

APPLICATION

Modelling temperature-dependent development rate and phenology in arthropods: The devRATE package for R

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Abstract

1. Thermal biologists are interested in generating paired data on development rates and temperatures, but they are in need of automated tools to accurately analyse this data.
2. Fed with a database of more than 30 existing development models, the devRATE package provides tools for plotting and visualizing data, selecting the most appropriate model, and mapping and forecasting ectotherm phenology using temperature time-series data. Most proposed models are for arthropods, mainly insects (e.g. Lepidoptera, Coleoptera, Hemiptera, Diptera, Hymenoptera).
3. This paper presents the main functions of the package and provides an example using an empirical dataset.
4. The devRATE package provides investigators with a unique set of tools and a database that allows them to fit development rate models, and to compare arthropod response to temperature.

KEYWORDS

life cycle, model fitting, performance, physiological process

1 | INTRODUCTION

The need to understand and predict future ecological effects of climate change has increased interest in studying the relationship between temperature and organisms' performances, such as development rate (Salis, Lof, Asch, & Visser, 2016). Small ectotherms, like arthropods, are particularly sensitive to their thermal environments, from the scale of microclimates to regional climates (Faye, Rebaudo, Yáñez-Cajo, Cauvy-Fraunié, & Dangles, 2016; Rebaudo, Faye, & Dangles, 2016). However, it is difficult to select the most appropriate of the many available models and to fit to empirical data without a centralized database of species performances studies.

Development rate is a fundamental feature of an ectotherm's life history (Taylor, 1981), and is an essential element in population dynamics models (Hilbert & Logan, 1983). Including development rate in a model makes it possible to estimate a species' emergence time, or its potential distribution in a particular environment (Moore & Remais, 2014), with practical applications for agriculture

(Kontodimas, Eliopoulos, Stathas, & Economou, 2004; Roy, Brodeur, & Cloutier, 2002) and epidemiology (Damos & Savopoulou-Soultani, 2011).

Mathematical models relating temperature and development rate in ectotherms began with the work of Reaumur in the 1730s and expanded greatly from there—there are now more than 30 published models (Figure 1, and Appendix S1 and S2, Moore & Remais, 2014). Choosing the most appropriate model for a specific set of requirements is a challenge. On the one hand, the straight-line equation of the form " $y = a \times x + b$ " (based on the cumulative degree-day concept, Campbell, Frazer, Gilbert, Gutierrez, & Mackauer, 1974) is easy to implement, but is known to be invalid at extreme temperatures (Harcourt & Yee, 1982; Hilbert & Logan, 1983; Logan, Wollkind, Hoyt, & Tanigoshi, 1976; Stinner, Gutierrez, & Butler, 1974). On the other hand, alternative models, such as nonlinear models, have been successfully used to describe development rates at both intermediate and extreme temperature values. However, nonlinear models are harder to fit, especially for

