(T)=0$), with one at $T = 0°C$. This

142   makes the Briere models unsuitable to describe TPCs of organisms that have nonzero

143   performance below freezing temperatures. Because of this, the Briere models are restricted to

144    $T_{min} \geq 0°C$ so that there are only two roots (T_{min} and T_{max}).

145

146   The optimum temperature of the Briere models is given by the following expression (Briere *et al.*
147   1999):
148

149    $$T_{opt} = \frac{(m+1)T_{min} + 2mT_{max} + \sqrt{4m^2T_{max}^2 + (m+1)^2T_{min}^2 - 4m^2T_{min}T_{max}}}{4m+2} \tag{2}$$

150

151   For the Briere1 model (where $m = 2$ is fixed), T_{opt} is a deterministic function of T_{min} and T_{max}.

152   In other words, it is impossible to vary T_{opt} when T_{min} and T_{max} are fixed: the Briere1 model

153   implicitly assumes a strong relationship between these parameters. To our knowledge, this

154   assumption has no biological basis, and as a result, enforcing it will lead to biased inference of

155   these parameters.

156
157
158   The flexTPC model
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160   The flexTPC model is defined as:

161

162    $$r(T) = \begin{cases} r_{max}\left[\left(\frac{T-T_{min}}{\alpha}\right)^{\alpha}\left(\frac{T_{max}-T}{1-\alpha}\right)^{1-\alpha}\left(\frac{1}{T_{max}-T_{min}}\right)\right]^{\frac{\alpha(1-\alpha)}{\beta^2}} & T_{min} < T < T_{max} \\ 0 & \text{otherwise} \end{cases} \tag{3}$$

163

164   where r_{max} is the maximum performance/value of the trait, and T_{min} and T_{max} are the minimum

165   and maximum temperatures, respectively. These three parameters determine the scaling of the

166   TPC in the temperature and performance axes (Figure 1, right panel). Two additional parameters

8

167   determine the shape of the curve. Parameter $\alpha \in [0,1]$ determines the location of the temperature

168   optimum T_{opt} relative to the maximum and minimum through the relationship

169

170

$$T_{opt} = \alpha T_{max} + (1 - \alpha) T_{min} \quad (4)$$

171

172   This makes it possible for flexTPC to describe unimodal curves of any skewness by varying α,

173   where e.g. $\alpha = 0.5$ corresponds to a symmetric curve, and $\alpha = 0$ and $\alpha = 1$ correspond to

174      $T_{opt} = T_{min}$ and $T_{opt} = T_{max}$, respectively.

175

176   The parameter $\beta > 0$ determines the upper thermal breadth (UTB) of the TPC, with larger values

177   corresponding to broader curves and smaller values to narrower curves. UTB, defined here as the

178   temperature range for which $r(T) > e^{-\frac{1}{8}} r_{max} \approx 0.88 r_{max}$ (see Supplemental Information), is

179   approximately

180

181

$$\text{UTB} \approx \beta (T_{max} - T_{min}) \quad (5)$$

182

183   As $T_{max} - T_{min}$ corresponds to the thermal breadth of nonzero performance (defined here as the

184   lower thermal breadth), β is the (approximate) ratio of the upper and lower thermal breadths.

185   This approximation has less than 10% relative error for TPCs that are not extremely skewed ($\alpha \in$

186      $[0.06, 0.94]$) and not too broad ($\beta \leq 0.5$), which encompass the majority of TPC shapes that are

187   likely to be encountered in practice (Figure S4). For large β, the interpretation of β as the upper

188   thermal breadth at 88% of the peak height, as approximated in Equation 5, will no longer be

189   accurate, but larger β always corresponds to broader TPCs, with the limit $\beta \to \infty$ corresponding

190   to a constant model where $r(T) = r_{max}$ in the $[T_{min}, T_{max}]$ temperature range. Varying α and β

191   makes it possible for flexTPC to describe unimodal curves with many different shapes (Figure 1,

192   left panel).

193

194   An alternate parametrization of the flexTPC model that replaces α (the relative position of the

195   thermal optimum) with the absolute optimum temperature T_{opt} and β (the relative approximate

196   upper thermal breadth) with the absolute approximate upper thermal breadth $B = \beta(T_{max} -$

197    $T_{min})$ can also be constructed:

198

199    $r(T)$

$$
200 \quad = \begin{cases} r_{max}\left[\left(\dfrac{T-T_{min}}{T_{opt}-T_{min}}\right)^{\frac{T_{opt}-T_{min}}{T_{max}-T_{min}}}\left(\dfrac{T_{max}-T}{T_{max}-T_{opt}}\right)^{\frac{T_{max}-T_{opt}}{T_{max}-T_{min}}}\right]^{\frac{(T_{opt}-T_{min})(T_{max}-T_{opt})}{B^2}} & T_{min} < T < T_{max} \\ 0 & \text{otherwise} \end{cases} \quad (6)
$$

201

202   where $T_{opt} \in [T_{min}, T_{max}]$ and $B > 0$. In general, we expect Equation 6 to be useful for applied

203   scientists who wish to automatically calculate confidence intervals on parameters of interest

204   (absolute T_{opt} and thermal breadth) using standard statistical software that performs nonlinear

205   least squares or maximum likelihood estimation. Using this parametrization will lead to a

206   confidence interval for T_{opt} with no additional effort from the user of the statistical software.

207   However, there can be numerical issues with estimation for highly skewed curves where T_{opt} is

208   close to either T_{min} or T_{max}. When numerical issues arise, Equation 3 can be used instead.

209

210   Equation 3 is likely to be more useful when fitting TPCs through Bayesian methods, as it is more

211   straightforward to provide a reasonable prior distribution for α (which lies in the interval from 0

212   to 1) than for T_{opt} (which lies in-between two unknown model parameters: T_{min} and T_{max}). It is

213   also simple to obtain posterior samples and credible intervals for T_{opt} from MCMC output

214   through Equation 4.

