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

Theme08 - Introduction to Systems Biology
Reproducing a Research Article

Figure 1: Gammarus fossarum

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Date: July 27, 2022

Abstract

Abstract

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1.1 Goal

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RMR was calculated as the slope of oxygen depletion over a ca 35 min timeframe, corrected for the mean linear trend over time of oxygen concentration in controls as follows: RMR = (ci – cf)/(ti – tf), where ci and cf are initial and final oxygen concentrations (μmol O2/L) in the wells and ti and tf are initial and final times points (day-1) of the respiration experiment. Values were converted into C release rate (μg C/day) assuming a respiratory coefficient of 0.78 (as estimated for Gammarus pulex, Wright & Wright, 1979).

Statistical Analysis Equations

The following equations were used to express the mass (M in mg) and temperature (T in Kelvin) dependence of individual RMR and IR:

$$I = \alpha M^b e^{Ea\left(\frac{T-T_0}{k_B T_0 T}\right)} \tag{1a}$$

$$I = \alpha M^b e^{p\left(\frac{T-T_0}{k_B T_0 T}\right) - q\left(\frac{T-T_0}{k_B T_0 T}\right)^2} \tag{1b}$$

The standard MTE formulation (1a) is simply a particular case of the quadratic formulation (1b) where $q = 0$ and the equation is reduced to the MTE model where p can thus be interpreted as the activation energy.

Energetic efficiency was also calculated as follows: $E = (IR/RMR) * A_T$, where the ratio of IR to RMR is the ingestion to metabolism efficiency and A_T is the assimilation efficiency at temperature T. The temperature (T in Kelvin) dependence of assimilation efficiency was expressed, using empirical equations and values for detritivores Assimilation efficiency was following a logistic equation with the MTE equation both at the numerator and the denominator With the following formulation, assimilation efficiency is confined between 0 and 1 (no or complete assimilation):

$$A_T = \frac{\alpha e^{Ea\left(\frac{T-T_0}{k_B T_0 T}\right)}}{1 + \alpha e^{Ea\left(\frac{T-T_0}{k_B T_0 T}\right)}} \tag{2}$$

Consumer-Resource Dynamics Model

Below are the ordinary differential equations describing temporal change in leaf litter standing stocks (L) and Gammarus population biomass (G) (Equation 3a and 3b).

$$\frac{dL}{dt} = I - f(L)_T G - k_T L \tag{3a}$$

$$\frac{dG}{dt} = G\left[f(L)_T A - RMR_T\right] \tag{3b}$$

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.

4.2 General conclusion and perspective

5 References

R Core Team. 2019. *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org.

Réveillon, Tom, Thibaut Rota, Éric Chauvet, Antoine Lecerf, and Arnaud Sentis. 2022. "Energetic Mismatch Induced by Warming Decreases Leaf Litter Decomposition by Aquatic Detritivores." *Journal of Animal Ecology* n/a (n/a). https://doi.org/https://doi.org/10.1111/1365-2656.13710.

