Energetic mismatch induced by warming decreases leaf litter decomposition by aquatic detritivores

 $\begin{array}{c} \textbf{Theme08 - Introduction to Systems Biology} \\ \textbf{Reproducing a Research Article} \end{array}$



Figure 1: Gammarus fossarum

Vincent Talen 389015 BFV2 June 26, 2023 Tsjerk Wassenaar (WATS)

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Theme08 - Introduction to Systems Biology Reproducing a Research Article

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Abstract

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List of Abbreviations

MTE ODE Metabolic Theory of Ecology

Ordinary differential equation

RMF IR	Routine metabolic rate Leaf ingestion rate	
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1 Introduction

Climate change is a rising threat to the earth, the average overall surface temperature is predicted to increase by 0.2°C per decade and up to 2–5°C by the end of this century, leading to massive disruptions at all levels of biological organization across ecosystems [1], [2]. Life-history traits, population dynamics, species interactions and ecological processes are strongly influenced by temperature [3]–[5], especially physiological traits related to energy acquisition and expenditure [6], such as metabolic rate [7], [8] and ingestion rate [9], [10], which together determine the energy balance of organisms. Furthermore, most organisms are ectotherms [11] on who temperature has an even greater effect [12], thus a key in understanding ecosystems' response to global warming is understanding the thermal physiology of ectotherms [13].

A powerful framework to investigate ecosystem functioning in the context of global warming is the Metabolic Theory of Ecology (MTE) [6]. It combines the effects of body mass and temperature on biochemical processes in order to predict individual physiological performances [14], [15], this can then be scaled up from individuals to population, community and ecosystem levels [16]. As metabolic losses increase exponentially with warming, organisms generally increase energy supply through nutrient ingestion [17], [18], but metabolism increases more rapidly than nutrient ingestion with temperature. The resulting mismatch causes a decreasing energetic efficiency as temperature rises [19], but has not been studied or measured directly.

Despite the functional significance and vulnerability to warming of detritivore populations [20], [21], most studies on the impact of global warming on consumer-resource dynamics have mainly focused on carnivore and herbivore populations. Detritivores are heterotrophs that consume plant litter and decompose them into smaller inorganic molecules, performing what is called the first stage of remineralisation. These inorganic compounds can then be used by primary producers, such as plants and algae, to synthesize new organic molecules, completing the nutrient cycle in the ecosystem. Thus, leaf litter decomposition by detritivores is a crucial process in the ecosystem as it allows the nutrients stored in organic matter to be recycled and reused by other organisms.

Previous studies have not yet fully explained how thermal constraints on detritivores scale up to their entire ecosystems. Thermal bio-energetic models are greatly relevant for studying the impact of temperature and body size changes on detritivore-resource dynamics [22]-[24] and understanding the balance between key physiological processes that determine detritivore fitness [25] is crucial for predicting the responses of populations and freshwater ecosystems to global warming [19], [26], [27].

The goal of this research is to reproduce and improve on the research done by $R\'{e}veillon$ et al. [28] on the modelling of the consumer-resource dynamics by greatly improving the model code written in R, resulting in better reproducibility of this research and it being more easily expandable. $R\'{e}veillon$ et al. investigated the thermal energetic mismatch between energy demand (i.e. metabolic rate) and supply (i.e. ingestion rate) and simulated the consequences of this thermal mismatch for seasonal population dynamics and carbon fluxes [28].

1.1 Theory

The consumer-resource model created by *Réveillon et al.* describes the seasonal dynamics of *Gammarus Fossarum* and Leaf Litter biomasses in a temperate stream, a diagram showing an overview of the system dynamics can be seen below in Figure 2. Even though the model assumes that all individuals of the population have the same body mass, the exploration on the effects of temperature-induced changes in population body size is still possible. The fluctuation in Gammarus population biomass is driven by the balance between carbon intake through food ingestion and carbon loss through respiration. Changes in leaf litter biomass are due to herbivory pressure of Gammarus on seasonal litter fall stock.

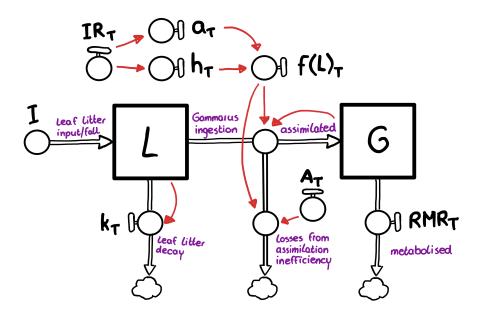


Figure 2: Diagram showing dynamics of the model (Made by Vincent Talen)

State variables

The model has two state variables, leaf litter standing stocks (L) and Gammarus population biomass (G), both in in $mg \, C/m^2$. Both state variables have an ordinary differential equation (ODE) that describes their temporal change, Equation 1a and 1b respectively.

$$\frac{dL}{dt} = I - f(L)_{\rm T}G - k_{\rm T}L \tag{1a}$$

$$\frac{dG}{dt} = G\left[f(L)_{\mathrm{T}}A_{\mathrm{T}} - RMR_{\mathrm{T}}\right] \tag{1b}$$

The standing stock of leaf litter is sustained by the seasonal leaf litter fall inputs (I) and decreases due to feeding activity by the Gammarus population $(f(L)_TG)$ and litter decomposition (k_TL) by other degradation processes (e.g. microbial decomposition and leaching). Dynamics of the Gammarus population is described as the balance of carbon intake through litter ingestion $(f(L)_T A_T)$ and loss through respiration (RMR_T) , henceforth Routine Metabolic Rate (RMR). Each of the parameters of these two ODEs is described by their own equation and dependent on temperature, except for leaf litter input, all parameters are shown in Table 1 below.

