

```
[ 'Input' 'ID' 'OriginalTraitName' 'OriginalTraitDef'
  'StandardisedTraitName' 'StandardisedTraitDef' 'OriginalTraitValue'
  'OriginalTraitUnit' 'OriginalErrorPos' 'OriginalErrorNeg'
  'OriginalErrorUnit' 'StandardisedTraitValue'
  'StandardisedTraitUnit'
  'StandardisedErrorPos' 'StandardisedErrorNeg'
  'StandardisedErrorUnit'
  'Replicates' 'Consumer' 'ConCommon' 'Habitat' 'Location'
  'LocationType'
  'LocationDate' 'CoordinateType' 'Latitude' 'Longitude' 'ConThermy'
  'ConStage' 'ConSize' 'ConSizeUnit' 'ConSizeType' 'ConDenValue'
  'ConDenUnit' 'ConTemp' 'ConTempUnit' 'ConTempMethod' 'Labfield'
  'Labtemp'
  'Labtempunit' 'Labtime' 'Labtimeunit' 'ArenaValue' 'ArenaUnit'
  'AmbientTemp' 'AmbientTempUnit' 'AmbientLight' 'AmbientLightUnit'
  'Resource' 'ResCommon' 'ResStage' 'ResThermy' 'ResTemp'
  'ResTempMethod'
  'ResSize' 'ResSizeUnit' 'ResDenValue' 'ResDenUnit' 'ResRepValue'
  'ResRepUnit' 'ObsTimeValue' 'ObsTimeUnit' 'EquilibTimeValue'
  'EquilibTimeUnit' 'AcclimFixTemp' 'AcclimFixTempUnit'
  'AcclimFixTempDur'
  'AcclimFixTempDurUnit' 'AcclimVarTemp' 'AcclimVarTempUnit'
  'AcclimVarTempDur' 'AcclimVarTempDurUnit' 'LabGrowthTemp'
  'LabGrowthTempUnit' 'LabGrowthDur' 'LabGrowthDurUnit' 'Citation'
  'FigureTable' 'Notes']
```

```
print(data.OriginalTraitUnit.unique()) #units of the response variable
```

```
['micromol m^-2 s^-1' 'mg o2 (10 minutes^-1)' 'micromol o2 dm^-2
min^-1'
'mg co2 dm^-2 h^-1' 'micromol co2 mg(Chl)^-1 h^-1' 'micro (day^-1)'
'% of maximum' 'mg co2 g(FW)^-1 h^-1' 'ng co2 cm^-2 s^-1' 'gh^-1
m^-2'
'nmol g^-1 s^-1' 'mg co2 g^-1 h^-1' 'nmol co2 cm^-2 s^-1'
'micromol co2 m^-2 s^-1' 'micromol o2 mg(Chl)^-1 h^-1'
'micromol co2 kg^-1 s^-1' 'mg co2 g(DW)^-1 h^-1'
'micromol o2 g(DW)^-1 min^-1' 'mg C g(DW)^-1 h^-1' 'mg o2 g(DW)^-2
h^-1'
'microg co2 m^-2 s^-1' 'micromol o2 g^-1 h^-1'
'microg co2 g(DW)^-1 min^-1' 'microl o2 g(DW)^-1 (10 minutes)^-1'
'mg co2 m^-2 s^-1' 'micromol o2 mg(Chl)^-1 min^-1'
'mg o2 10^-9 cells hour^-1' 'mmol e^- [mg chl a]^1 h^-1'
'microg o2 mg(Chl)^-1 min^-1' 'dpm 14C per 10^3 cells' 'mmol kg^-1
h^-1'
'microg C cm^-2 h^-1' 'g co2 m^-2 h^-1' 'microl co2 m^-2 s^-1'
'nmol cm^-2 s^-1' 'micromol co2 g(FW)^-1 h^-1' '?'