6 Appendices

Appendix A: 'model.R'

```r
## --------------------------
##
## Script name: model.R
##
## Purpose of script: Implements the biological model of consumer-resource dynamics
##
## Author: Vincent Talen
##
## Date Created: 20 June 2022
##
## Email: v.k.talen@st.hanze.nl
##
## -------------------------
##
## Notes:
##    - Goal: formulate formula functions in a more readable/recognizable manner
##
## --------------------------


#############
#   Libs    #
#############
library(deSolve)


#############
#   Code    #
#############
## ---- loading in data ----
# Dataframe with respiration rate and ingestion rate (µg C/hour)
input_file <- "Data_Mismatch.txt"
data <- read.table(input_file, header = TRUE, dec = ".")
data <- na.omit(data)

# Consider individuals as a qualitative variable
data$Indiv <- as.factor(data$Indiv)

# Suppress outlier individuals and rows with negative values
data <- data[!data$Indiv %in% c("12", "30", "76", "78"), ]
data <- data[data$Respi > 0 & data$Nutri > 0, ]


## ---- mte formulations ----
# Convert temperature into the Boltzmann term (°K)
boltz_const <- 8.62 * 10^-5
inverse_temps <- 1 / ((data$Temp + 273.15) * boltz_const)
mean_inverse_temp <- mean(inverse_temps)
```

```r
# Quadratic function for metabolic rate (µg C/day)
calcMetabolicRate <- function(T.C, M) {
  alpha <- exp(2.41599)      # metabolic expression level at reference temperature
  b <- 0.62308               # body mass-scaling exponent
  p <- 0.66731               # curve steepness (of the relationship)
  q <- 0.21153               # quadratic term
  T.K <- T.C + 273.15        # convert temperature from Celsius to Kelvin

  # Repeating part with temperatures
  temp_dependancy_part <- (1 / (T.K * boltz_const)) - mean_inverse_temp

  # Calculate metabolic rate with full formula
  metabolic_rate <- alpha * M^b * exp(-p * temp_dependancy_part) * exp(-q * temp_dependancy_part^2)
  return(metabolic_rate)
}

# Quadratic function for ingestion rate (µg C/day)
calcIngestionRate <- function(T.C, M) {
  alpha <- exp(5.26814)      # ingestion expression level at reference temperature
  b <- 0.81654               # body mass-scaling exponent
  p <- 0.31876               # curve steepness (of the relationship)
  q <- 0.18909               # quadratic term
  T.K <- T.C + 273.15        # convert temperature from Celsius to Kelvin

  # Repeating part with temperatures
  temp_dependancy_part <- (1 / (T.K * boltz_const)) - mean_inverse_temp

  # Calculate ingestion rate with full formula
  ingestion_rate <- alpha * M^b * exp(-p * temp_dependancy_part) * exp(-q * temp_dependancy_part^2)
  return(ingestion_rate)
}


## ---- assimilation efficiency ----
# Assimilation efficiency function based on exponential decay (quadratic model)
# Is a logistic equation with the MTE equation both at the numerator and the denominator
calcAssimEff <- function(temp) {
  mte_equation <- (exp(-0.84730) * exp(0.16400 * ((temp + 273.15) - 285.65) / (boltz_const * 285.65 * (
  return(mte_equation / (1 + mte_equation))
}


## ---- attack rate parameter ----
leaf_mass <- 10.25 * 1000      # Mean initial leaf discs mass: 10.25 ± 0.68 mg
leaf_mass <- leaf_mass * 0.45  # Converted from mg to in µgC with a factor: 0.45

# Attack rate function based on exponential decay (quadratic model)
calcAttackRate <- function(temp, mass) {
  expt_duration <- 2
  decay_rate <- -log(1 - calcIngestionRate(temp, mass) * expt_duration / leaf_mass)
  attack_rate <- decay_rate / expt_duration
  return(attack_rate)
}
```

```r
103
104
105  ## ---- handling time parameter ----
106  # Handling time function based on exponential decay (quadratic model)
107  calcHandlingTime <- function(temp, mass) {1 / (calcIngestionRate(temp, mass) / 1000) }
108
109  ## ---- leaf decomposition- and respiration rate ----
110  # Reference temperature
111  ref_temp <- 10
112
113  # Function for the leaf litter microbial decomposition rate
