Derivation of time-independent growth functions

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Introduction

Generally speaking, as time passes one expects the size of an organism to also grow. Growth, understood as the increase of the physical dimensions, or size, of an organism, characterizes the temporal evolution of many living entities more than many other features. By physical dimensions we mean quantities such as diameter, height, weight, volume, etc. that are directly related to the spatial space occupied by that organism. For example, we may speak about diameter or height for trees, weight or volume for mammals, etc.

Even under ideal conditions, growth is hampered by structural and physiologically constraints, which set in as the organism gets larger. Therefore, it may seem reasonable to assume that, for an organism, there is an upper limit to its size which is only reached under the most optimum climatic and environmental conditions. That upper limit is thus usually unknown but may be guessed by extrapolating observed trends in size. The assumption that size cannot attain absurdly high values also implies that, beyond some point, growth must slow down as time passes, becoming very small at large size.

Growth in size as time passes may slow down, stop or even reverse in some organisms depending on, for example, worsening environmental conditions or fiercer competition (EXAMPLES?).

hereby we will concern ourselves only with those cases where a physical dimension increases as time passes. In addition, we assume the existence of an upper limit to size.

Growth is usually measured as the increment in size between two time points. The assumption of an upper limit to size suggests that sigmoid-like curves may be a good analytical model to describe size as a function of time. Let $y(t)$ be that analytical curve, which depends on time or age t. Then we can define growth simply as $y(t_2) - y(t_1)$, where$t_1 < t_2$. Although convenient, this expression may be impractical most of the time since it also depends on time and we are usually not informed about the age of the organism. Rather, we seek to be able to express growth as a function only of the time difference between observations, $t_2 - t_1$, a quantity that is much easier to obtain.

Finding a growth function from which a simple time-independent expression can be derived is not an easy task. One is seeking for a functional expression where size at a time t_2 depends on previous size at time t_1, with $t_1 < t_2$, plus some set of free parameters. Those parameters, if not known beforehand, are usually calculated via a regression scheme.

Below we will derive time-independent (also known as age-independent) curves for several growth functions. These curves all share the characteristic of having a sigmoid shape, which implies that there is always asymptotic minimum and maximum sizes. This fits well with the general idea that,

Some of the curves are solutions of ordinary differential equations which have been used ***. Others, whoever, simply have a sigmoid shape which makes them appropriate for our objectives.

Some of the growth curves that are explained below are well-known and widely used (e.g. logistic, Schumacher, Gompertz, monomolecular) whereas others are more rarely employed (e.g. arctangent, hyperbolic tangent). The dependence of growth on explanatory variables like e.g. climatic, landscape, competition, etc. is conveyed through the growth rate parameter k, which is defined as a coefficient that explicitly multiplies time (or age) t. In addition, we allow for a term B which accounts for any offset in the growth curve. As we will see below, this summative offset nevertheless vanishes in all cases when size is expressed as a function of previous size (i.e. time or age-independence). Finally, diameter growth $y_2 - y_1 = 0$ when $t = 0$ or $k = 0$ in all cases, as expected.

The obvious non-linearity of the time-independent equations below makes it challenging to devise a regression scheme with which to fit those expressions to a set of observational data. Good starting guesses for the parameters of the fit become a key ingredient for a quick and satisfactory convergence of the regression algorithms. Otherwise, those algorithms may fail to converge, or do so to a local, rather than global, extreme. Therefore, we have extracted simple expressions for the so-called growth rate parameter k, which can be fitted in an initial step as linear expressions of the predictors. The coefficients thus calculated can then be used as first guesses for the full non-linear regression to the time-independent growth curves.

Logistic growth function The logistic curve is one of the most widely used functions to determine the growth of an individual plant or animal. In a general case, in which size depends on time t as well as on a set of predictors (e.g. climatic, topographic), the size y of an organism that obeys the logistic rule can be written:

$$y = \frac{A}{1 + e^{-(k \cdot t + B)}} \tag{1}$$

where A indicates the asymptotic value of y when $t \to \infty$, B is an offset parameter and k is the growth rate parameter. To obtain a time-independent growth equation that determines growth between two time points t_1 and t_2, $t_1 < t_2$, we start by rewriting t as:

$$e^{-(k \cdot t + B)} = \frac{A}{y} - 1 \tag{2}$$

$$t = \frac{1}{k} \cdot \ln\left(\frac{A - y}{y} - B\right) \tag{3}$$

Let us define a subscript notation whereby t_1 and t_2 indicate time points separated by Δ years, where $\Delta = t_2 - t_1$. Likewise, y_1 and y_2 will denote sizes at those time points, respectively. Then:

$$\Delta = t_2 - t_1 = \frac{1}{k} \cdot \left[\ln\left(\frac{y_2}{y_1} \cdot \frac{A - y_1}{A - y_2}\right)\right] \tag{4}$$