215

216   Equation 3 can also be used for maximum likelihood estimation: it is straightforward to obtain

217   confidence intervals for T_{opt} through bootstrap methods and any numerical issues regarding the

218   optimal temperature "crossing-over" past the maximum or minimum temperatures can be

219   avoided by constraining α to be in the unit interval. This parametrization also has the advantage

220   of clearly separating the parameters that determine the shape (α, β) and location/scaling

221    $(T_{min}, T_{max}, r_{max})$ of the TPC.

222
223   Datasets
224
225   To illustrate the predictive performance and applications of flexTPC, we compared it with the

226   Briere model in various real-world datasets.

227

228   The `botrana` dataset consists of the developmental time of various life stages of the grapevine

229   moth *Lobesia botrana* (eggs, instars 1-5, and pupae) measured at 14 temperatures, ranging from

230   8 to 34°C. This dataset, which was used to motivate development of the Briere models (Briere *et*

231   *al.* 1999), was taken from Table 1 in (Briere & Pracros 1998). This dataset is expected to be one

232   in which the Briere models perform well.

233

234   The `glacierbac` dataset consists of the temperature dependence of the growth rate of bacterial

235   *Arthrobacter* and *Pseudomonas* strains isolated from glacial deposits (Gounot 1976). This

236   dataset was chosen to highlight the advantage of flexTPC over Briere in describing TPCs from

237   organisms from cold environments.

238

239   The `abcoli` dataset (Cruz-Loya *et al.* 2021) consists of measurements of total growth after 24

240   hours of laboratory cultures of the bacterium *Escherichia coli* in the presence of various

241   antibiotic backgrounds at seven temperatures. These antibiotics either kill or slow down the

242   growth of *E. coli* in a temperature-dependent manner, modifying the shape of the TPC. This

243   dataset was chosen to highlight the ability of flexTPC to describe curves of different shapes.

244

245   The `lhculex` dataset (Shocket *et al.* 2020) corresponds to various mosquito temperature-

246   dependent life history traits (egg viability, probability of larval survival to adulthood,

247   development rate, and female adult lifespan) from *Culex pipiens* and *Culex quinquefasciatus*.

248   These traits have been previously modeled with different functional forms (linear, quadratic, and

249   Briere1). This dataset was chosen to highlight the ability of flexTPC to fit curves of various

250   shapes for which different functional forms were previously needed.

251

252   Parameter estimation

253   A nonlinear regression approach was used to fit the Briere1, Briere2, and flexTPC models to the

254   `botrana, glacierbac,` and `abcoli` datasets through maximum likelihood estimation.

255   The following model was used for the `botrana` and `glacierbac` datasets:

256

257
$$y_i \sim \text{Normal}(r_m(T_i; P_m), \sigma) \quad T \in (T_{min}, T_{max})$$

258
$$y_i = 0 \qquad\qquad\qquad \text{otherwise}$$

259

260 where y_i is the observed response at temperature T_i, σ the standard deviation of the data, r_m the

261 temperature response curve model (either Briere1, Briere2, or flexTPC), and P_m the set of all

262 parameters from the corresponding TPC model being fit. For example, $P_{\text{Briere1}} =$

263 $\{T_{min}, T_{max}, c\}$.

264

265 In the `abcoli` dataset, the response variable is optical density, which does not have zero

266 values. For this dataset the model used was:

267

268
$$y_i \sim \text{Normal}(r_m(T_i; P_m), \sigma)$$

269

270 As a criterion for model selection, we compared the negative log-likelihood obtained under leave

271 one out cross-validation (LOOCV-nLL) for all models in the datasets described above. This is a

272 measure of the predictive out-of-sample model performance that is asymptotically equivalent to

273 AIC (Stone 1977) but makes fewer assumptions, and has been recommended as the approach of

274 choice for model selection when computationally feasible (Yates *et al.* 2023). It consists of

275 removing each data point in turn, fitting the model with maximum likelihood on the remaining

276 data points, and evaluating the negative log-likelihood (nLL) in the removed data point (which is

277 a measure of the quality of the model prediction for a data point that was not used in fitting). We

278 report the mean nLL when each data point is removed in turn. Alternate model comparison

279 criteria (AIC and BIC) are reported in the Supplemental Information.

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280

Bayesian parameter estimation for mosquito trait data

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283 For the `lhculex` dataset, we followed a Bayesian approach for parameter estimation. This

284 makes it possible to fit curves with reasonable thermal limits for traits that lack data at low

285 temperatures using weakly informative prior distributions and illustrates the benefits of fitting

286 flexTPC in a Bayesian context. For each mosquito life history trait, flexTPC was compared to a

287 TPC functional form that was used previously to describe the data being modeled, which varied

288 by trait (Shocket *et al.* 2020). Deviance Information Criterion (DIC) (Spiegelhalter *et al.* 2002)

289 was used as a model selection criterion. For more details, see Table 1 and the Supplemental

290 Information.

291

292 Models were fit using Markov Chain Monte Carlo (MCMC) with the r2jags R package, an

293 interface for JAGS (Just Another Gibbs Sampler) (Plummer 2003). Four independent MCMC

294 chains were run for 300,000 iterations, discarding the first 50,000 iterations as burn-in. The

295 resulting MCMC chains were thinned, saving every eight iterations. Chain convergence was

296 monitored both by visual inspection of trace plots and density plots of the individual chains and

297 by ensuring the potential scale reduction factor $\hat{R} < 1.01$ for all parameters.