Table 1: Model state variables' parameters

Parameter	Equation	Unit	Explanation
$\overline{I \atop f(L)_{\mathrm{T}}}$	2	$mg C m^2$ $mg C mg C^{-1} day^{-1}$	Leaf litter input Gammarus functional response
$RMR_{ m T}$	3b	mgC/day	Gammarus routine metabolic rate
$A_{ m T}$	4	-	Gammarus assimilation efficiency
k_{T}	5	day^{-1}	Leaf litter microbial decomposition

Parameter equations

The first parameter that is used in both differential equations is the *Gammarus* population feeding rate, which follows the Holling type II functional response (Equation 2).

$$f(L)_T = \frac{a_T L}{1 + a_T h_T L} \tag{2}$$

with $a_{\rm T}$ being the Gammarus attack rate on leaves (mg^{-2}/day) , $h_{\rm T}$ the Gammarus handling time (day^{-1}) , both at temperature T, and with L being the leaf litter biomass in $mg~C/m^2$. Attack rate is estimated by assuming that the proportion of ingested leaf litter follows an exponential decay of time, which can be calculated as $DC_{\rm T} = -log(1 - IR_{\rm T} * t/M_L)$. Where $IR_{\rm T}$ is the daily leaf ingestion rate (IR) at temperature T $(mg~C~mg~C^{-1}~day^{-1})$ calculated with Equation 3b, t is the duration of the experiment (d) and M_L is the mean initial C mass of leaf discs in microcosms. After the decay rate is calculated the attack rate can finally be calculated by dividing the estimated decay rate by the experimental duration $(a_{\rm T} = DC_{\rm T}/t)$. The handling time is calculated as the inverse of the ingestion rate $(h_{\rm T} = 1/IR_{\rm T})$.

To express the mass (M) and temperature (T) dependence of the RMR and IR of individuals the following equations were used: To express the dependence of RMR and IR of individuals on mass (M) and temperature (T) the following equations using the MTE formula were used:

$$I = \alpha M^b e^{Ea\left(\frac{T - T_0}{k_B T_0 T}\right)} \tag{3a}$$

$$I = \alpha M^b e^{p\left(\frac{T - T_0}{k_B T_0 T}\right) - q\left(\frac{T - T_0}{k_B T_0 T}\right)^2}$$
(3b)

where α is the metabolic or the ingestion expression level at reference temperature T_0 , b is the mass-scaling exponent, M is the dry body mass (mg), Ea is the activation energy (eV) and k_B is the Boltzmann's constant $(8.62 * 10^{-5} eV K^{-1})$.

To allow for the investigation into the curvature strength of the relationship between the measured rate (I) and temperature, a deviation of the MTE expression is used within Equation 3b's exponential term. The curvature is described by the fitted polynomial first- and second-order terms p and q, respectively [29], [30]. If q = 0 is used in the quadratic formulation (Equation 3b) and the equation is reduced to the MTE model, then p can be interpreted as the activation energy [29]. This particular case is formulated as Equation 3a.

To express the temperature dependence of assimilation efficiency (A_T) , empirical equations and values for detritivores from $Lang\ et\ al.\ [31]$ are used. So the assimilation efficiency is confined between 0 and 1 (no assimilation or complete assimilation) a logistic equation is used where the MTE equation is used both at the numerator and denominator, resulting in Equation 4.

$$A_T = \frac{\alpha e^{Ea\left(\frac{T-T_0}{k_B T_0 T}\right)}}{1 + \alpha e^{Ea\left(\frac{T-T_0}{k_B T_0 T}\right)}} \tag{4}$$

where α is the normalization constant of assimilation efficiency, Ea is the activation energy (eV) and k_B is the Boltzmann's constant $(8.62 * 10^{-5} \ eV \ K^{-1})$.

The temperature dependence of microbial decomposition is expressed using the Arrhenius equation, since carbon fluxes in aquatic ecosystems are largely caused by microbial decomposition [32] causing leaf litter to also be affected by this.

$$k_T = k_{10^{\circ}C} e^{-Ea\left(\frac{1}{k_B T} - \frac{1}{283.15k_B}\right)}$$
 (5)

where $k_{10^{\circ}C}$ is the leaf litter decomposition rate at 10°C (283.15K), Ea is the activation energy (eV) and k_B is the Boltzmann's constant.

2 Materials and Methods

2.1 The software model

The model was implemented using the R programming language [33] (version 4.1.3), in combination with multiple packages/libraries that made it possible to perform the data manipulation and calculations. The table below (Table 2) shows the list of packages that were used for this project, including their exact versions. It is recommended to use the exact versions of the packages listed to guarantee compatibility when reproducing this project and model.

Software	Package	Version
\overline{R}		4.1.3
	data.table	1.14.2
	deSolve	1.3.4
	ggpubr	0.4.0
	lme4	1.1 - 29
	quantmod	0.4.20
	reshape2	1.4.4
	tidyverse	1.3.1

Table 2: Software and packages

The ode function from the deSolve [34] package is the core tool used to implement the model, it applies the ordinary differential equations (ODE), that make up the model, over time with parameters. All the data is placed into data.tables from the data.table library [35], allowing for fast and intuitive operations. To visualize the data and create plots the packages ggpubr [36], reshape2 [37] and tidyverse [38] were used. The lme4 [39] and quantmod [40] packages were used to create models and prediction data used for the actual lines in the plots.

2.2 Model configuration

Réveillon et al. performed multiple laboratory experiments and statistical analyses to estimate values for the initial state variables and the parameters that together accurately describe the dynamics to develop the consumer-resource model [28]. The experimental values that $Réveillon\ et\ al.$ used will also be used for this project in order to attain the goal of this project, namely to improve on the code implementation of the consumer-resource model. All values below will come from their research article ([28]).