114  calcLeafDecomp <- function(temp) { 0.00956 * exp(-0.37000 * (1 / ((temp + 273.15) * boltz_const) - ref_
115
116  # Function for the leaf litter respiration rate
117  calcLeafRespi <- function(temp) { 2.5 / 0.45 * 10^-3 * exp(-0.65000 * (1 / ((temp + 273.15) * boltz_cons
118
119
120  ## ---- consumer-resource model ----
121  GammLeafModel <- function(temp, gamm_indv_mass, leaf_fall, gamm_start_biomass) {
122    Nutri <- function(time, state, parms) {
123      with(as.list(c(state, parms)), {
124        fL <- a * L / (1 + a * h * L)           # Holling type II functional response
125        dL <- -fL * G - k * L                   # Biomass changes of leaf litter stock
126        dG <- G * (fL * A - M)                   # Biomass changes of Gammarus population
127        list(c(dL, dG))
128      })
129    }
130
131    # Leaf litter fall event function
132    leafFallEvent <- function(time, state, parms) {
133      with(as.list(c(state, parms)), {
134        return(c(L + leaf_fall, G))
135      })
136    }
137
138    # Get time points to trigger litter fall event (first 15 days of the year)
139    getFallTimesYearX <- function(year) { seq(year * 365 + 1, year * 365 + 15) }
140    leaf_fall_times <- unlist(lapply(seq(0, 6), getFallTimesYearX))
141
142    # Model parameters
143    parameters <- c(
144      M = calcMetabolicRate(temp, gamm_indv_mass) / 1000,   # Gammarus metabolic rate (in mgC/day)
145      a = calcAttackRate(temp, gamm_indv_mass),             # Gammarus attack rate (in mgC/day)
146      h = calcHandlingTime(temp, gamm_indv_mass),           # Gammarus handling time (in 1/day)
147      A = calcAssimEff(temp),                               # Gammarus assimilation efficiency
148      k = calcLeafDecomp(temp),                             # Leaf microbial decomposition (in 1/day)
149      Rl = calcLeafRespi(temp)                              # [UNUSED???] Leaf respiration (in mgC/mgleaf/
150    )
151
152    # Times and starting conditions
153    times <- seq(0, 365 * 7, by = 1)                        # Times in days for 7 years
154    state <- c(L = leaf_fall, G = gamm_start_biomass)       # Starting biomasses (in g/m2)
155
156    # Model output
```

```
157    out <- ode(time = times, func = Nutri, y = state, parms = parameters,
158               events = list(func = leafFallEvent, time = leaf_fall_times))
159
160    # Turn deSolve class object into dataframe and change very low and negative values to 0
161    data_table <- as.data.table(out) %>% mutate(across(c(L, G), ~ fifelse(.x < 10^-3, 0, .x)))
162    return(data_table)
163  }
164
165
166  ## ---- temperature-size rule models ----
167  # Average TSR response
168  calcTSR.Avg <- function(temp, mass) {
169    conv_fact <- 6.5                                    # Avg. conversion factor from dry to fresh mass
170    change_slope <- -3.90 - 0.53 * log10(mass)          # Slope of change in mass per carbon
171    change_prop <- log(1 + change_slope / 100)          # Proportion of change in mass per C
172    change_const <- exp(log(mass) - 12.5 * change_prop) # Constant of change in mass at 12.5°C
173
174    dry_mass <- change_const * exp(change_prop * (temp))  # Dry body mass (mg)
175    fresh_mass <- dry_mass / conv_fact                    # Fresh body mass (mg)
176    return(dry_mass)
177  }
178
179  # Maximum TSR response
180  calcTSR.Max <- function(temp, mass) {
181    conv_fact <- 6.5                                    # Avg. conversion factor from dry to fresh mass
182    change_slope <- -8.0                                # Slope of change in mass per carbon
183    change_prop <- log(1 + change_slope / 100)          # Proportion of change in mass per C
184    change_const <- exp(log(mass) - 12.5 * change_prop) # Constant of change in mass at 12.5°C
185
186    dry_mass <- change_const * exp(change_prop * (temp))  # Dry body mass (mg)
187    fresh_mass <- dry_mass / conv_fact                    # Fresh body mass (mg)
188    return(dry_mass)
189  }
```