Results

298
299
300 In this work, we present flexTPC—a flexible model for unimodal thermal performance curves

301 (TPCs) in which the optimum temperature can lie at any point in between the minimum and

302 maximum temperatures. This model is parameterized in terms of biologically meaningful

303 quantities and can describe TPCs of a wide variety of shapes (Figure 1). We compare the

304 performance of flexTPC to that of the Briere1 and Briere2 models (Equation 1), which are

305 phenomenological models for TPCs that are popular in applications in various real-world

306 datasets.

307
Insect developmental rates
308
309
310 The Briere models were initially developed to describe the thermal dependence of insect

311 developmental rates. We compared the flexTPC and Briere models for describing Briere and

312 Pacros's data on the rates of development of the life stages of the grapevine moth *Lobesia*

313 *botrana* (Figures 2 (left panel), S1) to evaluate the relative performance of these models in a real

314 dataset for which the Briere models would be typically used.

315

316 Based on leave-one-out cross validation (LOOCV), we found that flexTPC was the best

317 performing model for six life stages (eggs, instars 1, 2, 3, 5 and pupae) while the Briere2 model

318 was the best performing model for one life stage (instar 4; Table 1). The Briere1 model was the

319 worst performing model for all life stages in this dataset.

320
Organisms that live below freezing temperatures
321
322
323 The Briere models force trait performance to be zero at $T = 0°C$ and are thus unable to describe

324 thermal performance curves for traits of living organisms that function below freezing

325   temperatures. In order to provide a real-world example, we next compared the Briere and

326   flexTPC models for describing the growth rate of three facultative psychrophile bacterial strains

327   (*Arthrobacter sp* strain SI 55, *Arthrobacter sp* strain SI 60, and *Pseudomonas* strain SII 76) and

328   two obligate psychrophile strains (*Arthrobacter glacialis* strains SI 137 and SI 158) isolated from

329   glaciers (Gounot 1976) (Figures 2 (middle column), S2). We found that flexTPC provides better

330   fits than both Briere models for all bacterial species in the dataset (Table 1). This was especially

331   so for both *Arthrobacter glacialis* strains since they exhibit substantial growth at and below 0°C,

332   which is impossible to capture with the Briere models.

333
334   Thermal performance curves (TPCs) of varying shapes

335
336   Thermal performance curves (especially those for growth and developmental rates) are often left-

337   skewed, with the temperature optimum closer to the maximum than the minimum temperature

338   for the trait. However, some traits have symmetric or right-skewed TPCs, and environmental

339   stressors can change the shape of TPCs (Bestion *et al.* 2018; Brett *et al.* 1969; Cruz-Loya *et al.*

340   2021; Cuppers *et al.* 1997). As a real-world example, we next considered a dataset consisting of

341   the temperature-dependent growth of *Escherichia coli* under 12 different antibiotics, and a

342   control condition in the absence of antibiotics (Cruz-Loya *et al.* 2021). We again compared the

343   fit of the Briere1, Briere2, and flexTPC models (Figures 2 (right column), S3, Table 1).

344

345   While the TPC of *E. coli* growth is left-skewed in the absence of antibiotics, its shape can be

346   modified in their presence because antibiotic effectiveness can vary at different temperatures.

347   Some antibiotics give rise to left-skewed curves (e.g., TET, TMP, FOX), while others result in

348   curves that are closer to symmetric and can be either nearly flat (GEN, TOB, STR) or narrow

349   (ERY). FlexTPC was the best performing model for all 13 antibiotic backgrounds in this dataset

16

350   (Table 1) and is the only model out of the three that can describe TPCs that are symmetric or

351   right-skewed.

352

353   *Fitting thermal performance curves that vary in shape across multiple traits and species*

354

355   Organisms have multiple temperature dependent traits, giving rise to TPCs that can have

356   different shapes. In practice, this has often meant that a different TPC functional form (such as

357   Briere or quadratic) must be chosen for each trait, and sometimes even for the same trait in

358   different species. This raises the issue that the inferred parameters (like minimum, optimal, and

359   maximum temperatures) may differ across traits or species partially because of using different

360   functional forms rather than only because of the data. A flexible model such as flexTPC makes it

361   possible to compare TPCs of different shapes with the same model, allowing the direct

362   comparison of inferred parameters. In addition, having interpretable model parameters allows the

363   use of informative Bayesian priors based on curves fit to related species or knowledge of the

364   temperature range in the habitat of the species of interest.

365

366   As an example, we fit TPC models to a dataset with four life history traits (lifespan, egg

367   viability, larval survival to adulthood, and mosquito development rate) of the mosquitoes *Culex*

368   *pipiens* and *Culex quinquefasciatus* using a Bayesian approach (Figure 3). In a previous study

369   (Shocket *et al.* 2020), these data were analyzed using various different functional forms (linear,

370   quadratic, and Briere), depending on the trait and species (Table 1). We find that flexTPC gives

371   very similar fits to using these different models for lifespan, larval survival, and development

372   rate. Moreover, it provides substantially better fits for egg viability compared to the previous

373   models chosen in the literature (quadratic for *Cx. pipiens* and Briere1 for *Cx. quinquefasciatus*).

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17

375   For adult lifespan, flexTPC results in a near-identical fit to that of a piecewise linear model

376   (which was previously used to describe this trait) within the range of the data. Although this

377   dataset does not contain temperatures low enough to observe a reduction in lifespan, it must

378   necessarily decrease at lower temperatures, so it is likely more realistic to model this trait as a

379   right-skewed unimodal TPC (as can be done with flexTPC) rather than a linear model. If

380   Bayesian methods are used, this can be done even in cases where there is a lack of data near

381   temperature extremes.

382

383   In Bayesian approaches, uncertainty in model parameters is described by probability

384   distributions. Before the analysis, a prior distribution for each parameter is chosen that represents

385   how likely each parameter value is assumed to be *a priori* (before observing the data). Prior

386   distributions can be based on biological knowledge from previous experiments in related species

387   or known characteristics of the habitat of the population being studied. For example, as the

388   mosquito species of interest are ectotherms that live in temperate (*Cx. pipiens*) or

389   tropical/subtropical (*Cx. quinquefasciatus)* climates, we assume that T_{min} and T_{max} for adult

390   lifespan are *a priori* 95% likely to be in the interval (0°C, 10°C) and (25°C, 45°C), respectively.