Each scenario that has been simulated for this project has been done for the same five temperatures (5, 10, 15, 20 and 25 degrees Celsius) and were run for the same 7-year duration, of which the first year is excluded because of transient dynamics following the input of leaf litter and detritivores in the system. The annual leaf litter fall was represented as an event of 15 consecutive days at the beginning of each year, with an even amount of leaf litter fall each day as to mimic the phenology of forest vegetation in the study region [28]. It was also assumed that each Gammarus individual had the same body mass, meaning that a population size structure was not implemented.

Since the consumer-resource model consists of two state variables and almost each of their parameters are again expressed as equations which also have their own parameters, a lot of values were used to describe and simulate the system dynamics. Most of the equations' parameters are static between scenarios, with only the mass (M) and temperature (T) changing. The static parameter values will be listed in a separate table for each equation, beginning with the global parameter values used in almost every equation or formula in Table 3.

Table 3: Global parameter values

Parameter	Value	Unit	Explanation
\overline{T}	5, 10, 15, 20, 25	C	Temperatures simulations were run at
T_0	285.65	K	Reference temperature
k_B	$8.62*10^{-5}$	$eV K^{-1}$	Boltzmann's constant
M	4.26	mg	Gammarus mean individual dry body mass

Both the Metabolic- and Ingestion Rate are both calculated using Equation 3b, they thus do use the same parameters but not the same parameter values. The values that are used to calculate the metabolic rate are listed in Table 4 and the values used to calculate the ingestion rate are listed in Table 5.

Table 4: Metabolic Rate (3b) parameter values

Parameter	Value	Unit	Explanation
α	$e^{2.41599}$	-	Metabolic expression level at reference temperature T_0
b	0.62308	-	Mass-scaling exponent
p	0.66731	-	Curve steepness
q	0.21153	-	Quadratic term

Table 5: Ingestion Rate parameter values

Parameter	Value	Unit	Explanation
α	$e^{5.26814}$	-	Ingestion expression level at reference temperature T_0
b	0.81654	-	Mass-scaling exponent
p	0.31876	-	Curve steepness
q	0.18909	-	Quadratic term

For calculating the assimilation efficiency, estimates provided by $Lang\ et\ al.\ [31]$ and the rescaled intercept (α) by $R\'{e}veillon\ et\ al.\ [28]$ were used. These values are listed below in Table 6.

Table 6: Assimilation Efficiency parameter values

Parameter	Value	\mathbf{Unit}	Explanation
α	$e^{-0.84730}$	-	Normalization constant
Ea	0.16400	eV	Activation energy
T_0	285.65	K	Reference temperature

Parameter values used for the attack rate formula can be seen in Table 7. Initial mass of the leaf discs is derived from the pre-weighed batches of six dry leaf discs the individuals were allowed to feed on during the experiment. The mean dry mass of these batches was 10.25mg [28], which was then converted from dry mass to C content through the use of the the conversion factor (0.45) of dry mass to C content of leaf litter. Lastly the C mass was converted from mg to μg by multiplying by 1000.

Table 7: Attack rate formula static parameter values

Parameter	Value	Unit	Explanation
\overline{t}	2	day	Duration of the feeding experiment
M_L	4612.5	$\mu g C$	Initial C mass of leaf discs in microcosms

The parameter values used in the Arrhenius equation that expresses the microbial decomposition rate of leaf litter are listed in Table 8 and are in situ estimates provided by Follstad Shah et al. [41].

Table 8: Leaf Decomposition Rate parameter values

Parameter	Value	\mathbf{Unit}	Explanation
$ \begin{array}{c} \overline{k_{10^{\circ}C}} \\ Ea \end{array} $	0.00956 0.37000	$\begin{array}{c} day^{-1} \\ eV \end{array}$	Litter decomposition rate at 10°C (283.15°K) Activation energy

One of the attributes that was calculated as part of the analysis is the annual persistence time above thresholds for both litter standing stock and Gammarus stock, the threshold values that were used are listed in Table 9.

Table 9: Annual persistence time threshold values

Threshold	Value	\mathbf{Unit}	Explanation	
$\frac{L}{G}$	$6*10^4$ $5*10^3$	$mgC/m^2 \ mgC/m^2$	Threshold for litter standing stock Threshold for Gammarus stock	

Main analysis

For the main analysis three scenarios were simulated, the first was the reference scenario (TSR_R) with all its parameters values based on experimental estimates and the Gammarus mean body mass is constant across temperatures. Because body mass is temperature dependent [42] two other scenarios were simulated that implemented the dependency of temperature on body mass, these simulations were based on empirical results from a meta-analysis by Forster et al. ([43]): a scenario that uses the mean relationship between body mass and temperature for aquatic organisms (TSR_A) and a scenario that corresponds to the largest body size decrease with temperature (TSR_M) . The values used for the main analysis' scenarios are listed below in Table 10.

Table 10: Main analysis initial state variables biomass values

State variable	Value	Unit	Explanation
L	300 000	$mg C/m^2$	Leaf litter stock biomass
G	15	mgC/m^2	Gammarus population biomass density
I	300 000	$mg C m^{-2} year^{-1}$	Annual leaf litter input

3 Results

4 Discussion and Conclusion

4.1 Discussion

- Basically unreproducible in general, long pieces of code that were repeated over and over that could not be understood. No easy way to reproduce other than to immediately copy and paste multiple hundreds lines of code where only few values would be changed.
- Formulas for metabolic and ingestion rates were heavily rewritten from the base formula. They were unrecognizable so they were cleaned up to be understandable and resemble the actual formula more. It should also be noted that the position where the mean in the quadratic portion of the exponent is actually different from what would be done following the formula.
- When cleaning the data for calculating the means, standard deviation and persistence of the biomasses a mistake was made. The first 16 days of each year are when the leaf litter falls so these need to be removed as to not taint the results. This was then coded in the literal way as it was just said, however, the code behaves different than they likely expected so only 16 days were removed per year. Thus the removal only happened each year for the temperature of 5 degrees Celsius, this was easily fixed by grouping by year and temperature.
- To calculate the decreasing slopes the quantmod library's findPeaks and findValleys functions were used. These however have a flaw in them causing the peaks and valleys to always overshoot by 1 row, to fix this all indices were subtracted by 1.

