Supplemental information for

Divergent carbon use efficiency-growth rate tradeoff in popular biological growth models

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Introduction

Below we provide mathematical formulations of the different models used in the manuscript. All models are coded in Matlab, and can be found at https://github.com/jinyun1tang/cue_paper.

A. The modified Droop model (Thingstad, 1987)

The mDroop model is based on Thingstad (1987), who developed a model of bacteria that feeds on substrates containing carbon, nitrogen, and phosphorus. For simplicity, we removed the nitrogen and phosphorus components here, and adopted symbols that are more consistent with the remaining of this manuscript.

Specifically, the dynamics for structural biomass B_V is formulated as

$$\frac{dB_V}{dt} = \mu B_V, \tag{A1}$$

and that for total biomass B_X is formulated as

$$\frac{dB_X}{dt} = \left(j_A \frac{Q_{max}-Q}{Q_{max}-Q_{min}} - R\right) B_V. \tag{A2}$$

where the specific substrate uptake is down-regulated from j_A by the carbon quota limiter $(\frac{Q_{max}-Q}{Q_{max}-Q_{min}})$.

Based on equations (A1) and (A2), the dynamics of carbon quota Q is

$$\frac{dQ}{dt} = \frac{d}{dt}\left(\frac{B_X}{B_V}\right) = \frac{1}{B_V}\frac{dB_X}{dt} - \frac{B_X}{{B_V}^2}\frac{dB_V}{dt} = j_A \frac{Q_{max}-Q}{Q_{max}-Q_{min}} - R - Q\mu, \tag{A3}$$

Note that carbon quota Q has its maximum and minimum defined as Q_{max} and Q_{min}, respectively. Because structural biomass B_V is part of B_X, we have $Q_{min} \geq 1$.

Accordingly, the specific growth rate μ is computed as a function of carbon quota via

$$\mu = \mu_{max}\left(1 - \frac{Q_{min}}{Q}\right), \tag{A4}$$

and the specific respiration R is computed as

$$R = c_1 Q\mu + c_2(Q - Q_{min}). \tag{A5}$$

where coefficient c_1 relates respiration R to growth, and coefficient c_2 relates respiration R to maintenance.

Exponential growth

For exponential growth, since $\frac{dQ}{dt} = 0$, one has

$$j_A \frac{Q_{max}-Q}{Q_{max}-Q_{min}} - R - Q\mu = 0, \tag{A6}$$

which when combined with equation (A5) leads to

$$\frac{j_A Q_{max}}{Q_{max}-Q_{min}} = \left[(1 + c_1)\mu + c_2 + \frac{j_A}{Q_{max}-Q_{min}}\right] Q - c_2 Q_{min}. \tag{A7}$$

By defining $\Delta Q = Q_{max} - Q_{min}$, Q can be solved from equation (A7) as

$$Q = \frac{j_A Q_{max} + c_2 Q_{min}\Delta Q}{[(1+c_1)\mu + c_2]\Delta Q + j_A}. \tag{A8}$$

When equation (A8) is combined with (A4), the specific growth rate is computed as a function of substrate uptake j_A through

$$\frac{\mu}{\mu_{max}} = \frac{j_A \Delta Q}{j_A Q_{max} + [c_2 + (1+c_1)\mu_{max}]Q_{min}\Delta Q}. \tag{A9}$$

Meanwhile, by rewriting equation (A4) as

$$Q = Q_{min}\frac{\mu_{max}}{\mu_{max}-\mu}, \tag{A10}$$

then using equations (A3) and (A5), we can compute the actual substrate uptake q as

$$\begin{aligned} q &= j_A \frac{Q_{max}-Q}{Q_{max}-Q_{min}} = R + Q\mu = [(1 + c_1)\mu + c_2]Q - c_2 Q_{min}, \\ &= \left([(1 + c_1)\mu + c_2]\frac{\mu_{max}}{\mu_{max}-\mu} - c_2\right)\frac{Q_{min}}{Y_S}, \\ &= \frac{(1+c_1)\mu_{max} + c_2}{\mu_{max}-\mu}\frac{Q_{min}}{Y_S}\mu. \end{aligned} \tag{A11}$$

where Y_S is the reserve biomass yield from assimilating the substrate, which leads to the equation of $q(S)$ in Table 1 of the main text.