391   Choosing reasonable prior distributions based on biological knowledge is much easier when the

392   model parameters are interpretable (e.g., for minimum and maximum temperatures and the

393   maximum trait value) rather than mathematical constants with no direct biological meaning.

394   Because of its interpretable parameters (Figure 4 and Box 1), flexTPC is well-suited for

395   Bayesian parameter estimation.

Discussion

In this work we introduce flexTPC, a flexible mathematical model for thermal performance curves (TPCs) that can describe unimodal TPCs of various shapes (including left-skewed, symmetric, and right-skewed curves). FlexTPC is mathematically equivalent to the Beta model (Yin *et al.* 1995), but is reparametrized to be biologically interpretable and better suited for applied ecology and infectious disease applications. We show that this model addresses various limitations of the Briere models, such as not being able to describe TPCs from species that can survive below freezing temperatures, or TPCs that vary in skewness/thermal breadth. This leads to better predictive performance in various real-world datasets. Based on these results, we propose flexTPC as a general-purpose descriptive model to describe unimodal TPCs.

FlexTPC is parametrized in terms of biologically meaningful quantities that are of interest to ecologists: the minimum and maximum temperatures, the maximum value of the trait, a choice of either the relative or absolute position of the optimum temperature, and a choice of the approximate relative or absolute upper thermal breadth. This has several advantages when compared to models in which some parameters are mathematical constants without a clear interpretation. First, the model behaves more predictably when changing its parameter values, since these quantities can be kept constant or modified intentionally as opposed to changing in possibly unintuitive ways as other parameters vary (Figure 4). This aids in the clear interpretation of parameter sensitivity analysis and facilitates modeling how TPCs change over time and/or space (Box 1). Second, it simplifies finding reasonable initial values for the parameters when fitting the model with optimization-based methods (e.g., least squares or maximum likelihood estimation). Third, statistics such as confidence intervals can often be

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420   obtained automatically with standard software when a quantity of interest is an explicit

421   parameter of the model. Lastly, an interpretable parametrization makes it easier to incorporate

422   information from previous experiments in similar species or other sources (e.g., the

423   environmental temperature range from the habitat of the organism) when using informative

424   priors in Bayesian approaches to parameter inference.

425

426   FlexTPC has several important advantages over other popular models like the Briere models.

427   First, in any model describing TPCs, at least three parameters are necessary in order to set the

428   curve height and the minimum and maximum temperatures independently. Because of this, the

429   optimal temperature in any TPC model that has three parameters or fewer (like the Briere1

430   model or the quadratic model) will necessarily be a deterministic function of some subset of

431   these parameters. This may lead to biased estimates for the optimum temperature (and the other

432   parameters involved in the deterministic relationship) whenever the true relationship between

433   these parameters deviates from the implicit assumption made by the TPC functional form, which

434   often lacks a biological justification in phenomenological models. FlexTPC (and Briere2) can

435   vary the optimum temperature for fixed values of the minimum and maximum temperature and

436   are thus likely better suited for estimating optimal temperatures, especially when thermal limits

437   are tightly constrained by the data. Conversely, when using the Briere1 function to describe a

438   TPC where most data are near the optimum, the estimated thermal minimum and maximum

439   might be inaccurate due to the constraints imposed by the functional form.

440

441   Second, organisms may function below freezing temperatures, and while the Briere1 and the

442   Briere2 models cannot describe positive performance below freezing, flexTPC can describe

20

443   TPCs at any temperature range (Figures 2, S2). Although it is possible to use the Briere models

444   in these cases by shifting the model in the temperature axis, this requires choosing an arbitrary

445   temperature shift, and the shape of the resulting TPC depends on the chosen shift (Figure S5).

446

447   Another advantage of flexTPC over the Briere models is its ability to describe TPCs of many

448   different shapes. This will be especially useful in studies comparing multiple TPCs from

449   different traits and/or from different organisms. Currently, different functional forms are

450   commonly used in these studies when the TPC shape changes across species or traits. This can

451   potentially introduce issues when comparing inferred parameters, as parameters might vary

452   between conditions partially due to the use of a different model rather than because of

453   meaningful differences in the data. This issue can be avoided by using a flexible model that

454   allows fitting all conditions with the same functional form.

455

456   As flexTPC is a more complex model that the Briere models, with five free parameters, it is

457   natural to consider whether it can be used in data-limited situations where measurements are only

458   available at a few temperatures, as frequently occurs in lab and field data. In this work we show

459   that, despite this additional complexity, flexTPC has better predictive performance than the

460   Briere1 and Briere2 models in many real-world scenarios. Moreover, as illustrated in the data for

461   mosquito lifespan (Figure 3), flexTPC can be used in situations with limited data at some

462   temperature ranges when using Bayesian methods. Even in cases with severe data limitations, the

463   use of a flexible model with Bayesian methods with strongly informative priors based on

464   biological knowledge of the species being modeled and its habitat may be preferable to the use of

465   a more parsimonious model that assumes a strong relationship between the optimal, minimum,

466 and maximum temperatures without biological justification, especially when the main purpose of

467 the analysis is to estimate an optimal temperature. However, more parsimonious models can be

468 obtained from the flexTPC equation for researchers under severe data constraints that do not

469 wish to take a Bayesian approach to parameter inference (see Supplemental Information).