4.2 General conclusion and perspective

5 References

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6 Appendices

Appendix A: 'model.R'

```
## Copyright (c) 2023 Vincent Talen.
   ## Licensed under GPLv3. See LICENSE file.
   ## ~~~~~~~
   ## Script name: model.R
   ## Purpose of script: Implements the biological model of consumer-resource dynamics
   ## Author: Vincent Talen
   ## Date Created: 09 Jan 2023
11
12
   ## Email: v.k.talen@st.hanze.nl
13
   ## ~~~~~~~
16
   ## Notes:
   ## - Goal: formulate formula functions in a more readable/recognizable manner
18
19
   ## ~~~~~~~
20
21
22
   # ######## #
  # Libs #
24
   library(deSolve)
28
   # ######## #
  # Code #
30
  # ###############
   # Define Boltzmann term (°K)
   boltz_const <- 8.62 * 10^-5
33
   # Define mean inverse temperature (calculated from Data_Mismatch.txt)
   mean inverse temp <- 40.5941593143742
36
37
   ## ---- mte formulations ----
   # Quadratic function for metabolic rate (\mu g C/day)
39
   calcMetabolicRate <- function(T.C, M) {</pre>
     alpha \leftarrow exp(2.41599)
                             # metabolic expression level at reference temperature
41
     b <- 0.62308
                               # mass-scaling exponent
     p <- 0.66731
                               # curve steepness (of the relationship)
43
     q <- 0.21153
                                # quadratic term
     T.K \leftarrow T.C + 273.15
                                # convert temperature from Celsius to Kelvin
45
     # Repeating part with temperatures
47
     temp_dependancy_part <- (1 / (T.K * boltz_const)) - mean_inverse_temp</pre>
```

```
49
      # Calculate metabolic rate with full formula
      metabolic_rate <- alpha * M^b * exp(-p * temp_dependancy_part) * exp(-q * temp_dependancy_part^2)
51
      return(metabolic_rate)
52
    }
53
54
    # Quadratic function for ingestion rate (\mu q C/day)
55
    calcIngestionRate <- function(T.C, M) {</pre>
      alpha \leftarrow exp(5.26814)
                                     # ingestion expression level at reference temperature
57
      b <- 0.81654
                                     # mass-scaling exponent
58
      p <- 0.31876
                                     # curve steepness (of the relationship)
59
                                     # quadratic term
      q <- 0.18909
60
      T.K \leftarrow T.C + 273.15
                                     # convert temperature from Celsius to Kelvin
61
62
       # Repeating part with temperatures
63
      temp_dependancy_part <- (1 / (T.K * boltz_const)) - mean_inverse_temp</pre>
64
65
      # Calculate ingestion rate with full formula
66
      ingestion_rate <- alpha * M^b * exp(-p * temp_dependancy_part) * exp(-q * temp_dependancy_part^2)
      return(ingestion_rate)
68
    }
69
70
71
    ## ---- assimilation efficiency ----
72
    # Assimilation efficiency function based on exponential decay (quadratic model)
    # Is a logistic equation with the MTE equation both at the numerator and the denominator
74
    calcAssimEff <- function(T.C) {</pre>
                                  # normalization constant of assimilation efficiency
      alpha \leftarrow exp(-0.84730)
76
      Ea <- 0.16400
                                   # activation energy
77
      T.0 <- 285.65
                                  # reference temperature of 12.5 degrees Celsius in Kelvin
      T.K \leftarrow T.C + 273.15
                                  # convert temperature from Celsius to Kelvin
79
80
      mte_equation <- alpha * exp( Ea * (T.K - T.0) / (boltz_const * T.0 * T.K) )</pre>
81
      return(mte_equation / (1 + mte_equation))
    }
83
84
85
    ## ---- attack rate parameter ----
    # Attack rate function based on exponential decay (quadratic model)
87
    calcAttackRate <- function(temp, mass) {</pre>
                     # Experiment duration
89
      M.L <- 4612.5 # Mean initial C mass of leaf discs in microcosms (\mu q C)
      decay_rate <- -log(1 - calcIngestionRate(temp, mass) * t / M.L)</pre>
91
      return( decay_rate / t )
92
    }
93
94
95
    ## ---- handling time parameter ----
96
    # Handling time function based on exponential decay (quadratic model)
97
    calcHandlingTime <- function(temp, mass) {1 / (calcIngestionRate(temp, mass) / 1000) }</pre>
98
99
    ## ---- leaf decomposition- and respiration rate ----
100
    # Function for the leaf litter microbial decomposition rate (Arrhenius equation)
101
    calcLeafDecomp <- function(T.C) {</pre>
```

```
k.10C <- 0.00956
                                   # litter decomposition rate at 10°C (283.15°K)
103
      Ea <- 0.37000
                                   # activation energy
104
      T.K <- T.C + 273.15
                                   # convert temperature from Celsius to Kelvin
105
       # return( k.10C * exp(-Ea * (1 / (boltz_const * T.K - 283.15 * boltz_const))) )
106
      return( k.10C * exp(-Ea * (1 / (boltz_const * T.K) - 10)) )
107
108
109
110
    ## ---- consumer-resource model ----
