

# *ATNr*: Allometric trophic models in R

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This document presents the mathematical definitions of the different models available in *ATNr*. ATN stands for Allometric Trophic Models. This name refers to the fact that these models describe the dynamic of populations that interact trophically with interaction strength determined by biological rates (like attack rate, handling time, ...) derived from allometric relationships (i.e. body mass relationships). Since the seminal work from Yodzis and Innes in 1992 ([Yodzis and Innes, 1992]), different implementations were developed through time and the *ATNr* package propose three versions that are classically used in food web studies. Despite their differences, all *ATNr* models describe the biomass dynamic of trophically interacting species by estimating their growth rates at different point in time using a similar set of hypotheses:

- Growth rates of species are positively affected by what they consume (i.e. the models are based on energetic transfers between a resource and its consumer)
- Growth rates of species are negatively affected by consumers that feed upon them and by metabolic expenses.

The growth rate of non basal species over time can be formalised by a set of differential equations:

$$\frac{dB_i}{dt} = B_i \sum_j F_{ji} e_j - \sum_j B_j F_{ij} - X_i B_i, \quad (1)$$

where  $\frac{dB_i}{dt}$  is the growth rate of the biomass of species  $i$  at a point in time  $t$ ,  $B_i$  is the biomass of species  $i$ ,  $F_{ij}$  is the per capita feeding rate of species  $j$  on

species  $i$  ( $F_{ij} = 0$  if  $j$  does not feed on  $i$ ),  $e_i$  is the assimilation efficiency of resource  $i$  when consumed and  $X_i$  is the per gram metabolic rate of species  $i$ . The growth rate of basal species is defined as:

$$\frac{dB_i}{dt} = r_i G_i B_i - \sum_j B_j F_{ij} - X_i B_i, \quad (2)$$

where  $r_i$  is the mass-specific growth rate of species  $i$ ,  $G_i$  its net growth rate.

The three different versions of ATN models proposed in the package all derive from this set of equations, and only differ by how the feeding rate (i.e. species functional response)  $F_{ij}$  of non basal species and net growth rate of basal species  $G_i$  are calculated. For instance, a major difference in the calculation of  $G_i$  among models is whether or not the dynamic of the nutrient pool is considered.

Overall, the models currently proposed in the *ATNr* package provide the means to generate the biomass dynamics of populations depending on their trophic interactions. As it stands, the package is focused on such population dynamics in local communities, which excludes the modeling of spatial processes driven by immigration and emigration [Ryser et al., 2019], ontogenetic shifts in stage- or size-structured populations [DeR, 2008], other types of interactions like mutualism [Thébault and Fontaine, 2010] or socio-economic factors [Werner et al., 2022]. While the approach of bioenergetic population dynamic modeling is generally flexible to include all of these aspects, we have kept the model of the package relatively simple as adding any of these processes to the package would come at the cost of the necessity to parameterize them. However, the flexibility in the definition of the parameters associated with the processes in the current version of the model allows users to address a large set of questions related to the links between food web and community structure, behavioural aspects and environmental gradients, such as temperature or productivity. For the different models, the package proposes a by-default parametrisation that was so far mainly used for theoretical studies [Schneider et al., 2016, Binzer et al., 2016]. It is however possible to adapt it to more specific usage (such as specific sets of species or ecosystem types). The use of allometric relationships permits to decrease the amount of parameters to estimate and the recent release of large datasets now allows for these more specific usages [Uiterwaal et al., 2022, Dell et al., 2011].

Here we present the formulation of feeding rate and net growth rate used by the different models and depict how the different variables are usually defined by proposing a default parametrisation based on what is used in the

literature. As a convention, for all parameters that depend on both resources and consumers, like  $F_{ij}$ , the first index refers to the resource and the second to the consumer. In other words, double subscripts read as “*from a resource to a consumer*”. This matches the data structure used in the package, where all matrices are defined such as rows represent resources and columns represent consumers.

## 1 Unscaled version

This version implements the model as in [Binzer et al., 2016]. It does not scale the time of the biological rate according to the growth rate of the smallest basal species, explaining its denomination (see section 2 for the scaled version). This model also does not include nutrient dynamics (see section 3).

### 1.1 functional response

In this version, the functional response  $F_{ij}$  describing the feeding rate of consumer  $j$  on resource  $i$  is informed by 4 different ecological processes:

- Clearance rate  $a_{ij}$ , (sometimes described as attack rate).
- Growth rates of species are negatively affected by consumers that feed upon them and by metabolic expenses.

is written as:

$$F_{ij} = \frac{a_{ij} B_i^{q_j}}{1 + c_j B_j + \sum_k h_{kj} a_{kj} B_k^{q_j}} \frac{1}{m_j}. \quad (3)$$

Here,  $B_i$  is the biomass of species  $i$ ,  $a_{ij}$  is the attack rate of  $j$  on  $i$ ,  $q$  is the hill exponent determining the shape of the functional response (for type II,  $q = 1$ ; for type III,  $q \in ]1, 2]$ ),  $c$  sets the interference competition (the proportion of time that a consumer spends encountering con-specifics) and  $h_{ij}$  is the handling time of consumer  $j$  on resource  $i$ .