470

471 Our work shows that flexTPC is a general-purpose model for unimodal TPCs that is well-suited

472 for comparing populations or experimental conditions where the curves may vary in thermal

473 breadth and skewness. To our knowledge, flexTPC is the first descriptive TPC model to

474 simultaneously have an explicit parameter corresponding to all of the main TPC features of

475 interest for ecologists—the temperature minimum, maximum, and optimum, along with the

476 maximum trait performance value and thermal breadth. This inclusion of parameters of interest

477 results in a model that is both flexible and interpretable, which we believe will be useful for both

478 fitting empirical data and for theoretical work that models how TPCs change under evolution or

479 in the presence of external factors like other stressors. FlexTPC can also be used as a flexible

480 functional form to describe the response of biological traits to other environmental factors (e.g.,

481 precipitation or humidity) when these responses are unimodal.

22

Acknowledgements

Data and code availability

All data and code are provided in a GitHub repository.

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628

629   Figures, Tables and Boxes

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631
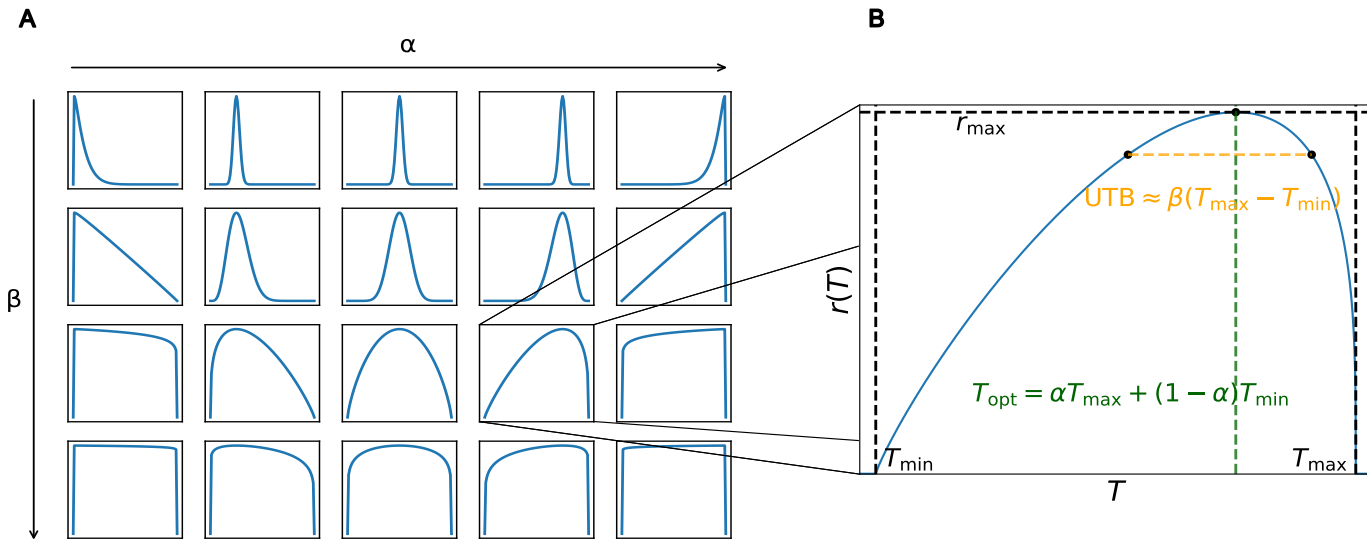
Figure 1. The flexTPC model can describe unimodal thermal performance curves of various shapes. *A.* The flexTPC model (Equation 3) has two parameters that determine the shape of the curve: α (varying from left to right) corresponds to the position of the temperature optimum relative to the minimum and maximum temperatures while β (varying from top to bottom) determines the thermal breadth near the top of the curve. *B.* Three additional parameters determine how the curve is scaled in the temperature and trait performance axes: the minimum and maximum temperatures (T_{min} and T_{max}, respectively), and the maximum value of the response r_{max}. The optimum temperature T_{opt} can be at any point between T_{min} and T_{max}: its position is determined by parameter $\alpha \in [0,1]$. The upper thermal breadth (UTB), defined as the temperature range where $r(T) > e^{-\frac{1}{8}} r_{max} \approx 0.88 r_{max}$, is approximately the product of β and the lower thermal breadth $T_{max} - T_{min}$ where $r(T) > 0$ (for details on the accuracy of this approximation, see Methods and Figure S4).
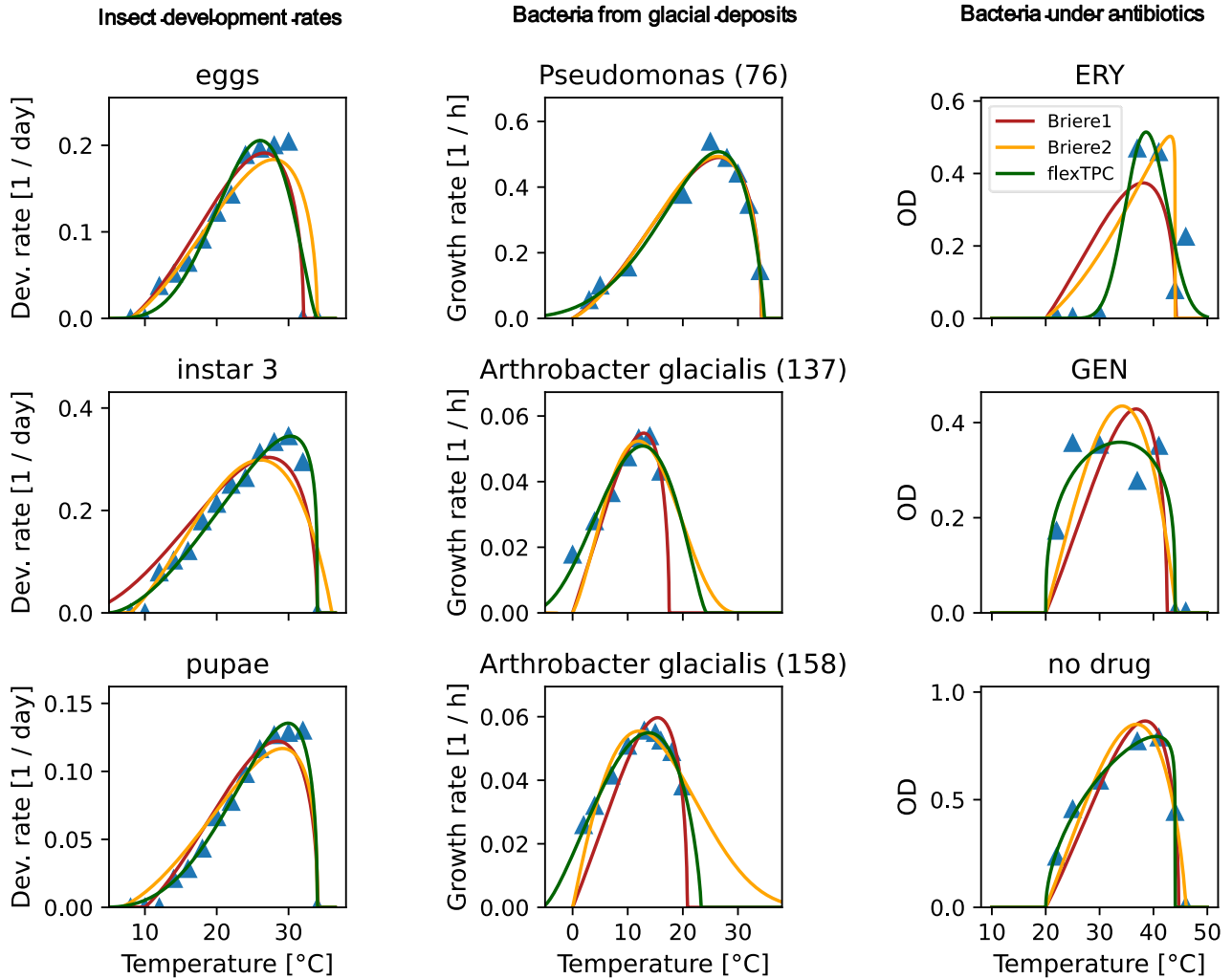
Figure 2. FlexTPC outperforms the Briere1 and Briere2 models in various real-world datasets. Data (shown as blue triangles) and fitted TPC models (Briere1: red lines, Briere2: yellow lines, flexTPC: green lines) for selected examples from various real-world datasets (`botrana`, `glacierbac` and `abcoli`, see Methods). *Left column.* Rate of development of various life stages of the grapevine moth *Lobesia botrana*. A subset of the life stages (eggs, instar 3 and pupae) is shown. *Middle column.* Growth rate of psychrophile bacterial species (*Pseudomonas* and *Arthrobacter glacialis*) isolated from glacial deposits. *Right column.* Optical density (OD, a proxy for the number of bacteria) of *Escherichia coli* cultures after 24-hour growth under various antibiotic backgrounds (ERY: erythromycin, GEN: gentamycin, no drug:

28

654   growth media without antibiotics). The fitted TPC models for all traits in each dataset are shown

655   in Figures S1-S3 in the Supplemental Information.

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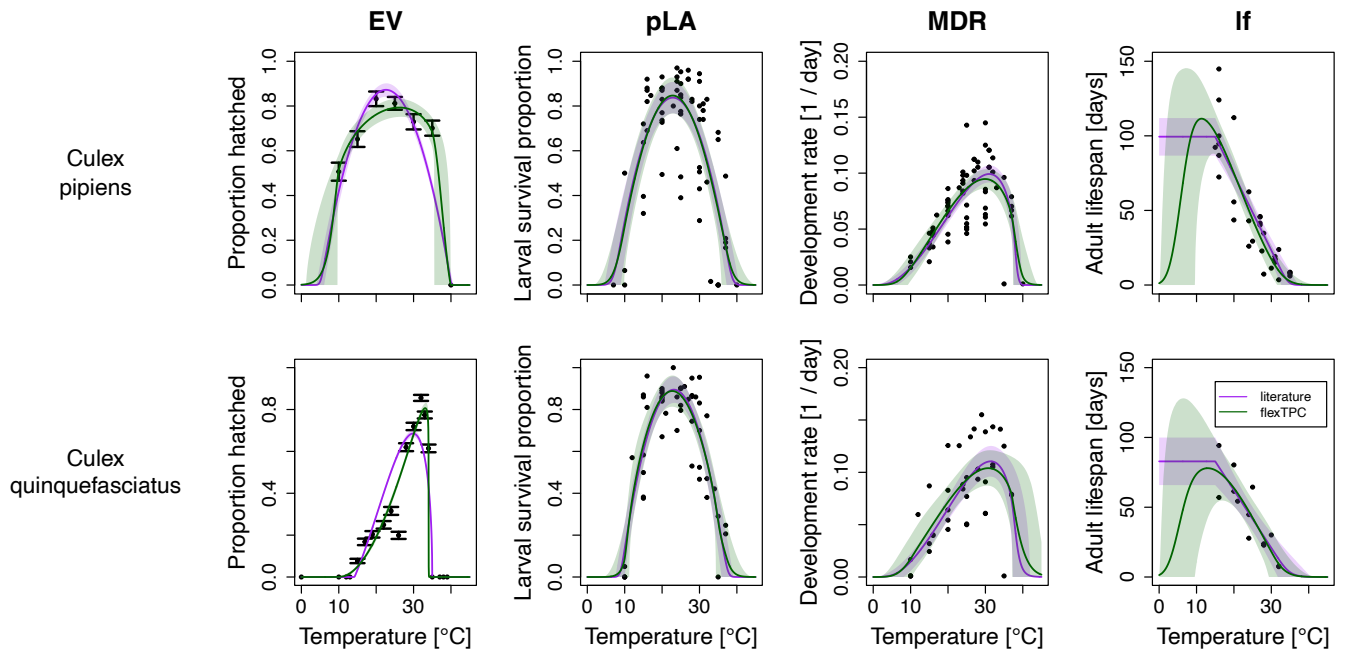
657
658
659 **Figure 3. FlexTPC can be used to fit the thermal performance of multiple traits with**