For the structural biomass yield Y_V, it can be computed as

$$Y_V = \frac{\mu}{q} = \frac{\mu_{max} - \mu}{(1+c_1)\mu_{max} + c_2} \frac{Y_S}{Q_{min}}. \tag{A12}$$

Following this, the total biomass yield is

$$Y_B = Y_V Q = Y_V Q_{min} \frac{\mu_{max}}{\mu_{max} - \mu} = \frac{\mu_{max}}{(1+c_1)\mu_{max} + c_2} Y_S, \tag{A13}$$

which is the equation shown in Table 1 of the manuscript.

B. The variable-internal-stores model

This model is based on the microbial model in Williams (1967) and plant model in Thornley (1972). Since this model assumes that the metabolic demands for maintenance $m_V B_V$ and growth $B_V \frac{v_E x}{K+x}$ are parallelly met by reserve biomass turnover, it computes the reserve biomass as

$$\frac{dB_X}{dt} = j_A B_V - m_V B_V - B_V \frac{v_E x}{K+x}, \tag{B1}$$

where x is the reserve density defined as $x = B_X / B_V$.

Accordingly, the structural biomass growth is computed as,

$$\frac{dB_V}{dt} = Y_{RV} B_V v_E \frac{x}{K+x}. \tag{B2}$$

To ease the model intercomparison, we simplify the nonlinear kinetics with linear kinetics, such that

$$\frac{dB_X}{dt} = j_A B_V - m_V B_V - B_V v_E x, \tag{B3}$$

and

$$\mu = \frac{1}{B_V} \frac{dB_V}{dt} = Y_{RV} v_E x. \tag{B4}$$

Accordingly, the reserve density dynamics x becomes

$$\frac{dx}{dt} = \frac{1}{B_V} \frac{d}{dt}(B_X) + B_X \frac{d}{dt}\left(\frac{1}{B_V}\right) = j_A - m_V - (\mu + v_E)x. \tag{B5}$$

Exponential growth

Under exponential growth, the reserve density is at steady state $\frac{dx}{dt} = 0$, which leads to

$$j_A = m_V + (\mu + v_E)x, \tag{B6}$$

and

$$x = \frac{\mu}{Y_{RV} v_E}. \tag{B7}$$

The combination of equations (B6) and (B7) leads to

$$j_A = \frac{\mu(\mu+v_E)}{Y_{RV}v_E} + m_V = \frac{\mu(1+\mu/v_E)}{Y_{RV}} + m_V, \tag{B8}$$

which can be rewritten as

$$\mu^2 + v_E\mu - (j_V - m_V)v_E Y_{RV} = 0, \tag{B9}$$

from which μ can be solved as a function of substrate uptake as

$$\mu = \frac{v_E}{2}\left(-1 + \sqrt{1 + \frac{4(j_A - m_V)Y_{RV}}{v_E}}\right). \tag{B10}$$

Additionally, one can compute the structural biomass yield as

$$Y_V = \frac{\mu}{j_A}Y_S = \frac{\mu Y_S Y_{RV}}{(1+\mu/v_E)\mu + m_V Y_{RV}}, \tag{B11}$$

and the total biomass yield as

$$Y_B = Y_V(1+x) = \frac{\mu Y_S}{(1+\mu/v_E)\mu + m_V Y_{RV}}\left(Y_{RV} + \frac{\mu}{v_E}\right). \tag{B12}$$

C. Standard DEB model

Following Kooijman (2009) and Tang and Riley (2023), the standard DEB (sDEB) model assumes that reserve biomass is mobilized via the first order kinetics when the reserve biomass density ($x = B_X/B_V$) is used as control variable. Specifically, the reserve density dynamics is formulated as

$$\frac{dx}{dt} = j_A - v_E x. \tag{C1}$$

Accordingly, the structural biomass growth μ is driven by the mobilized reserve biomass flux $(v_E - \mu)x$ after subtracting the demand from maintenance m_V/Y_{RV}, such that

$$(v_E - \mu)x - \frac{m_V}{Y_{RV}} = \frac{\mu}{Y_{RV}}, \tag{C2}$$

which leads to

$$\frac{1}{B_V}\frac{dB_V}{dt} = \mu = \frac{Y_{RV}v_E x - m_V}{1 + Y_{RV}x}, \tag{C3}$$