The B coefficient has conveniently disappeared from the equation. Now we can easily deduce the following expression for k:

$$k = \frac{1}{\Delta} \cdot \left[\ln\left(\frac{y_2}{y_1} \cdot \frac{A - y_1}{A - y_2}\right)\right] \tag{5}$$

Since $t_2 = t_1 + \Delta$, we can arrive at an expression for y_2 as a function of y_1, Δ and the coefficients a_i:

$$y_2 = \frac{A}{1 + e^{-(k \cdot t_1 + B)} \cdot e^{-k \cdot \Delta}} = \frac{A}{1 + \left(\frac{A}{y_1} - 1\right) \cdot e^{-k \cdot \Delta}} \tag{6}$$

Schumacher growth function The Schumacher growth curve can be expressed as:

$$y = A \cdot e^{-\frac{1}{k \cdot t + B}} \tag{7}$$

For this curve to make ecological sense, $k \cdot t + B > 0$ always. We have departed from the more standard Schumacher function $y = A \cdot e^{-\frac{1}{k \cdot t}}$ to allow for an extra offset parameter B in the exponent. Then, we can express t as:

$$t = \frac{1}{k} \cdot \frac{1}{\ln\left(\frac{A}{y}\right)} - \frac{1}{k} \cdot B \tag{8}$$

Now, following the same notation as shown above, we write:

$$\Delta = \frac{1}{k} \cdot \left[\frac{1}{\ln\left(\frac{A}{y_2}\right)} - \frac{1}{\ln\left(\frac{A}{y_1}\right)} \right] \tag{9}$$

As above, the offset B has vanished from the equation. Then:

$$k = \frac{1}{\Delta} \cdot \left[\frac{1}{\ln\left(\frac{A}{y_2}\right)} - \frac{1}{\ln\left(\frac{A}{y_1}\right)} \right] \tag{10}$$

Therefore:

$$y_2 = A \cdot e^{-\left[\frac{1}{\frac{1}{\ln\left(\frac{A}{y_1}\right)} + k \cdot \Delta} \right]} \tag{11}$$

This is exactly Equation [9] in Tomé et al. (2006), Canadian Journal of Forest Research.

Gompertz growth function

$$y = A \cdot e^{-e^{-(k \cdot t + B)}} \tag{12}$$

B is an offset.

$$t = \frac{1}{k} \cdot \left[\ln\left(\frac{1}{\ln\left(\frac{A}{y}\right)} \right) - B \right] \tag{13}$$

$$\Delta = \frac{1}{k} \cdot \ln\left(\frac{\ln\left(\frac{A}{y_1}\right)}{\ln\left(\frac{A}{y_2}\right)} \right) \tag{14}$$

$$k = \frac{1}{\Delta} \cdot \ln\left(\frac{\ln\left(\frac{A}{y_1}\right)}{\ln\left(\frac{A}{y_2}\right)} \right) \tag{15}$$

$$y_2 = A \cdot \left(\frac{y_1}{A}\right)^{e^{-k \cdot \Delta}} \tag{16}$$

Monomolecular growth function

$$y = A \cdot \left(1 - e^{-(k \cdot t + B)}\right) \tag{17}$$

$$t = \frac{1}{k} \cdot \left[\ln\left(\frac{A}{A-y}\right) - B\right] \tag{18}$$

$$\Delta = \frac{1}{k} \cdot \left[\ln\left(\frac{A-y_1}{A-y_2}\right)\right] \tag{19}$$

$$k = \frac{1}{\Delta} \cdot \left[\ln\left(\frac{A-y_1}{A-y_2}\right)\right] \tag{20}$$

$$y_2 = A - (A - y_1) \cdot e^{-k \cdot \Delta} \tag{21}$$

Arctangent growth function The arctangent is another sigmoid curve from which a time-independent growth function can be derived relatively easily. We start by expressing growth as a function of time:

$$y = A \cdot \left(\frac{1}{\pi} \cdot \arctan\left(k \cdot t + B\right) + 0.5\right) \tag{22}$$

Thus, growth $y \in [0, A]$ and B has been included to allow for any possible offset in the curve. We can easily get:

$$k \cdot t = \tan\left[\left(\frac{y}{A} - 0.5\right) \cdot \pi\right] - B \tag{23}$$