660 **different shapes that typically require the choice of different TPC models.** We show

661 Bayesian fits to egg viability (EV), probability of larval survival to adulthood (pLA), mosquito

662 development rate (MDR), and female adult lifespan (lf) for *Culex pipiens* (top row) and *Culex*

663 *quinquefasciatus* mosquitoes (bottom row). These traits have very different shapes and different

664 TPC models have been used in the past to fit data from these traits. We compare the flexTPC
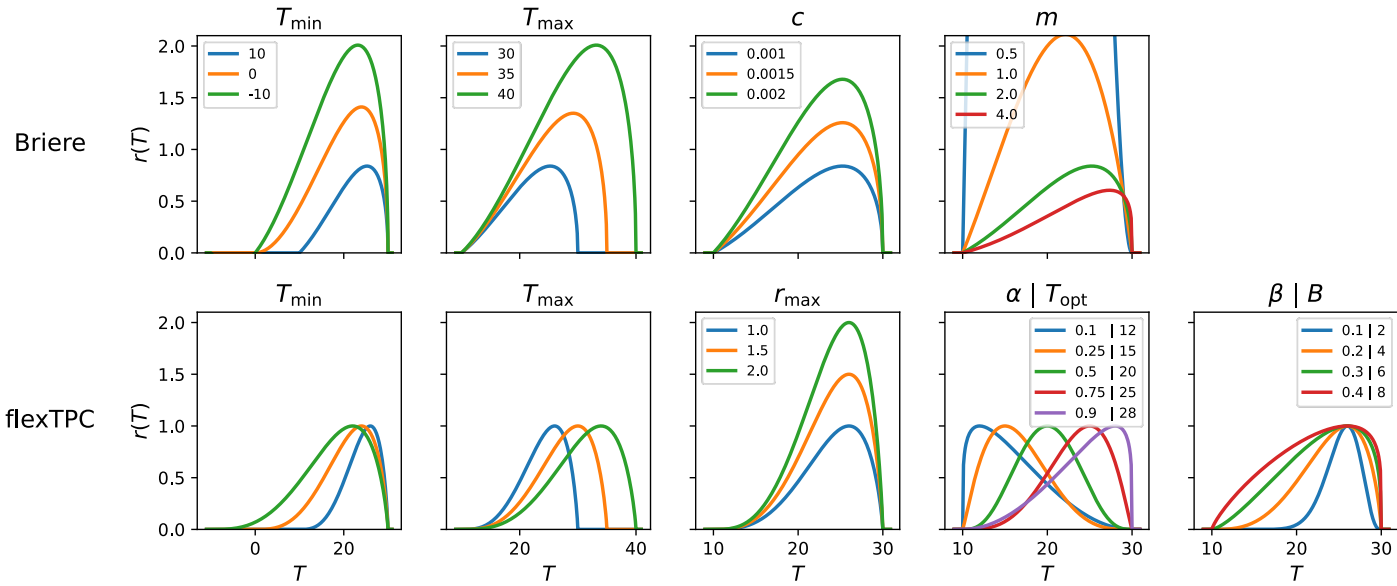
665 model (green) with a previously used TPC functional form that varies by trait and species

666 (purple, see Table 4 for the specific model for each trait). Lines correspond to posterior means

667 and shaded regions to 95% credible intervals, which represent the uncertainty of the true value of

668 the TPC at each temperature.

669

Figure 4. Single parameter changes in the Briere and flexTPC models. In each panel, we show the effects on the thermal performance curve when a single parameter of the corresponding TPC model is changed while keeping all other parameters constant. For parameters other than m in the Briere model, a fixed value of $m = 2$ is used (corresponding to the Briere1 model). We show the parameter values for both parametrizations of flexTPC (Equations 3 and 6), which differ on whether the optimal temperature and approximate upper thermal breadth are in unitless (α, β) or dimensional (T_{opt}, B) form, but are otherwise identical and describe the same set of curves. Since flexTPC has biologically interpretable parameters, changing a single parameter (e.g., T_{min}) will change the thermal performance curve in a predictable way (as the rest of the parameters that are kept constant correspond to known curve properties). In contrast, in a model where some parameters are mathematical constants without a direct biological interpretation, changing a parameter can lead to unintuitive and possibly unintended changes in the thermal performance curve (e.g., changing T_{min} also leads to changes on the height of the curve for the Briere model). This has important consequences when modeling changes in TPCs due to

685   evolutionary or environmental factors, and when interpreting sensitivity analyses of derived

686   quantities from TPC models (see Box 1). Note that decreasing parameter T_{min} to negative values

687   in the Briere model does not lead to models with positive performance below 0°C (see Methods).