### 1.2 growth rate

The net growth rate  $G_i$  of basal species  $i$  is defined as:

$$G_i = 1 - \frac{s_i}{K_i}, \quad (4)$$

where  $K_i$  is the carrying capacity of species  $i$  and  $s_i$  depends on the ratio between plants inter- and intra-specific competition for resources  $\alpha_{ij}$ :

$$s_i = \sum_j \alpha_{ij} B_j \quad (5)$$

The diagonal elements  $\alpha_{ii}$  define intraspecific competition and the off-diagonal elements interspecific competition. The identity matrix ( $\alpha_{ii} = 1, \alpha_{ij} = 0 \forall i \neq j$ ) corresponds to the model for which each basal species has its own resource (therefore, adding new basal species increases the total amount of resources available in the system). The matrix of ones ( $\alpha_{ij} = 1 \forall i, j$ ) corresponds to a scenario where all basal species share the same resource pool.

Overall, this equation defines a saturating response: when the species biomass is low, net growth rate approaches 1. When the biomass is approaching the carrying capacity, the net growth rate tend to 0.

### 1.3 default parametrisation and units

A summary of the above parameters and their derivation can be found in Tables 1 and 2.

Variable	Mathematical expression	Name in the package	Definition
$a_{ij}$	$a_{ij} = a_0 m_i^{a_1} m_j^{a_2} e^{E_a \frac{T_0 - T}{k T T_0}}$	\$a	Attack rate
$h_{ij}$	$h_{ij} = h_0 m_i^{h_1} m_j^{h_2} e^{E_h \frac{T_0 - T}{k T T_0}}$	\$h	Handling time
$c_i$	Free parameter	\$c	Interference competition
$K_i$	$K_i = k_0 m_i^{k_1} e^{E_k \frac{T_0 - T}{k T T_0}}$	\$K	Carrying capacity
$r_i$	$r_i = r_0 m_i^{r_1} e^{E_r \frac{T_0 - T}{k T T_0}}$	\$r	Maximum growth rate
$X_i$	$X_i = x_0 m_i^{x_1} e^{E_x \frac{T_0 - T}{k T T_0}}$	\$X	Metabolic rate
$q_i$	Free parameter	\$q	Hill exponent (functional response type)
$\alpha_{ij}$	$\begin{cases} 0, i \neq j \\ 1, i = j \end{cases}$	\$alpha	competition for resources

Table 1: Parameter used for the unscaled model.

Variable (units)	parameter used	values
$a_{ij} \text{ (} m^2 \cdot s^{-1} \text{)}$	$a_0$	$e^{-13.1}$
	$a_1$	0.25
	$a_2$	-0.8
	$E_a$	-0.38
$h_{ij} \text{ (} s \text{)}$	$h_0$	$e^{9.66}$
	$h_1$	-0.45
	$h_2$	0.47
	$E_h$	0.26
$c_i \text{ (} m^2 \cdot s^{-1} \text{)}$	$c$	0.8
$K_i \text{ (} g \cdot m^{-2} \text{)}$	$k_0$	Free parameter
	$k_1$	0.28
	$E_k$	0.71
$r_i \text{ (} g \cdot m^{-2} \text{)}$	$r_0$	$e^{-15.68}$
	$r_1$	-0.25
	$E_r$	-0.84
$X_i \text{ (} J \cdot s^{-1} \text{)}$	$x_0$	$e^{-16.54}$
	$x_1$	-0.31
	$E_x$	-0.69
$q_i$	-	0.2

Table 2: Parameter units and default values used by the package *ATNr* for the model as in [Binzer et al., 2016].

## 2 Scaled version

This model, which corresponds to the one implemented in the julia package *BioEnergeticFoodWebs* ([Delmas et al., 2017]) refers to the *scaled* version of the ATN model. It means that the time unit of the different biological rates used (like metabolic rate, maximum feeding rate, ...) are scaled to the growth rate of the smallest basal species (more details in 2.3). This redefinition of the variables implies a redefinition of the equations describing the dynamics of species, which introduce the scaled metabolic rate  $x_i$  and the maximum

feeding rate of species relative to their metabolic rate  $y_i$ :

$$\frac{dB_i}{dt} = B_i r_i G_i - x_i B_i - \sum_j x_j y_j B_j F_{ij} \quad (6)$$

$$\frac{dB_i}{dt} = x_i y_i B_i \sum_j F_{ji} e_j - x_i B_i - \sum_j x_j y_j B_j F_{ij}, \quad (7)$$