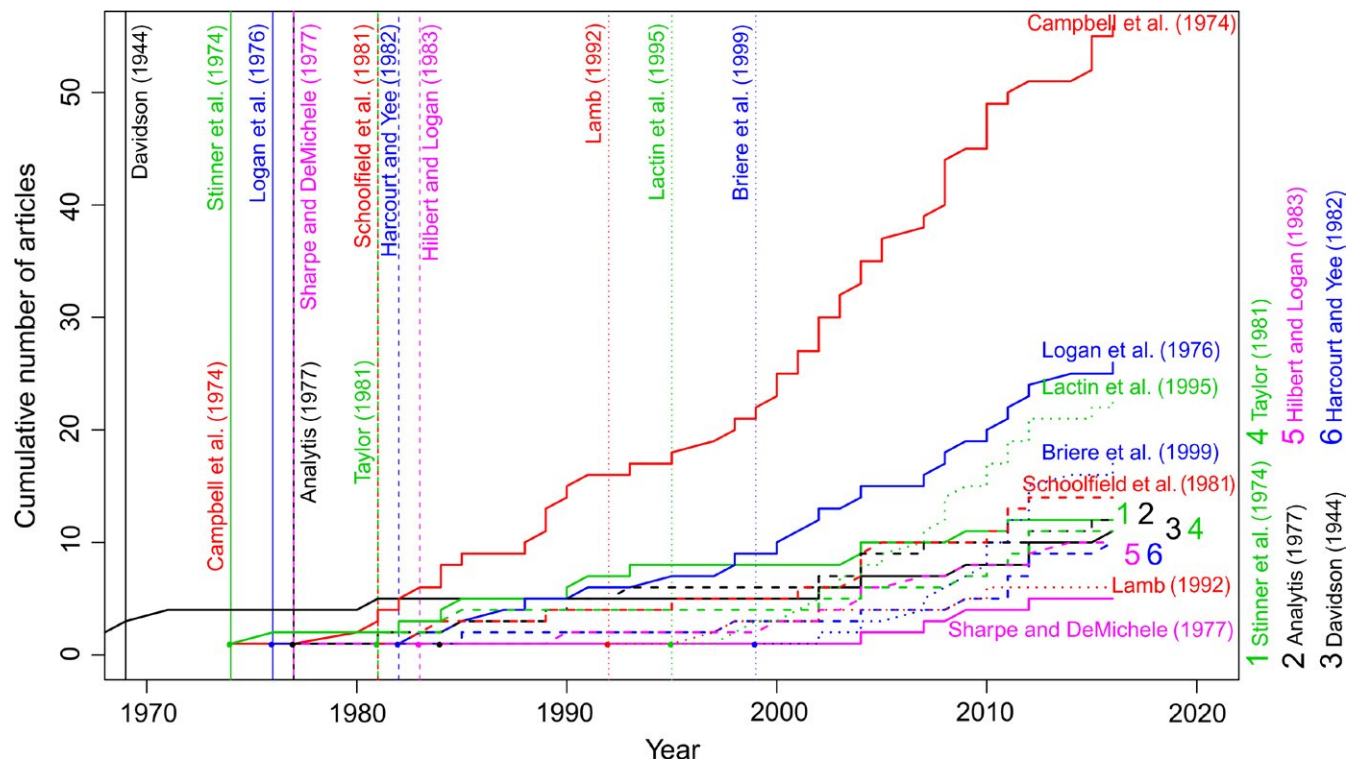


FIGURE 1 Model development and use through time. The time frame represents the most widely used models (used in at least in 5% of the literature review) to relate development rate with ambient temperature in ectotherms as a function of time. Each curve corresponds to the cumulative number of articles in which the models were fitted to empirical data. Vertical lines represent the date on which each model was published. This figure is the result of 100 articles selected randomly from the literature

small datasets (Logan et al., 1976), due to the number of parameters (Taylor, 1981)—even when parameters have a biological meaning (Schoolfield, Sharpe, & Magnuson, 1981).

Without tools to easily fit nonlinear models to empirical data, biologists had largely adopted the straight-line equation (Figure 1), despite substantial limitations at extreme temperatures. Moreover, while several studies have reviewed available development rate models (Damos & Savopoulou-Soultani, 2011; Golizadeh & Zalucki, 2012; Kontodimas et al., 2004; Moore & Remais, 2014; Roy et al., 2002; Shi, Reddy, Chen, & Ge, 2016), none has offered a set of tools that would allow (1) applying models to empirical data (e.g. Tonnang et al., 2013 with the ILCYM software) and (2) browsing parameters from the literature to estimate sound starting values in the fitting process. To meet this need, we have developed “DEVRate,” an R package (R Core Team 2017) aimed to (1) determine the relationship between development rate and temperature using models and parameter estimates from the literature, and (2) forecast and compare ectotherm phenology from different temperature datasets. DevRate functions (1) fit both linear and nonlinear models to empirical data (from more than 30 models to date), (2) plot fitted models from other studies retrieved from a large literature review of arthropods, which is included in the package database (essential for estimating starting values in the fitting process and for contextualizing results; Figure 2), (3) forecast ectotherm phenology over time and (4) build distribution maps from fitted models.

2 | DEVRate ARCHITECTURE AND MODEL DATABASE

DEVRate is an R package to fit development rate models to empirical data and build phenology models. It includes a database of models characterizing the relationship between development rate and temperature in arthropods, and facilitating its parameters estimation with parameter estimates from the literature. A list of the temperature-dependent development rate models included is given in Appendix S1 and Table 1. The package uses a function that fit models to empirical datasets through nonlinear least-square estimates. While the function may be considered as a wrapper for “nls” function from the “STATS” package, the DEVRate package offers many additional functions to model arthropods phenology, and organizes its output to facilitate interpretation and presentation of developmental models, all while considering potential outlier problems.