Appendix B: 'functions.R'

```
1   ## ---------------------------
2   ##
3   ## Script name: functions.R
4   ##
5   ## Purpose of script: Functions
6   ##
7   ## Author: Vincent Talen
8   ##
9   ## Date Created: 20 June 2022
10  ##
11  ## Email: v.k.talen@st.hanze.nl
12  ##
13  ## --------------------------
14  ##
15  ## Notes:
16  ##   - x
```

```r
##
## --------------------------

#############
#   Libs    #
#############
library(data.table)
library(ggpubr)
library(reshape2)
library(tidyverse)
source("r_code/model.R")



#############
# Functions #
#############
# ---- scenario data gathering and preparations ----
getScenarioDataList <- function(gamm_indv_mass, leaf_fall, gamm_start_biomass) {
  # 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) %>%
    setNames(temperatures)
  return(data_list)
}

prepareBigDataFrame <- function(df_list) {
  # Function to get the population metabolism for a temperature with the population biomass
  getPopMetabolism <- function(cur_temp, gamm_pop_biomass) {
    # Get metabolic rate for current temperature
    meta_rate    <- calcMetabolicRate(cur_temp, gamm_indv_mass) / 1000  # Gammarus metabolic rate (in mg
    # Calculate population metabolism
    pop_metabolism <- meta_rate * gamm_pop_biomass
    return(fifelse(pop_metabolism < 0, 0, pop_metabolism))
  }
  # Function to get the population ingestion for a temperature with the population- and leaf biomasses
  getPopIngestion <- function(cur_temp, leaf_biomass, gamm_pop_biomass) {
    # Get ingestion- and attack rates for current temperature
    ingest_rate <- calcIngestionRate(cur_temp, gamm_indv_mass) / 1000  # Gammarus ingestion rate (in mg
    attack_rate <- calcAttackRate(cur_temp, gamm_indv_mass)            # Gammarus attack rate (in mg C/
    # Calculate population leaf ingestion
    pop_ingestion <- (attack_rate * leaf_biomass / (1 + attack_rate * 1 / (ingest_rate / 1000) * leaf_b
    return(fifelse(pop_ingestion < 0, 0, pop_ingestion))
  }

  # Bind all dataframes from list to single big one and
  # drop last days to have 2555 days/rows left per temperature
  big_df <- rbindlist(df_list)[!time == 2555] %>%
    # Rename 'time' column to conform to naming scheme
    setnames("time", "Time") %>%
    # Add temperature and year columns to facilitate future calculations
    "$<-"(Temp, rep(temperatures, each = 2555)) %>%
    "$<-"(Year, rep(rep(1:7, each = 365), 5)) %>%
    # Add population metabolism and leaf ingestion columns
```

```r
     "$<-"(M, getPopMetabolism(.$Temp, .$G)) %>%
     "$<-"(I, getPopIngestion(.$Temp, .$L, .$G)) %>%
     # Set column order to a nicer one
     setcolorder(c("Time", "L", "G", "M", "I", "Temp", "Year"))
   return(big_df)
}

# ---- plotting list of scenario dataframes ----
createPlotForTemp <- function(cur_temp, cur_data) {
  # Divide L & G values to create a better readable plot
  divided_data <- copy(cur_data)
  set(divided_data, i = NULL, "L", divided_data$L / 10^5)
  set(divided_data, i = NULL, "G", divided_data$G / 10^5)

  # Create plot
  plot <- ggplot(divided_data, aes(x = time, y = value)) +
    # Set axis limits and step size
    scale_x_continuous(breaks = seq(0, 7 * 365, 365)) +
    ylim(NA, ceiling(max(divided_data[, -1])) + 1) +
    # Add the data (lines)
    geom_line(aes(y = L, color = "Leaf Litter Biomass")) +
    geom_line(aes(y = G, color = "Gammarus Fossarum Biomass")) +
    # Add styling
    labs(title = sprintf("%s°C", cur_temp), x = "", y = "") +
    # theme(plot.title = element_text(hjust = 0.075, vjust = -11)) +
    #theme(plot.margin = margin(0.1, 0.25, 0, 0, "cm")) +
    scale_color_manual(name = "", values = c("black","tomato2"),
                       limits = c("Leaf Litter Biomass", "Gammarus Fossarum Biomass"))
  return(plot)
}

plotScenario <- function(data, image_title, file_out) {
  # Use lapply to create plots for each temperature in the list and collect the legend from a plot
  plot_list <- lapply(seq_along(data), function(i) { createPlotForTemp(names(data)[i], data[[i]]) })
  plot_legend <- get_legend(plot_list[[1]])

  # 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") }) %>%
    "[[<-"(length(plot_list) + 1, plot_legend)

  # Place plots and legend in an arranged grid
  col_num <- 3
  my.grid <- ggarrange(plotlist = plot_list, ncol = col_num, nrow = ceiling(length(plot_list) / col_num
    annotate_figure(top = text_grob(image_title), bottom = text_grob("Time (d)"),
                    left = text_grob(bquote("Biomass "(10^5~ mg~ C~ m^-2)), rot = 90))

  # Save the created arranged grid with the lossless 'lzw' compression that greatly reduces file size
  ggsave(file_out, bg = "white", width=15, height=8, units="in", dpi=300, compression = "lzw")
  dev.off()
}
```