'micromol mg(Chl a)^-1 h^-1' 'micromol g(DW)^-1 h^-1' 'g o2 cm^-2
h^-1'
'microg o2 cm^-2 h^-1' '%' 'micromol o2 mg(Chl a)^-1 h^-1'
'micromol co2 g^-1 min^-1' 'cpm (microg protein)^-1'
'microg o2 g(DW)^-1 min^-1' 'microl o2 mg(DW)^-1 h^-1'
'fmol C cell^-1 min^-1' 'microl o2 mg(Chl)^-1 h^-1'
'microl o2 g(DW)^-1 h^-1' 'mm^3 o2 cm^-2 h^-1' 'nmol o2 g(DW)^-1
s^-1'
'micromol o2 g(DW)^-1 h^-1' 'microg co2 dm^-2 (both sides) min^-1'
'mg o2 g^-1 h^-1' 'mg c g(DW)^-1' 'microl o2 g(FW)^-1 h^-1'
'microW mg^-1' 'nmol g(DW)^-1 s^-1' 'nmol co2 g(DW)^-1 s^-1'
'micromol g^-1 h^-1' 'microl o2 g(FW)^-1 min^-1' 'nmol co2 g^-1
s^-1'
'micromol g^-1 s^-1' 'pgC cell^-1 h^-1' 'pg C pg(chl a)^-1 h^-1'
'micromol O2 g^-1 h^-1' 'micromol o2 g(FW)^-1 h^-1' nan
'mg o2 g(DW)^-1 h^-1' 'nmol CO2 cm^-2 s^-1' 'micromol o2 m^-2 s^-1'
'% of max' 'micromol dm^-2 min^-1' 'microg C g^-1 h^-1'
'mg o2 dm^-2 h^-1' 'mg co2 h^-1 g^-1' 'g C g(Chl a)^-1 h^-1']
```

```
print(data.ConTempUnit.unique()) #units of the independent variable
```

```
['celsius' 'Celsius']
```

```
print(data.ID.unique()) #units of the independent variable
```

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[ 1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17
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19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35
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37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53
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757 758 759 760 761 762 763 764 765 766 767 768 769 770 771 772 773
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775 776 777 778 779 780 781 782 783 784 785 786 787 788 789 790 791
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900
901 902 903]

```

```

data_subset = data[data['ID']==110]
data_subset.head()

```

	Input	ID	OriginalTraitName	OriginalTraitDef	StandardisedTraitName
800	Richard	110	net photosynthesis	NaN	net photosynthesis r:
801	Richard	110	net photosynthesis	NaN	net photosynthesis r:
802	Richard	110	net photosynthesis	NaN	net photosynthesis r:
803	Richard	110	net photosynthesis	NaN	net photosynthesis r:
804	Richard	110	net photosynthesis	NaN	net photosynthesis r:

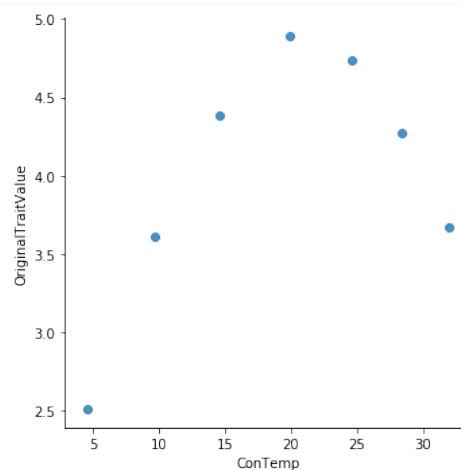
5 rows × 78 columns

```

sns.lmplot("ConTemp", "OriginalTraitValue", data=data_subset,
fit_reg=False)

```

```
<seaborn.axisgrid.FacetGrid at 0x7fd8af63a1f0>
```



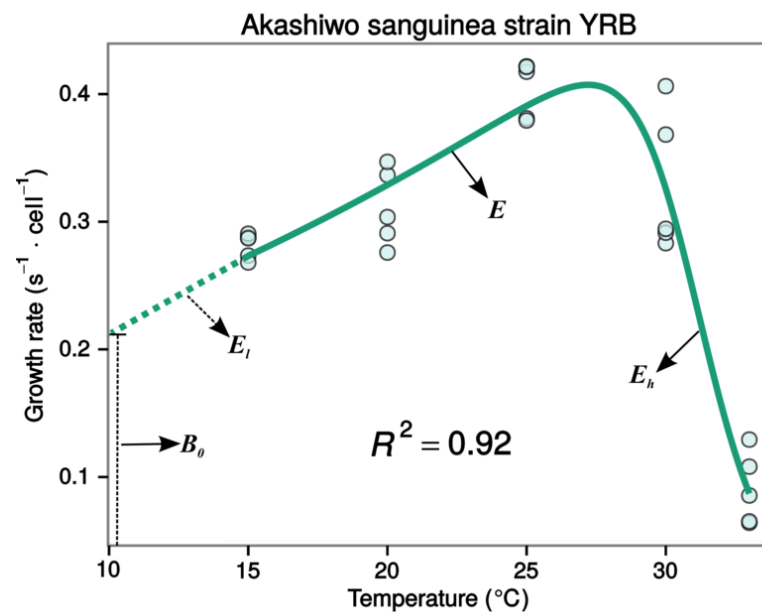
All the following parameters and variables are in SI units.