The nonlinear regression has many advantages: a broad range of functions can be fitted with solid estimates of parameters even when datasets are relatively small; prediction and calibration intervals for estimates of parameters, and criteria for comparing models are easily computed; and the object returned by the function includes many elements (see ?nls) readily usable by other functions (e.g. “confint”) and packages (e.g. “NLSTOOLS”; Baty et al., 2015). However, this function is sensitive to outliers, which may affect the results of a nonlinear analysis. Also, it uses iterative optimization procedures so that the user

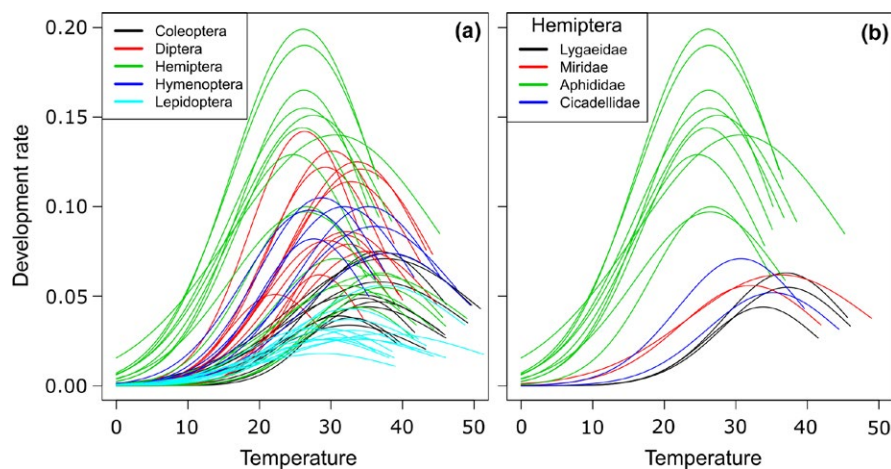


FIGURE 2 Development rate curves following the Taylor model from the package database, using the `devRatePlotInfo()` function. Curves are sorted by Order in (a) and family within the Hemiptera Order in (b). Seventy-one curves are represented here from five distinct Orders of arthropods. The curves are truncated to the right according to the Taylor model (lethal effects of short exposures to high temperatures)

needs to choose reasonably good starting values for the parameters or the algorithm may converge to a local minimum rather than the global minimum, or not converge at all.

To guide the choice of reasonably good starting values, the package includes a database of parameter estimates from the literature with more than 600 entries, mainly from the insect orders Lepidoptera, Coleoptera, Hemiptera, Diptera and Hymenoptera. Before attempting to fit any model to empirical data, the database can be explored through dedicated functions used to search for previous modelling studies on closely related orders, families or species. Then, the parameter estimates from the literature can be retrieved and used as first guess starting values. This database is therefore helpful for proper model building. If no closely related species are documented in the database, a separate script is available to visually adjust the parameters until the fit of the function to the data looks reasonable (see Appendix S3 and the GitHub website, using the “MANIPULATE” package in Rstudio; <https://github.com/frareb/devRate/>).

For each development stage, the empirical data can be fitted to any model in the database and then plotted against the fitted model. Development rate should be provided in day^{-1} and temperature in $^{\circ}\text{C}$. For model comparison, all functions compatible with an “nls” object can be used (e.g. “AIC”, “BIC” and “logLik” functions for model selection). The Akaike information criterion (AIC) can be used to compare models fitted using the same dataset (caution that the “nls” fit assumes the data are normal IID, so computing the AIC to compare models will only be valid if the normal IID assumption holds). Once models have been selected for each development stage, the “devRateIBM” function can be used to forecast phenology over time.