Therefore:

$$t = \frac{1}{k} \cdot \tan\left[\left(\frac{y}{A} - 0.5\right) \cdot \pi\right] - B \tag{24}$$

$$\Delta = \frac{1}{k} \cdot \left[\tan\left(\left(\frac{y_2}{A} - 0.5\right) \cdot \pi\right) - \tan\left(\left(\frac{y_1}{A} - 0.5\right) \cdot \pi\right)\right] \tag{25}$$

Thus, the offset term B has vanished from the equation. An equivalent expression for k is:

$$k = \frac{1}{\Delta} \cdot \left[\tan\left(\left(\frac{y_2}{A} - 0.5\right) \cdot \pi\right) - \tan\left(\left(\frac{y_1}{A} - 0.5\right) \cdot \pi\right)\right] \tag{26}$$

Finally, we derive:

$$\tan\left(\left(\frac{y_2}{A} - 0.5\right) \cdot \pi\right) = \tan\left(\left(\frac{y_1}{A} - 0.5\right) \cdot \pi\right) + k \cdot \Delta \tag{27}$$

and then:

$$y_2 = A \cdot \left[\frac{1}{\pi} \cdot \arctan\left\{\tan\left(\left(\frac{y_1}{A} - 0.5\right) \cdot \pi\right) + k\Delta\right\} + 0.5\right] \tag{28}$$

Hyperbolic tangent growth function

$$y = \frac{A}{2} \cdot [\tanh(k \cdot t + B) + 1] = \frac{A}{2} \cdot \frac{e^{2\cdot(k\cdot t+B)} - 1}{e^{2\cdot(k\cdot t+B)} + 1} = A \cdot \frac{e^{2\cdot k\cdot t}}{e^{2\cdot k\cdot t} + e^{-2\cdot B}} \tag{29}$$

$$e^{2\cdot k\cdot t} = \frac{y}{A-y} \cdot e^{-2\cdot B} \tag{30}$$

$$t = \frac{1}{2\cdot k} \cdot \left[\ln\left(\frac{y}{A-y}\right) - 2\cdot B\right] \tag{31}$$

$$\Delta = \frac{1}{2\cdot k} \cdot \ln\left(\frac{y_2}{y_1} \cdot \frac{A-y_1}{A-y_2}\right) \tag{32}$$

$$k = \frac{1}{2\cdot \Delta} \cdot \ln\left(\frac{y_2}{y_1} \cdot \frac{A-y_1}{A-y_2}\right) \tag{33}$$

Since $t_2 = t_1 + \Delta$:

$$y_2 = A \cdot \frac{e^{2\cdot k\cdot t_1} \cdot e^{2\cdot k\cdot \Delta}}{e^{2\cdot k\cdot t_1} \cdot e^{2\cdot k\cdot \Delta} + e^{-2\cdot B}} \tag{34}$$

Thus:

$$y_2 = A \cdot \frac{\frac{y_1}{A-y_1} \cdot e^{2\cdot k\cdot \Delta}}{\frac{y_1}{A-y_1} \cdot e^{2\cdot k\cdot \Delta} + 1} \tag{35}$$

Finally:

$$y_2 = A \cdot \frac{y_1}{y_1 + (A-y_1) \cdot e^{-2\cdot k\cdot \Delta}} \tag{36}$$

Growth rate parameter We assume that the dependence of the growth rate parameter on a given set of predictors X_i is linear. Then, k can then be expressed as:

$$k = \sum_{i=1}^{n} a_i \cdot X_i \tag{37}$$

where the coefficients a_i are unknown and must be calculated. There are cases where we wish to impose a strict positivity on k. At the same time, we prefer an expression that does not lead to unrealistically high values for k. Examples of this behaviour may come about, for example, when computing projections for X_i values that are very different from the ones used during calibration. In those instances, we can force k to be strictly positive by expressing it as a logistic function of the variables X_i. In this case, we replace the lineal expression from above with the following:

$$k = \frac{C}{1 + e^{-\sum_{i=1}^{n} a_i \cdot X_i}} \tag{38}$$

A new transformation is thus needed to obtain a linear expression. After some algebra, we get:

$$\sum_{i=1}^{n} a_i \cdot X_i = \ln\left(\frac{k}{k_{max} - k}\right) \tag{39}$$

Using a logistic function for k has the advantage of not letting k reach absurdly low or high values, since $k \in [0, C]$ always. A new parameter k_{max} is, however, necessary to set an upper limit to k.