    GammLeafModel <- function(temp, gamm_indv_mass, leaf_fall, gamm_start_biomass, tsr_model) {</pre>
112
       # Apply TSR Model to Gammarus individual mass
113
      if (!is.null(tsr model)) {
114
        gamm indv mass <- tsr model(temp, gamm indv mass)</pre>
115
116
117
      Nutri <- function(time, state, parms) {</pre>
118
        with(as.list(c(state, parms)), {
119
           fL <- a * L / (1 + a * h * L)
                                                    # Holling type II functional response
120
           dL \leftarrow -fL * G - k * L
                                                    # Biomass changes of leaf litter stock
121
           dG \leftarrow G * (fL * A - M)
                                                    # Biomass changes of Gammarus population
122
           list(c(dL, dG))
123
        })
124
      }
125
126
      # Leaf litter fall event function
127
      leafFallEvent <- function(time, state, parms) {</pre>
        with(as.list(c(state, parms)), {
129
           return(c(L + leaf_fall, G))
130
        })
131
      }
132
133
       # Get time points to trigger litter fall event (first 15 days of the year)
134
      getFallTimesYearX <- function(year) { seq(year * 365 + 1, year * 365 + 15) }</pre>
135
      leaf_fall_times <- unlist(lapply(seq(0, 6), getFallTimesYearX))</pre>
136
137
      # Model parameters
138
      parameters <- c(
139
        M = calcMetabolicRate(temp, gamm_indv_mass) / 1000, # Gammarus metabolic rate (in mqC/day)
140
        a = calcAttackRate(temp, gamm_indv_mass),
                                                                  # Gammarus attack rate (in mqC/day)
        h = calcHandlingTime(temp, gamm_indv_mass),
                                                                  # Gammarus handling time (in 1/day)
142
                                                                  # Gammarus assimilation efficiency
        A = calcAssimEff(temp),
143
        k = calcLeafDecomp(temp),
                                                                  # Leaf microbial decomposition (in 1/day)
144
145
146
       # Times and starting conditions
      times \leftarrow seq(0, 365 * 7, by = 1)
                                                                  # Times in days for 7 years
148
      state <- c(L = leaf_fall, G = gamm_start_biomass)</pre>
                                                                  # Starting biomasses (in g/m2)
149
150
       # Model output
151
      out <- ode(time = times, func = Nutri, y = state, parms = parameters,
152
                  events = list(func = leafFallEvent, time = leaf_fall_times))
153
154
      # Turn deSolve class object into dataframe and change very low and negative values to 0
155
```

```
data_table <- as.data.table(out) %>% mutate(across(c(L, G), ~ fifelse(.x < 10^-3, 0, .x)))
       return(data_table)
157
    }
158
159
160
    ## ---- temperature-size rule models ----
161
    # Average TSR response
    calcTSR.Avg <- function(temp, mass) {</pre>
163
       conv fact <- 6.5
164
                                                                    # Avg. conversion factor from dry to fresh mas
       change_slope \leftarrow -3.90 - 0.53 * log10(mass)
                                                                    # Slope of change in mass per carbon
165
       change_prop <- log(1 + change_slope / 100)</pre>
                                                                    # Proportion of change in mass per C
166
       change_const <- exp(log(mass) - 12.5 * change_prop)</pre>
                                                                   # Constant of change in mass at 12.5°C
167
168
       dry_mass <- change_const * exp(change_prop * (temp))</pre>
                                                                    # Dry body mass (mq)
169
       fresh_mass <- dry_mass / conv_fact</pre>
                                                                    # Fresh body mass (mq)
170
       return(dry_mass)
171
172
173
    # Maximum TSR response
174
    calcTSR.Max <- function(temp, mass) {</pre>
       conv_fact <- 6.5</pre>
                                                                    # Avg. conversion factor from dry to fresh mas
176
       change_slope <- -8.0
                                                                    # Slope of change in mass per carbon
177
       change_prop <- log(1 + change_slope / 100)</pre>
                                                                    # Proportion of change in mass per C
178
       change_const <- exp(log(mass) - 12.5 * change_prop)</pre>
                                                                    # Constant of change in mass at 12.5°C
180
       dry_mass <- change_const * exp(change_prop * (temp))</pre>
                                                                    # Dry body mass (mg)
       fresh_mass <- dry_mass / conv_fact</pre>
                                                                    # Fresh body mass (mg)
182
       return(dry_mass)
183
    }
184
```