$$B = B_0 + B_1 x + B_2 x^2 \quad (11)$$

These are phenomenological models, with the parameters B_0 , B_1 , B_2 and B_3 lacking any mechanistic interpretation. x is the independent variable (in this case Temperature, T)

$$B = B_0 T(T - T_0) \sqrt{T_m - T}$$
$$B = \frac{B_0 e^{-\frac{E_a}{k} \left(\frac{1}{T} - \frac{1}{283.15} \right)}}{1 + e^{\frac{E_L}{k} \left(\frac{1}{T_L} - \frac{1}{T} \right)} + e^{\frac{E_h}{k} \left(\frac{1}{T_h} - \frac{1}{T} \right)}} \quad (13)$$

Here, k is the Boltzmann constant ($8.617 \times 10^{-5} \text{ eV} \cdot \text{K}^{-1}$), B the value of the trait at a given temperature T (K) ($\text{K} = ^\circ\text{C} + 273.15$), while B_0 is the trait value at 283.15 K (10°C) which stands for the value of the growth rate at low temperature and controls the vertical offset of the curve. E_l is the enzyme's low-temperature de-activation energy (eV) which controls the behavior of the enzyme (and the curve) at very low temperatures, and T_l is the at which the enzyme is 50% low-temperature deactivated. E_h is the enzyme's high-temperature de-activation energy (eV) which controls the behavior of the enzyme (and the curve) at very high temperatures, and T_h is the at which the enzyme is 50% high-temperature deactivated. E is the activation energy (eV) which controls the rise of the curve up to the peak in the "normal operating range" for the enzyme (below the peak of the curve and above T_h).



Example of the full Sharpe-Schoolfield model (Eqn. (13)) fitted to the thermal response curve of a metabolic trait x with resource abundance.

In many cases, a simplified Schoolfield model would be more appropriate for thermal response data, because low temperature inactivation is weak, or is undetectable in the data because low-temperature measurements were not made.

$$B = \frac{B_0 e^{\frac{-E}{k}(\frac{1}{T} - \frac{1}{283.15})}}{1 + e^{\frac{E_h}{k}(\frac{1}{T_h} - \frac{1}{T})}} \quad (14)$$

In other cases, a different simplified Schoolfield model would be more appropriate, because high temperature inactivation was not detectable in the data because measurements were not made at sufficiently high temperatures:

$$B = \frac{B_0 e^{\frac{-E}{k}(\frac{1}{T} - \frac{1}{283.15})}}{1 + e^{\frac{E_i}{k}(\frac{1}{T_i} - \frac{1}{T})}} \quad (15)$$

Note that the cubic model (Eqn. (12)) has the same number of parameters as the the reduced Schoolfield models (Eqn. (14) & (15)). Also, the temperature parameter (T) of the cubic model (Eqn. (12)) is in °C, whereas the Temperature parameter in the Schoolfield model is in K.

Additional models and questions you can tackle

In all three options above, you may try to tackle fitting to additional models you find in the literature. Some Readings have been provided for each of the three data types below.

You may choose to tackle some biological hypotheses or explore patterns by considering additional covariates. For example,

Do different taxa show different functional responses?

Does temperature or taxon identity affect which population growth rate model fits best?

Do different models fit different types of thermal performance curves (e.g., Photosynthesis vs Respiration)?

You may also choose to revisit the results of another paper that has done comparisons of the models you have chosen with your new dataset (but remember, that may well become too ambitious a project given the time you have).

Readings & Resources

Many of these papers are in pdf format in the Readings directory on TheMulQuaBio repository.

General

- Levins, R. (1966) The strategy of model building in population biology. *Am. Sci.* 54, 421–431.