Appendix C: 'scenarios.R'

```r
## ---------------------------
##
## Script name: scenarios.R
##
## Purpose of script: Simulate scenarios using functions from the functions.R module
##
## Author: Vincent Talen
##
## Date Created: 20 June 2022
##
## Email: v.k.talen@st.hanze.nl
##
## --------------------------
##
## Notes:
##   - x
##
## ---------------------------
#setwd("BIN2-P8/endreport")


#############
#   Libs    #
#############
source("r_code/functions.R")


#############
#   Code    #
#############
# Temperatures to do simulations of
temperatures <- c(5, 10, 15, 20, 25)

######################################
### SCENARIO 0: STANDARD SCENARIO ###
######################################
# Gammarus mean body mass = 4.26 mgDM
# Annual leaf fall        = 300 gC/m2/an = 300 000 mgC/m2/an
# Gammarus density        = 30 mgDM/m2   = 15 mgC/m2

# Duration of the leaf fall in days
fall_duration_in_days <- 15

# Define scenario values
gamm_indv_mass <- 4.26
leaf_fall <- 300000 / fall_duration_in_days
gamm_start_biomass <- 15

# Get data for temperatures with values of current scenario
scen_df_list <- getScenarioDataList(gamm_indv_mass, leaf_fall, gamm_start_biomass)
```

```
52  # Create plots in an arranged grid
53  file_out <- "figures/Population Dynamics Standard Scenario.tiff"
54  image_title <- "Standard Scenario: Population Dynamics over 7 years"
55  plotScenario(scen_df_list, image_title, file_out)
56
57  # Combine dataframes into one and add temperature, year, population metabolism- and ingestion columns
58  TestSD <- prepareBigDataFrame(scen_df_list)
59
60  ####################################################################################################
61  CutSD <- as.data.frame(setDT(TestSD)[TestSD[, tail(.I, -16), by = Year]$V1])
62  CutSD <- CutSD[!CutSD$Year == "1", ]
63
64  #############################
65  ### Mean annual biomasses ###
66  #############################
67  # Calculate litter and Gammarus mean annual biomasses
68  MeanL=as.data.frame(setDT(CutSD)[, .(MeanL=mean(L)), by=list(Temp,Year)])
69  MeanG=as.data.frame(setDT(CutSD)[, .(MeanG=mean(G)), by=list(Temp,Year)])
70
71  # Calculate means and deviations over 6 years for annual biomasses
72  MeanLSD=as.data.frame(setDT(MeanL)[, .(MeanL=mean(MeanL), SdL=sd(MeanL)), by=list(Temp)])
73  MeanGSD=as.data.frame(setDT(MeanG)[, .(MeanG=mean(MeanG), SdG=sd(MeanG)), by=list(Temp)])
74
75  ##############################################################
76  ### Mean annual persistence times above biomass thresholds ###
77  ##############################################################
78  # Calculate litter and Gammarus mean annual persistence times
79  ThLSD=CutSD[CutSD$L>60000,]
80  ThGSD=CutSD[CutSD$G>5000,]
81
82  TimeLSD=as.data.frame(setDT(ThLSD)[, .(TimeL=length(Time)), by=list(Temp,Year)])
83  TimeGSD=as.data.frame(setDT(ThGSD)[, .(TimeG=length(Time)), by=list(Temp,Year)])
84
85  # Calculate means and deviations over 6 years for the thresholds
86  TimeLSD=as.data.frame(setDT(TimeLSD)[, .(MeanTimeL=mean(TimeL), SdTimeL=sd(TimeL)), by=list(Temp)])
87  TimeGSD=as.data.frame(setDT(TimeGSD)[, .(MeanTimeG=mean(TimeG), SdTimeG=sd(TimeG)), by=list(Temp)])
88
89  #####################################################
90  ### Mean biomass maximums and biomass decreases ###
91  #####################################################
92  # Find biomass maximums and minimums
93  CycleLSD=as.data.frame(setDT(TestSD)[, .(MaxLSD=findPeaks(L), MinLSD=findValleys(L)[seq(2,14,2)]), by=l:
94  CycleGSD=as.data.frame(setDT(TestSD)[, .(MaxGSD=findPeaks(G), MinGSD=c(findValleys(G),2555)), by=list(T:
```

13