Appendix B: 'functions.R'

```
## Copyright (c) 2023 Vincent Talen.
   ## Licensed under GPLv3. See LICENSE file.
   ## Script name: functions.R
   ## Purpose of script: Functions
   ## Author: Vincent Talen
10
   ## Date Created: 09 Jan 2023
12
   ## Email: v.k.talen@st.hanze.nl
14
   ## ~~~~~~~
16
   ## Notes:
   ##
      - x
18
```

```
20
21
22
   Libs
24
   # ####### #
   library(data.table)
   library(ggpubr)
   library(reshape2)
28
   library(tidyverse)
   source("src/model.R")
31
32
   # ####### #
33
   # Functions #
34
   # ######## #
35
   # ---- Scenario data gathering and preparations ----
   getScenarioDataList <- function(gamm_indv_mass, leaf_fall, gamm_start_biomass, tsr_model) {</pre>
37
      # Get data for given values for each temperature using the model function that performs an ode
     data_list <- lapply(temperatures, GammLeafModel, gamm_indv_mass, leaf_fall, gamm_start_biomass, tsr_m
39
        setNames(temperatures)
     return(data list)
41
   }
42
43
   createLongDataFrame <- function(df_list, tsr_model) {</pre>
44
     if (is.null(tsr_model)) { tsr_model <- function(temp, mass) {return(mass)} }</pre>
45
46
     # Function to get the population metabolism for a temperature with the population biomass
47
     getPopMetabolism <- function(cur_temp, gamm_pop_biomass) {</pre>
48
        # Get metabolic rate for current temperature
49
                    <- calcMetabolicRate(cur_temp, tsr_model(cur_temp, gamm_indv_mass)) / 1000 # Gammarus</pre>
50
        # Calculate population metabolism
       pop_metabolism <- meta_rate * gamm_pop_biomass</pre>
52
        return(fifelse(pop_metabolism < 0, 0, pop_metabolism))</pre>
54
      # Function to get the population ingestion for a temperature with the population- and leaf biomasses
     getPopIngestion <- function(cur_temp, leaf_biomass, gamm_pop_biomass) {</pre>
56
        # Get ingestion- and attack rates for current temperature
        ingest_rate <- calcIngestionRate(cur_temp, tsr_model(cur_temp, gamm_indv_mass)) / 1000</pre>
58
        attack_rate <- calcAttackRate(cur_temp, tsr_model(cur_temp, gamm_indv_mass))
                                                                                                     # Gammarus
59
        # Calculate population leaf ingestion
60
       pop_ingestion <- (attack_rate * leaf_biomass / (1 + attack_rate * 1 / ingest_rate * leaf_biomass))</pre>
61
       return(fifelse(pop_ingestion < 0, 0, pop_ingestion))</pre>
62
     }
63
64
      # Bind all dataframes from list to single big one and
65
      # drop the last days to have 2555 days/rows left per temperature
66
     big_df <- rbindlist(df_list)[!time == 2555] %>%
67
        # Rename 'time' column to conform to naming scheme
        setnames("time", "Time") %>%
69
        # Add temperature and year columns to facilitate future calculations
        "$<-"(Temperature, rep(temperatures, each = 2555)) %>%
71
        "$<-"(Year, rep(rep(1:7, each = 365), 5)) %>%
```

```
# Add population metabolism and leaf ingestion columns
73
         "$<-"(M, getPopMetabolism(.$Temperature, .$G)) %>%
        "$<-"(I, getPopIngestion(.$Temperature, .$L, .$G)) %>%
75
        # Set column order to a nicer one
        setcolorder(c("Time", "L", "G", "M", "I", "Temperature", "Year"))
77
      return(big_df)
78
    }
79
80
    # ---- Plot list of scenario dataframes ----
81
    createPlotForTemp <- function(cur_temp, cur_data) {</pre>
82
      # Divide L & G values to create a better readable plot
83
      divided_data <- copy(cur_data)</pre>
84
      set(divided_data, i = NULL, "L", divided_data$L / 10^5)
      set(divided_data, i = NULL, "G", divided_data$G / 10^5)
86
      # Create plot
88
      plot <- ggplot(divided_data, aes(x = time, y = value)) +</pre>
        # Set axis limits and step size
90
        scale_x_continuous(breaks = seq(0, 7 * 365, 365)) +
        ylim(NA, ceiling(max(divided_data[, -1])) + 1) +
92
        # Add the data (lines)
        geom_line(aes(y = L, color = "Leaf Litter Biomass")) +
94
        geom_line(aes(y = G, color = "Gammarus Fossarum Biomass")) +
95
        # Add styling
96
        labs(title = sprintf("%s°C", cur_temp), x = "", y = "") +
97
        # theme(plot.title = element_text(hjust = 0.075, vjust = -11)) +
98
        \#theme(plot.margin = margin(0.1, 0.25, 0, 0, "cm")) +
99
        scale_color_manual(name = "", values = c("black", "tomato2"),
100
                             limits = c("Leaf Litter Biomass", "Gammarus Fossarum Biomass"))
101
      return(plot)
102
103
104
    plotScenarioDynamics <- function(data, image_title, file_out) {</pre>
105
      # Use lapply to create plots for each temperature in the list and collect the legend from a plot
106
      plot_list <- lapply(seq_along(data), function(i) { createPlotForTemp(names(data)[i], data[[i]]) })</pre>
107
      plot_legend <- get_legend(plot_list[[1]])</pre>
109
      # Remove legends from the plots and add extracted legend to end of the list
      plot_list <- lapply(plot_list, function(cur_plot) { cur_plot + theme(legend.position = "none") }) %>%
111
        "[[<-"(length(plot_list) + 1, plot_legend)
112
113
      # Place plots and legend in an arranged grid
114
      col_num <- 3
115
      my.grid <- ggarrange(plotlist = plot_list, ncol = col_num, nrow = ceiling(length(plot_list) / col_num
116
        annotate_figure(top = text_grob(image_title), bottom = text_grob("Time (d)"),
117
                         left = text_grob(bquote("Biomass "(10^5~ mg~ C~ m^-2)), rot = 90))
118
      # Save the created arranged grid with the lossless 'lzw' compression that greatly reduces file size
120
      ggsave(paste("figures/", file_out, sep=""), bg = "white", width=15, height=8, units="in", dpi=300, co
121
      dev.off()
122
    }
123
124
    # ---- Create prediction data ----
```

```
createPredictionData <- function(huidige_data, scenario_names) {</pre>
      # Get vector from lowest temperature to highest temperature with steps of 0.5
127
      Temperature <- seq(head(temperatures, n=1), tail(temperatures, n=1), by=0.5)
      # Create vector with scenario names times the number of temperature steps
129
      Scenario <- rep(scenario_names, each=length(Temperature))</pre>
      # Create dataframe
131
      Pred <- data.table(Temperature, Scenario)</pre>
133
      # Each column with 'Mean' should get their predicted values for smooth lines
      for(cname in colnames(huidige_data)) {
135
        if (startsWith(cname, "Mean")) {
136
          new_col_name <- gsub("Mean", "Pred", cname)</pre>
137
          predicted_data <- predict(lmList(get(cname) ~ poly(Temperature, 2)|Scenario, data=huidige_data),</pre>
138
          Pred[ , (new_col_name) := predicted_data]
139
140
      }
141
      return(Pred)
142
143
```