3 | EXAMPLE

In this example, data from Crespo-Pérez, Rebaudo, Silvain, and Dangles (2011) were retrieved on the potato tuber moth *Tecia solanivora* (Lepidoptera: Gelechiidae) previously studied by the authors. It illustrates the use of the package on an insect pest to determine its thermal performance curve and forecast its phenology using a theoretical temperature time series. The dataset is included in the

package together with model fits, and can be built from scratch as a user would do with experimental data (see the package vignette for further details). Here, the dataset is used to simplify the example throughout the course of this section.

```
> data(exTropicalMoth)
```

3.1 | Model selection and fit

If there is no a priori model selection (e.g. guided by a specific research question), model selection is facilitated by an automated search process to match to a given taxa a model and parameter estimates from the literature. In order to identify a candidate model, it is possible to browse the database with the “devRateFind” function. In this example, the Taylor model (Taylor, 1981) was applied twice to the Gelechiidae family by Sporleder, Schaub, Aldana, and Kroschel (2016) to fit the development rates of *Symmetrischema tangolias*, a closely related tuber moth (or alternatively the lactin1_95 model with *Phthorimaea operculella*; see the package vignette).

```
> devRateFind(familySP = “Gelechiidae”)
R> taylor_81 2
```

To obtain the development rate relative to temperature from the empirical dataset, the package determines the nonlinear least-squares estimates of the parameters of a nonlinear model using R “nls” function. Appropriate starting values for parameter estimates are essential for the algorithm to converge. Given the phylogenetic similarities between the study example and *S. tangolias* in the database, nearby starting values provide a good first guess. Parameter estimates from the literature can be retrieved with the “devRateInfo” function.

```
> devRateInfo(eq = taylor_81)
R> ... genSp stage param.Rm param.Tm param.To ref
R> 64 ... S. tangolias pupa 0.0990 31.8000 11.1000
Sporleder et al. 2016
```

It is now possible to proceed to the model fit using retrieved parameter estimates with the “devRateModel” function, and plot the result with the “devRatePlot” function (Figure 3a,b,c).

TABLE 1 Most widely used models to relate development rate with ambient temperature, where rT is the development rate and T the temperature

Equation	Model name	Variables definition	References
$rT = aa + bb \times T$	campbell_74	aa: intercept of the line bb: slope of the line	Campbell et al. (1974)
$rT = \phi \times \left(e^{\frac{(bb \times T)}{(T_{max} - T)/\Delta T}} - e^{(bb \times T_{max} - (T_{max} - T)/\Delta T)} \right)$	logan6_76	ϕ : developmental rate at some base temperature above developmental threshold T_{max} : maximum temperature ΔT : width of the high temperature boundary layer bb: a constant	Logan et al. (1976)
$rT = \alpha \times \left(\frac{1}{1 + cc \times e^{(-bb \times T)}} - e^{(-((T_{max} - T)/\Delta T))} \right)$	logan10_76	T_{max} : the maximum temperature ΔT : width of the high temperature boundary layer α , bb : constants	
$rT = e^{\frac{(aa \times T)}{\Delta T}} - e^{\frac{(aa \times T_{max} - (T_{max} - T)/\Delta T)}{\Delta T}}$	lactin1_95	aa: a constant T_{max} : maximum temperature ΔT : width of the high temperature boundary layer	Lactin, Holliday, Johnson, and Craigen (1995)
$rT = e^{\frac{(aa \times T)}{\Delta T}} - e^{\frac{(aa \times T_{max} - (T_{max} - T)/\Delta T)}{\Delta T}} + bb$	lactin2_95	aa, bb: constants T_{max} : maximum temperature ΔT : width of the high temperature boundary layer	
$rT = aa \times T \times (T - T_{min}) \times (T_{max} - T)^{(1/2)}$	briere1_99	T_{min} : low temperature developmental threshold T_{max} : maximum temperature aa: a constant	Briere, Pracros, Le Roux, and Pierre (1999)
$rT = aa \times T \times (T - T_{min}) \times (T_{max} - T)^{(1/bb)}$	briere2_99	T_{min} : low temperature developmental threshold T_{max} : maximum temperature aa, bb: constants	
$rT = \frac{p25 \times (T + 273.16)/298 \times e^{\frac{(aa/R \times (1/298 - 1/(T+273.16))))}{(1 + e^{\frac{(bb/R \times (1/cc - 1/(T + 273.16)))}{(T + 273.16))}} + e^{\frac{(dd/R \times (1/ee - 1/(T + 273.16)))}{(T + 273.16))}}}$	schoolfield_81	p25: development rate at 25°C assuming no enzyme inactivation aa: enthalpy of activation of the reaction that is catalysed by the enzyme bb: change in enthalpy associated with low temperature inactivation of the enzyme cc: temperature at which the enzyme is 1/2 active and 1/2 low temperature inactive dd: change in enthalpy associated with high temperature inactivation of the enzyme ee: temperature at which the enzyme is 1/2 active and 1/2 high temperature inactive	Schoolfield et al. (1981)

```

> nlsPupaTaylor <- devRateModel(eq = taylor_81, temp
= exTropicalMoth$raw$pupa[,1], devRate = exTropical
Moth$raw$pupa[,2], startValues = list(Rm = 0.099, Tm
= 31.8, To = 11.1))
> devRatePlot(eq = taylor_81, nlsDR = nlsPupaTaylor,
temp=exTropicalMoth$raw$pupa[,1], devRate=exTropical
Moth$raw$pupa[,2])