## 2.1 functional response

In this model, the functional response can be expressed as:

$$F_{ij} = \frac{w_{ij} B_i^q}{B_0^q + c_j B_j + \sum_k w_{kj} B_k^q}. \quad (8)$$

where  $y_i$  is the maximum feeding rate of species  $i$  relative to its mass-specific metabolic rate  $x_i$ .  $w_{ij}$  is  $j$ 's relative consumption rate when consuming  $i$ , such as  $\sum_i w_{ij} = 1$ .  $c_j$  is the interference competition factor.  $q$  is the hill exponent determining the shape of the functional response (type II while  $q = 1$ , type III when  $q > 1$  and  $q \leq 2$ )

## 2.2 growth rate

The net growth rate of basal species is here defined in the same way as for the unscaled version of the model:

$$G_i = 1 - \frac{s_i}{K_i}, \quad (9)$$

where  $K_i$  is the carrying capacity of species  $i$ .  $s_i$  depends on the ratio between plants inter- and intra-specific competition for resources  $\alpha_{ij}$ :

$$s_i = \sum_j \alpha_{i,j} * B_j \quad (10)$$

The diagonal elements  $\alpha_{ii}$  define intraspecific competition and the off-diagonal elements interspecific competition. The identity matrix ( $\alpha_{ii} = 1, \alpha_{ij} = 0$  for all  $(i, j)$ ) correspond to the model for which each basal species has its own resource (therefore, adding new basal species increases the total amount of resources available in the system). The matrix of ones ( $\alpha_{ij} = 1$  for all  $(i, j)$ ) correspond to a scenario where all basal species shared the same resource pool.

Overall, this equation defines a saturating response: when the species biomass is low, net growth rate approaches 1. When the biomass is approaching the carrying capacity, the net growth rate tend to 0.

### 2.3 parametrisation and units

As in the previous models, the biological rates are based on allometric relationships (but here, with an exponent of  $-0.25$ ). However, the rates used in the model correspond to scaled version of the natural biological rates. The scaling is done to express biological rates relative to the growth rate of the smallest basal species. Thereafter, and consistently with the notation used in the functional response, we use capital letters for the natural rates and small letters for their scaled versions. As before, the natural biological rates are defined as:

$$R_i = r_0 M_i^{-0.25} \quad (11)$$

and the same definitions hold for mass-specific  $X_i$  metabolic rate and maximum feeding rate  $Y_i$ :

$$X_i = x_0 M_i^{-0.25}, \quad (12)$$

$$Y_i = y_0 M_i^{-0.25}, \quad (13)$$

Then the scaling is done using the following transformations, assuming that the smallest basal species is species 1:

$$r_i = \frac{r_0 M_i^{-0.25}}{r_0 M_1^{-0.25}} = \frac{M_i^{-0.25}}{M_1^{-0.25}}, \quad (14)$$

$$x_i = \frac{x_0 M_i^{-0.25}}{r_0 M_1^{-0.25}} = \frac{x_0}{r_0} \left( \frac{M_i}{M_1} \right)^{-0.25}. \quad (15)$$

$y_i$  is the maximum consumption rate of population  $i$  relative to its metabolic rate:

$$y_i = \frac{y_i}{x_i} = \frac{\frac{y_0 M_i^{-0.25}}{r_0 M_1^{-0.25}}}{\frac{x_0 M_i^{-0.25}}{r_0 M_1^{-0.25}}} = \frac{y_0}{x_0}. \quad (16)$$

The values associated to these parameters are presented in table 3.

Variable	parameter used	values	Variable name in the package
$x_i$	$\frac{x_0}{r_0}$	0.314	\$X
$y_i$	$\frac{a_y}{a_x}$	8	\$max.feed
$K_p$	$K$	10	\$K
$q_i$	-	1.2	\$q

Table 3: values and units of variables as set by the package default parametrisation for the scaled version

### 3 Unscaled version with nutrient dynamic

For this model, described in [Schneider et al., 2016], the definition of the feeding rate is based on the unscaled version (i.e. like in [Binzer et al., 2016], described in section 1), with a slight difference in the way the attack rate is defined. It strongly departs from the models presented before in the way the net growth rate of plants is calculated: instead of considering a maximum carrying capacity for basal species, the growth rate of plants is determined by their interactions with a nutrient pool for which the dynamics of nutrient concentrations are explicitly modeled (using differential equations, such as for species biomass dynamics).