Appendix C: 'scenarios.R'

```
## Copyright (c) 2023 Vincent Talen.
   ## Licensed under GPLv3. See LICENSE file.
   ## Script name: scenarios.R
6
   ## Purpose of script: Simulate scenarios using functions from the functions.R module
   ## Author: Vincent Talen
10
   ## Date Created: 09 Jan 2023
11
12
   ## Email: v.k.talen@st.hanze.nl
13
14
   ## ~~~~~~~~
15
16
17
       - Energetic efficiency plot needs to be added (back from creating the model section)
19
   ## ~~~~~~~
20
21
22
   # ######## #
23
       Libs
24
   # ######## #
25
   source("src/functions.R")
   source("src/simulateScenario.R")
27
   # ######## #
```

```
# Code
31
   # ######## #
32
   33
   # Temperatures to do simulations of
   temperatures < c(5, 10, 15, 20, 25)
35
   # Duration of the leaf fall in days
37
   fall_duration_in_days <- 15
38
39
   # Gammarus mean body mass = 4.26 mgDM
40
   gamm_indv_mass <- 4.26</pre>
41
  # Annual leaf fall = 300 \text{ qC/m2/an} = 300 \text{ 000 mqC/m2/an}
42
   leaf_fall <- 300000 / fall_duration_in_days</pre>
   # Gammarus density = 30 mqDM/m2 = 15 mqC/m2
44
   gamm_start_biomass <- 15</pre>
46
   48
   # Get data for temperatures with values of current scenario
   scen_df_list <- getScenarioDataList(gamm_indv_mass, leaf_fall, gamm_start_biomass, NULL)</pre>
50
   # Create plots in an arranged grid
52
   file out <- "Population Dynamics Standard Scenario.tiff"
   image title <- "Standard Scenario: Population Dynamics over 7 years"
54
   plotScenarioDynamics(scen_df_list, image_title, file_out)
56
   # Combine dataframes into one and add temperature, year, population metabolism- and ingestion columns
57
   TestSD <- createLongDataFrame(scen_df_list, NULL)</pre>
   # Simulate scenario and get final dataframes for both types of masses
   DataSD <- simulateScenario(TestSD, "SD")</pre>
61
62
   63
   # Get data for temperatures with values of current scenario
   scen_df_list2 <- getScenarioDataList(gamm_indv_mass, leaf_fall, gamm_start_biomass, calcTSR.Avg)</pre>
65
   # Create plots in an arranged grid
67
   file out <- "Population Dynamics Average TSR.tiff"
   image title <- "Average Temperature-Size Rule Response: Population Dynamics over 7 years"
69
   plotScenarioDynamics(scen_df_list2, image_title, file_out)
71
   # Combine dataframes into one and add temperature, year, population metabolism- and ingestion columns
   TestTSRA <- createLongDataFrame(scen_df_list2, calcTSR.Avg)</pre>
73
   # Simulate scenario and get final dataframes for both types of masses
   DataTSRA <- simulateScenario(TestTSRA, "TSRA")</pre>
76
   78
   # Get data for temperatures with values of current scenario
   scen_df_list3 <- getScenarioDataList(gamm_indv_mass, leaf_fall, gamm_start_biomass, calcTSR.Max)</pre>
80
   # Create plots in an arranged grid
   file_out <- "Population Dynamics Maximum TSR.tiff"
```

```
image_title <- "Maximum Temperature-Size Rule Response: Population Dynamics over 7 years"</pre>
84
    plotScenarioDynamics(scen_df_list3, image_title, file_out)
86
    # Combine dataframes into one and add temperature, year, population metabolism- and ingestion columns
    TestTSRM <- createLongDataFrame(scen df list3, calcTSR.Max)</pre>
    # Simulate scenario and get final dataframes for both types of masses
    DataTSRM <- simulateScenario(TestTSRM, "TSRM")</pre>
90
    92
    Data <- rbind(DataSD, DataTSRA, DataTSRM)</pre>
93
    Pred <- createPredictionData(Data, c("SD", "TSRA", "TSRM"))</pre>
94
95
    lossePlot <- function(deze_data, deze_pred, col_names, plot_title) {</pre>
97
      # y-axis limits
      max_lim <- round(max(deze_data[,get(col_names["Mean"])])/10^4+1)</pre>
99
      break_by <- ifelse(max_lim <= 4, 1, 2)</pre>
101
      plot <- ggplot(deze_data, aes(x=Temperature, y=!!sym(col_names["Mean"])/10^4, group=Scenario)) +
103
        geom point(aes(color=Scenario), size=3, position=position dodge(0.5)) +
        geom_line(data=deze_pred, aes(x=Temperature, y=!!sym(col_names["Pred"])/10^4, color=Scenario, linet
105
        geom_errorbar(color="grey50", width=0.75, position=position_dodge(0.5),
106
                      aes(ymin=(!!sym(col_names["Mean"]) - !!sym(col_names["Sd"]))/10^4,
107
                          ymax=(!!sym(col_names["Mean"]) + !!sym(col_names["Sd"]))/10^4)) +
108
        # Axis (text) styling
109
        labs(x = "Temperature (\u00B0C)", y = expression('Mean biomass'~'('*10^4~mg~C~m^-2*')'), title = pl
110
        theme(axis.text.y=element_text(size=10, colour="black"), axis.text.x=element_text(size=10, colour="
111
              plot.title = element_text(size=12), legend.title=element_text(face="bold")) +
112
        scale_y_continuous(breaks=seq(0, max_lim, by=break_by), limits=c(0, max_lim)) +#, labels=function(x
113
        # Color and types of plotted data elements
114
        scale_color_manual(values=c(SD="black", TSRA="steelblue2", TSRM="tomato2")) +