```

3.2 | Model results and comparison

Model results can be checked directly from the “nls” object returned by the “devRateModel” function, or using the “devRatePrint” function. The latter also checks the assumptions associated with the nls fit (normal distribution of the residuals and IID; see the package vignette for the output).

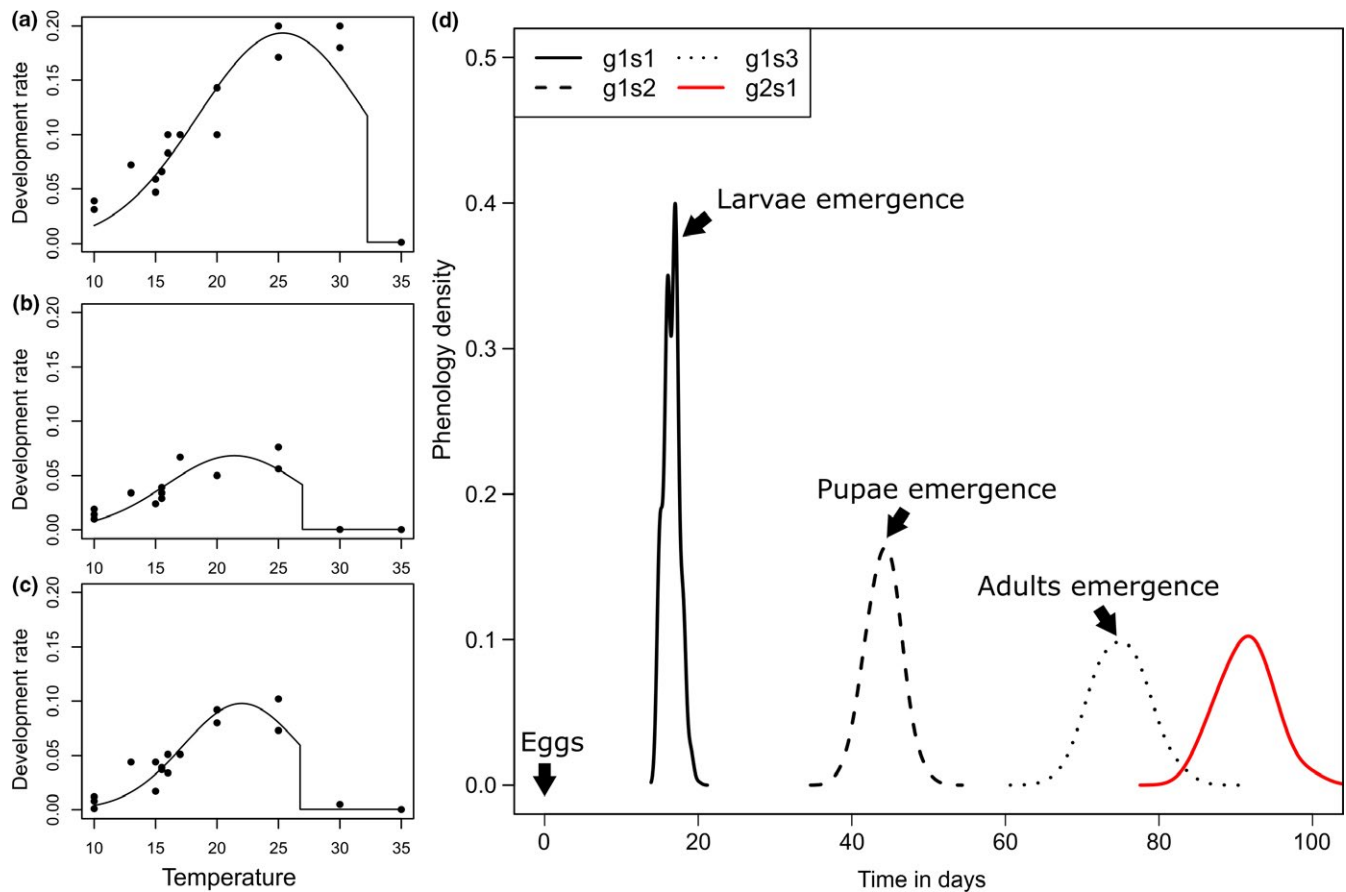


FIGURE 3 Development rate as a function of temperature and life stages. The potato tuber moth (*Tecia solanivora*) data were extracted from Crespo-Pérez et al. (2011) (black points; (a) for eggs, (b) for larvae and (c) for pupae), and the Taylor model was fitted to the empirical data (solid lines, using the `devRatePlot()` function). Phenology is represented as a function of time in days (d), with “g” for generation, and “s” for life stage (e.g. “g1s1” for larva, “g1s2” for pupa and “g1s3” for adults), with a different colour for each generation, and a different line type for each life stage, using the `devRateIBM()` and `devRateIBMPlot()` functions

```
> devRatePrint(myNLS = nlsPupaTaylor, temp = exTropicalMoth$raw$pupa[,1], devRate = exTropicalMoth$raw$pupa[,2])
```

For models comparison, the Lactin1 model (Lactin et al., 1995) was fitted using a similar approach, to compare with the Taylor model previously fitted. The AICs can be obtained using the “AIC” function (see also BIC with “BIC” and log-likelihood with “logLik” functions).

```
> nlsPupaLactin <- devRateModel(eq = lactin1_95,
exTropicalMoth$raw$pupa[,1], devRate=exTropicalMoth$raw$pupa[,2],
startValues = list(aa = 0.12, Tmax = 34, deltaT = 8.1))
> c(AIC(nlsPupaTaylor), AIC(nlsPupaLactin))
R> [1] -94.51292 -73.21501
```

3.3 | Forecasting phenology with empirical temperature datasets

From the model fit, one can predict the insect phenology over time using a temperature dataset. In this example, the temperature