688

689

Dataset				
botrana	**life stage**	**Briere1**	**Briere2**	**flexTPC**
LOOCV-nLL	*eggs*	2.00	-1.79	**-2.20**
	instar 1	-1.46	-2.32	**-2.64**
	instar 2	-2.24	-2.88	**-3.08**
	instar 3	7.16	-1.55	**-2.60**
	instar 4	2.14	**-2.61**	-2.51
	instar 5	-0.48	-3.04	**-3.12**
	pupae	10.80	-2.95	**-3.95**
glacierbac	**species (strain)**	**Briere1**	**Briere2**	**flexTPC**
LOOCV-nLL	*Arthrobacter sp (55)*	0.27	-3.35	**-3.61**
	Arthrobacter sp (60)	2.53	-3.13	**-3.79**
	Pseudomonas (76)	inf	-2.23	**-2.71**
	Arthrobacter glacialis (137)	0.70	-3.49	**-4.46**
	Arthrobacter glacialis (158)	-2.64	-4.23	**-5.68**
abcoli	**antibiotic**	**Briere1**	**Briere2**	**flexTPC**
LOOCV-nLL	*AMP*	-0.97	-1.33	**-2.08**
	CLI	-1.43	-1.47	**-1.67**
	CPR	-0.78	-1.23	**-1.70**
	ERY	-0.34	-0.70	**-1.21**
	FOX	-1.87	-1.88	**-2.36**
	GEN	-0.80	-1.00	**-1.68**
	LVX	-1.50	-1.50	**-1.74**
	NTR	-1.72	-1.89	**-2.10**
	STR	-0.96	-1.24	**-1.78**
	TET	-1.65	-1.70	**-1.92**
	TMP	-1.90	-1.91	**-2.59**
	TOB	-1.08	-1.39	**-2.10**
	no drug	-0.96	-1.17	**-2.67**
lhculex		***Culex pipiens***		
DIC	**trait**	**lit. function**	**lit. model**	**flexTPC**
	EV	quadratic	105.7	**47.4**
	pLA	quadratic	**-17.3**	-14.8
	MDR	Briere1	**-313.9**	-312.8
	lf	linear	280.7	**280.0**
		Culex quinquefasciatus		
	trait	**lit. function**	**lit. model**	**flexTPC**
	EV	Briere1	979.0	**370.2**

33

pLA	quadratic	**-42.6**	-39.2
MDR	Briere1	**-152.0**	-149.5
lf	linear	**110.3**	113.5

690

691 **Table 1. Model comparison in real-world datasets.** We compare the predictive performance of

692 flexTPC and Briere models. The best performing model has its values highlighted in bold. The

693 model comparison criteria are indicated below the corresponding dataset. For datasets that were

694 fit with a maximum likelihood approach (`botrana`, `glacierbac`, `lhculex`), we use mean

695 leave one out cross-validated negative log-likelihood (LOOCV-nLL, lower is better) as the

696 model comparison criterion to compare between the Briere1, Briere2, and flexTPC models. For

697 the `lhculex` dataset, which was fit with a Bayesian approach, we use the Deviance Information

698 Criterion (DIC, lower is better) as a model comparison criterion between a TPC functional form

699 that was previously used in the literature to describe that trait (lit.function) and flexTPC.

700 Box 1: Advantages of thermal performance curve models with biologically interpretable

701 parameters

702

703 For many applications (for example, studying the evolution of TPCs or predicting the effect of

704 thermal adaptation on infectious disease spread), it is of interest to model how thermal

705 performance curves change across time, across space, in the presence of a stressor other than

706 temperature, and/or when exposed to other factors that vary across populations. It is natural to do

707 this by making assumptions about how parameters of interest (e.g., minimum, optimum, or

708 maximum temperatures) change as a function of the variable of interest. However, when some

709 parameters in the chosen TPC functional form are mathematical constants without a clear

710 biological interpretation, this can lead to unintuitive changes in the predicted values for the TPC,

711 even when the parameter being modified is interpretable.

712

713 To illustrate this, we show the effects of changing a single parameter while keeping all other

714 parameters constant for the Briere and flexTPC models (Figure 4). In the Briere model there is a

715 multiplicative constant c that is proportional to the height of the curve when all other model

716 parameters are fixed. Changing the value of c while keeping the other model parameters constant

717 will change the TPC in a predictable way by modifying its height while keeping the same

718 minimum and maximum temperatures. However, changing the value of a different model

719 parameter in the Briere model (e.g., T_{min} or T_{max}, which are interpretable parameters) while

720 keeping all other parameters constant will not keep the height of the curve constant, as the value

721 of c that is needed to keep the same height changes when the other model parameters change. In

722 contrast, in the flexTPC model the maximum trait value r_{max} (i.e., the curve height) is explicitly

35

723   a model parameter. Thus, keeping r_{max} constant will keep the same TPC height regardless of the

724   values of the other parameters. When modeling changes in TPCs, it is advantageous to choose a

725   functional form where parameters are biologically interpretable, especially if it is of interest to

726   assume certain aspects of the TPC remain constant or change in a predictable way. This will lead

727   to a clearer interpretation of changes in model parameters which is not confounded by changes in

728   other aspects of the TPC that are not of interest.

729

730   Using TPC models where some of the parameters are mathematical constants without a

731   biological interpretation can lead to potentially misleading conclusions in applications that

732   require the interpretation of partial derivatives of the model or quantities derived from them.

733   Importantly, this includes sensitivity analyses of mathematical models that include TPCs as a

734   submodel (such as infectious disease or predator-prey models) with respect to the underlying

735   parameters of the TPC functional form. For example, sensitivity analysis based on partial

736   derivatives might indicate that the transmission of a disease is very sensitive to the parameter

737   T_{max} of a TPC modeled with the Briere1 function. However, as increasing T_{max} (while keeping

738   all other parameters constant) also increases the height of the TPC, this could be either due to the

739   increased maximum temperature or the increased curve height. In contrast, using a model where

740   all parameters have a clear biological interpretation (and where the maximum value of the TPC

741   is an explicit parameter) enables separating the effect of increasing the maximum temperature

742   and increasing the curve height.

743

744   In general, parametrizing models in terms of biologically interpretable quantities is useful as it

745   makes it possible to keep them constant or to change them in specified ways when varying other

746   parameters (as needed for modeling change in TPCs). It is also advisable to explore the effects of

747   changing individual parameters in the TPCs to be aware of what aspects of the curve are being

748   modified by the parameter in question when interpreting sensitivity analyses.