        scale_linetype_manual(values=c("SD"="dotted", "TSRA"="solid", "TSRM"="solid"))
116
      return(plot)
117
    }
118
    plotGridOfColumn <- function(deze_data, deze_pred, col_name) {</pre>
120
      # Create plots and put them in a list
      plot_list <- lapply(c("L", "G"), function(l_or_g) {</pre>
122
        plot_title <- ifelse(l_or_g == "L", "Leaf Litter", "Gammarus")</pre>
        lossePlot(deze_data, deze_pred, sapply(c("Mean", "Sd", "Pred"), paste, l_or_g, sep=col_name), plot_
124
      })
125
126
      # Return the plots in an arranged grid with the legend at the bottom
127
      arranged_plots <- ggpubr::ggarrange(plotlist=plot_list, ncol=2, nrow=1, common.legend=TRUE, legend="b
128
      return(arranged_plots)
129
    }
130
131
    createPlotImageForColumn <- function(column_name, image_title, out_file) {</pre>
      plotGridOfColumn(Data, Pred, column name) %>%
133
               annotate_figure(top = text_grob(image_title, size=16, face="bold"))
      ggsave(paste("figures/", out_file, sep=""), bg="white", width=3840, height=2160, units="px", dpi=300,
135
      dev.off()
```

```
}
137
138
    createPlotImageForColumn("Biom", "Mean Biomass Scenarios", "Mean Biomass Scenarios.tiff")
139
140
    141
    lossePlot2 <- function(deze data, deze pred, col names, correction, plot title, y label) {</pre>
142
      # y-axis limits
      max lim <- round( max(deze data[,get(col names["Mean"])]) + correction )</pre>
144
      break by <- ifelse(max lim <= 4, 1, 2)
146
      plot <- ggplot(deze_data, aes(x=Temperature, y=abs(!!sym(col_names["Mean"])), group=Scenario)) +
147
        # Plot data
148
        geom_point(aes(color=Scenario), size=3, position=position_dodge(0.5)) +
149
        geom_line(data=deze_pred, aes(x=Temperature, y=abs(!!sym(col_names["Pred"])), color=Scenario, linet
150
        geom_errorbar(color="grey50", width=0.75, position=position_dodge(0.5),
151
                      aes(ymin=(abs(!!sym(col_names["Mean"]) - !!sym(col_names["Sd"]))),
152
                           ymax=(abs(!!sym(col_names["Mean"]) + !!sym(col_names["Sd"]))))) +
153
        # Axis (text) styling
154
        labs(x = "Temperature (\u00B0C)", y = y_label, title = plot_title) +
155
        theme(axis.text.y=element_text(size=10, colour="black"), axis.text.x=element_text(size=10, colour="
              plot.title = element_text(size=12), legend.title=element_text(face="bold")) +
157
        scale_y_continuous(labels=function(x){x/correction}) + expand_limits(y = 0) +
158
        #scale_y_continuous(breaks=seq(0, max_lim, by=break_by), limits=c(0, max_lim)) +#, labels=function(
159
        # Color and types of plotted data elements
        scale color manual(values=c(SD="black", TSRA="steelblue2", TSRM="tomato2")) +
161
        scale linetype manual(values=c("SD"="dotted", "TSRA"="solid", "TSRM"="solid"))
162
      return(plot)
163
    }
164
165
    plotGridOfColumn2 <- function(deze_data, deze_pred, col_info) {</pre>
166
      # Create plots and put them in a list
167
      plot_list <- lapply(c("L", "G"), function(l_or_g) {</pre>
168
        plot_title <- ifelse(l_or_g == "L", "Leaf Litter", "Gammarus")</pre>
169
        full_column_names <- sapply(c("Mean", "Sd", "Pred"), paste, l_or_g, sep=col_info$col_name)
170
        lossePlot2(deze_data, deze_pred, full_column_names, col_info$correction, plot_title, col_info$y_lab
      })
172
173
      # Return the plots in an arranged grid with the legend at the bottom
174
      arranged_plots <- ggpubr::ggarrange(plotlist=plot_list, ncol=2, nrow=1, common.legend=TRUE, legend="b
      return(arranged plots)
176
    }
177
178
    createPlotImageForColumn2 <- function(cur_col_info, cur_data) {</pre>
      cur pred <- createPredictionData(cur data, c("SD", "TSRA", "TSRM"))</pre>
180
      plotGridOfColumn2(cur_data, cur_pred, cur_col_info) %>%
181
        annotate_figure(top = text_grob(cur_col_info$image_title, size=16, face="bold"))
182
      ggsave(paste("figures/", cur_col_info$image_title, ".tiff", sep=""), bg="white", width=3840, height=2
183
      dev.off()
184
    }
185
186
    column_info <- list(</pre>
187
      list(col_name = "Biom",
188
           correction = 10<sup>4</sup>,
189
```

```
y_label = expression('Mean biomass'~'('*10^4~mg~C~m^-2*')'),
190
           image_title = "Mean Biomass Scenarios"),
191
      list(col_name = "PersTime",
192
           correction = 1,
193
           y_label = "Persistance time (days)",
           image_title = "Persistance Time Scenarios"),
195
      list(col_name = "Slope",
           correction = 10^4,
197
           y_label = expression('Mean biomass slope'~'('*10^4~mg~C~m^-2~day^-1*')'),
           image_title = "Mean Biomass Slope Scenarios")
199
    )
200
201
    for (cur_col_info in column_info) {
202
      createPlotImageForColumn2(cur_col_info, Data)
203
    }
204
205
    # createPlotImageForColumn2(column_info[[3]], Data)
206
```