dataset was built from a normal distribution ($\mu = 15$, $\sigma = 1$), with a daily time step over 100 days. The development models used were those previously fitted with the Taylor model for the three life stages (egg, larva and pupa). Five hundred individuals were simulated, with individual plasticity in development rate modelled from a normal distribution centred on the development rate value with a standard deviation of 0.015. The “`devRateIBM`” function returns a list with (1) a table with all life stages for all individuals as a function of time in time steps, (2) the models used and (3) the temperature dataset.

```
> forecastTsolanivora <- devRateIBM(tempTS = rnorm(n = 100, mean = 15, sd = 1), timeStepTS = 1, models = exTropicalMoth$NLSmodel, numInd = 500, stocha = 0.015)
```

The results can be plotted using the “`devRateIBMPlot`” function (Figure 3d).

```
> devRateIBMPlot(ibm = forecastTsolanivora, typeG = "density")
```


4 | CONCLUSIONS

The `DEVRate` package was built to provide a set of tools to choose and fit development rate models to empirical data using a transparent and freely available code, to provide a way to predict ectotherm life stages in relation to temperature and to centralize fitted model parameters found in the literature in one tool. Centralization is particularly critical for contextualizing results for a specific order, family or species, for tackling the challenge of choosing the appropriate model and for easing the process of fitting the model. Additionally, as the database grows, it should facilitate meta-analyses on how ectotherms respond to temperature, thereby contributing to the understanding of this essential process, and promoting the importance of temperature choice and temperature resolution in forecasting accuracy.

AUTHORS' CONTRIBUTIONS

F.R. conceived the ideas and designed methodology; F.R. collected the data; F.R. and Q.S. analysed the data; F.R. and O.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Documentation and source code are freely available on CRAN (<https://cran.r-project.org/package=devRate>) and GitHub (<https://github.com/frareb/devRate>). The R package "DEVRate" can be installed in R with the following command: `install.packages("devRate")`.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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