#### 3.1 functional response

The functional response  $F_{ij}$  describing the feeding rate of consumer  $j$  on resource  $i$  is written as:

$$F_{ij} = \frac{w_{ij}b_{ij}B_i^q}{1 + c_jB_j + \sum_k w_{kj}h_{kj}b_{kj}B_k^q} \frac{1}{m_j}. \quad (17)$$

As before,  $q$  is the hill exponent determining the shape of the functional response (type II while  $q = 1$ , type III when  $q > 1$  and  $q \leq 2$ ),  $c$  sets the interference competition and  $h_{ij}$  is the handling time of consumer  $j$  on resource  $i$ . Here, the attack rate  $a_{ij}$  has been substituted by a resource specific capture coefficient  $b_{ij}$  (see section 3.3 on parameters for more details).  $w_{ij}$  is  $j$ 's relative consumption rate when consuming  $i$ , such as  $\sum_i w_{ij} = 1$ .  $m_i$  corresponds to the body mass of species  $i$ .



### 3.2 growth rate

The net growth rate of plant species  $G_i$  is not defined from a parameter corresponding to a carrying capacity but from concentrations of a set of nutrients for which the dynamic over time is explicitly modeled. when plants acquire nutrients from  $n$  different nutrient pools,  $G_i$  is defined as:

$$G_i = \min \left( \frac{N_1}{K_{1i} + N_1}, \dots, \frac{N_n}{K_{ni} + N_n} \right) \quad (18)$$

where  $k_{ni}$  determines the nutrient uptake efficiency of plant  $i$  on nutrient  $n$ . The smaller  $k_{ni}$  is, the more efficient plant  $i$  is to uptake nutrient  $n$ .  $N_n$  is the concentration of nutrient  $n$ , which dynamically changes over time and is described by another set of differential equations:

$$\frac{dN_n}{dt} = D(S_n - N_n) - v_{ni} \sum_i r_i G_i B_i. \quad (19)$$

Here,  $D$  is the global turnover rate that determines the rate by which the nutrients are refreshed.  $S_n$  is the maximal concentration of nutrient  $n$ .  $v_{ni}$  sets the relative content of nutrient  $n$  in plant  $i$ .

### 3.3 parametrisation and units

Variable	Mathematical expression	Name in the package	Definitions
$L_{ij}$	$L_{ij} = \left( \frac{m_j}{m_i R_{opt}} e^{1 - \frac{m_j}{m_i R_{opt}}} \right)$	\$L	Attack rate
$b_{ij}$	$b_{ij} = b_0 m_i^{b_1} m_j^{b_2} e^{E_b \frac{T_0 - T}{k T T_0}} L_{ij}$	\$b	Attack rate
$h_{ij}$	$h_{ij} = h_0 m_i^{h_1} m_j^{h_2} e^{E_h \frac{T_0 - T}{k T T_0}}$	\$h	Handling time
$r_i$	$r_i = m_i^{r_1} e^{E_r \frac{T_0 - T}{k T T_0}}$	\$r	Maximum growth rate
$X_i$	$X_i = x_0 m_i^{x_1} e^{E_x \frac{T_0 - T}{k T T_0}}$	\$X	Metabolic rate
$K_{np}$	Free parameter	\$K	Uptake efficiency
$v_{np}$	Free parameter	\$V	Plants relative nutrient content
$S_n$	Free parameter	\$S	Maximal level for nutrients
$c$	Free parameter	\$c	Interference competition
$q_i$	Free parameter	\$q	Hill exponent (functional response type)
$D$	Free parameters	\$D	Turnover rate of the nutrients

Table 4: variables used in the unscaled with nutrient version

Variable (units)	parameter used	values
$b_{ij}$ ( $m^2.s^{-1}$ )	$b_0$	50
	$b_1$	$\mathcal{N}(0.15, 0.03)$
	$b_2$	$\mathcal{N}(0.47, 0.04)$
	$E_a$	-0.38
$h_{ij}$ ( $s$ )	$h_0$	0.4
	$h_1$	$\mathcal{N}(-0.66, 0.02)$
	$h_2$	$\mathcal{N}(-0.48, 0.03)$
	$E_h$	0.26
$c_i$ ( $s$ )	$c$	$\mathcal{N}(0.8, 0.2)$
$K_{np}$ ( $g.m^{-2}$ )	$k$	$\mathcal{U}(0.1, 0.2)$
$v_{np}$ (unitless)	$v$	$\mathcal{U}(1, 2),   \sum_n (v_{np} = 1)$
$S_n$ ( $g.m^{-2}$ )	$s$	$\mathcal{N}(10, 2)$
$r_p$ ( $s^{-1}$ )	$r_1$	-0.25
	$E_r$	-0.84
$X_i$ ( $J.s^{-1}$ )	$x_0$	0.138 ( $i$ is a plant)
	$x_0$	0.314 ( $i$ is an animal)
	$x_1$	-0.25
	$E_x$	-0.69
$q_i$	-	0.2
$D$	-	0.25

Table 5: values and units of variables as set by the package default parametrisation for the unscaled with nutrient version

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