- Johnson, J. B. & Omland, K. S. (2004) Model selection in ecology and evolution. *Trends Ecol. Evol.* 19, 101–108.
- Motulsky, H. & Christopoulos A. (2004) Fitting models to biological data using linear and nonlinear regression: a practical guide to curve fitting. Oxford University Press, USA.
- Bolker, B. M. et al. (2013) Strategies for fitting nonlinear ecological models in R, AD Model Builder, and BUGS. *Methods Ecol. Evol.* 4, 501–512.

Functional responses

- Holling, C. S. 1959. Some Characteristics of Simple Types of Predation and Parasitism. *The Canadian Entomologist* 91 (7): 385–98.
<https://doi.org/10.4039/Ent91385-7>.
- Holling, C. S. 1966. The Functional Response of Invertebrate Predators to Prey Density. *Mem. Entomol. Soc. Canada* 48 (48): 1–86.
- Aljetlawi, A. A., E. Sparrevik, and K. Leonardsson. 2004. Prey-predator size-dependent functional response: derivation and rescaling to the real world. *J. Anim. Ecol.* 73, 239–252.
- Jeschke, J. M., M. Kopp & R. Tollrian. 2002. Predator functional responses: Discriminating between handling and digesting prey. *Ecol. Monogr.* 72, 95–112.
- Pawar, S., A. I. Dell, and V. M. Savage. 2012. Dimensionality of Consumer Search Space Drives Trophic Interaction Strengths. *Nature* 486 (7404): 485–89.
<https://doi.org/10.1038/nature11131>.
- Pritchard, D. W., R. A. Paterson, H. C. Bovy, and D. Barrios-O'Neill. 2017. frair: an R package for fitting and comparing consumer functional responses. *Methods Ecol. Evol.* 8, 1528–1534.

Population Growth

- Zwietering, M. H., I. Jongenburger, F. M. Rombouts, and K. Van't Riet. 1990. Modeling of the Bacterial Growth Curve. *Applied and Environmental Microbiology* 56 (6): 1875–81.
- Buchanan, R. L., R. C. Whiting, and W. C. Damert. 1997. When Is Simple Good Enough: A Comparison of the Gompertz, Baranyi, and Three-Phase Linear Models for Fitting Bacterial Growth Curves. *Food Microbiology* 14 (4): 313–26.
<https://doi.org/10.1006/fmic.1997.0125>.
- Grijspeerdt, K. and P. Vanrolleghem. 1999. Estimating the parameters of the Baranyi model for bacterial growth. *Food Microbiol.* 16, 593–605.
- Micha, P., and M. G. Corradini. 2011. Microbial Growth Curves: What the Models Tell Us and What They Cannot. *Critical Reviews in Food Science and Nutrition*.
<https://doi.org/10.1080/10408398.2011.570463>.

Thermal Performance Curves

- Schoolfield, R. M., P. J. H. Sharpe, and C. E. Magnuson. 1981. Non-Linear Regression of Biological Temperature-Dependent Rate Models Based on Absolute Reaction-Rate Theory. *Journal of Theoretical Biology* 88 (4): 719–31. [https://doi.org/10.1016/0022-5193\(81\)90246-0](https://doi.org/10.1016/0022-5193(81)90246-0).
- Zwietering, M. H., J. T. de Koos, B. E. Hasenack, J. C. de Witt, and K. van't Riet. 1991. Modeling of bacterial growth as a function of temperature. *Appl. Environ. Microbiol.* 57, 1094–101.
- Briere J. F., Pracros P., Le Roux A. Y., Pierre J. S. 1999. A novel rate model of temperature-dependent development for arthropods. *Environ Entomol* 28: 22–29.
- Dell, A. I., S. Pawar, and V. M. Savage. 2011. Systematic Variation in the Temperature Dependence of Physiological and Ecological Traits. *Proceedings of the National Academy of Sciences of the United States of America* 108 (26): 10591–10596. <https://doi.org/doi:10.1073/pnas.1015178108>.
- DeLong, J. P., J. P. Gibert, T. M. Luhring, G. Bachman, B. Reed, A. Neyer, and K. L. Montooth. 2017. The Combined Effects of Reactant Kinetics and Enzyme Stability Explain the Temperature Dependence of Metabolic Rates. *Ecology and Evolution* 7 (11): 3940–50. <https://doi.org/10.1002/ece3.2955>.

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