Exponential growth

For exponential growth, since $\frac{dx}{dt} = 0$, one has

$$j_A = v_E x, \tag{C4}$$

which leads to

$$\mu = \frac{Y_{RV}j_A - m_V}{1 + Y_{RV}j_A/v_E}. \tag{C5}$$

From equations (C4) and (C5), the structural biomass yield is computed as

$$Y_V = \frac{\mu}{j_A} Y_S = \frac{\mu}{m_V+\mu}\left(1-\frac{\mu}{v_E}\right) Y_S Y_{RV}, \tag{C6}$$

And the total biomass yield is computed as

$$Y_B = Y_V(1+x) = \frac{\mu}{m_V+\mu}\left(1-\frac{\mu}{v_E}\right)\left(Y_{RV}+\frac{m_V+\mu}{v_E-\mu}\right) Y_S, \tag{C7}$$

D. Modified DEB model

The mDEB model differs from the sDEB model by allowing the reserve biomass to be mobilized via nonlinear kinetics without involving the growth-induced dilution effect (Tang and Riley, 2025), instead, the growth-induced dilution acts to lower the reserve density. When taking the linear approximation (for easier model comparison), the reserve density dynamics is

$$\frac{dx}{dt} = j_A - v_E x - \mu x, \tag{D1}$$

where the term $-\mu x$ signifies the dilution effect that is absent from that for the sDEB model (see eq. (C1)).

The corresponding equation of structural biomass is

$$\frac{1}{B_V}\frac{dB_V}{dt} = \mu = Y_{RV} v_E x - m_V, \tag{D2}$$

Exponential growth

For exponential growth, since $\frac{dx}{dt} = 0$, one has

$$j_A = (v_E + \mu)x, \tag{D3}$$

which when entered in equation (D3), one has

$$\mu = Y_{RV} v_E \frac{j_A}{v_E+\mu} - m_V. \tag{D4}$$

Equation (D4) can be rewritten as

$$\mu^2 + (m_V + v_E)\mu - (j_A Y_{RV} - m_V)v_E = 0, \tag{D5}$$

and has the solution

$$\mu = \frac{m_V+v_E}{2}\left(-1+\sqrt{1+\frac{4v_E(j_A Y_{RV}-m_V)}{(m_V+v_E)^2}}\right). \tag{D6}$$

By combining equations (D3) and (D4), one may obtain

$$j_A = \left(1+\frac{\mu}{v_E}\right)\left(\frac{\mu+m_V}{Y_{RV}}\right), \tag{D7}$$

which can be used to compute the specific substrate uptake

$$q = \left(\frac{v_E+\mu}{v_E}\right)\left(\frac{\mu+m_V}{Y_{RV}Y_S}\right) = \left(\frac{v_E+\mu}{v_E}\right)\left(\frac{\mu+m_V}{\mu}\right)\frac{\mu}{Y_{RV}Y_S}. \tag{D8}$$

Thence, the structural biomass yield is

$$Y_V = \frac{\mu}{q} = \frac{v_E\mu}{(\mu+v_E)(\mu+m_V)}Y_{RV}Y_S. \tag{D9}$$

And the total biomass yield is

$$Y_B = (1+x)Y_V = \left(1+\frac{\mu+m_V}{Y_{RV}v_E}\right)\frac{v_E\mu Y_{RV}Y_S}{(\mu+v_E)(\mu+m_V)} = \frac{(Y_{RV}v_E+\mu+m_V)\mu}{(\mu+m_V)(\mu+v_E)}Y_S. \tag{D10}$$

E. Soil carbon model

The six soil carbon models used for the analysis of dynamic CUE under month-to-month varying carbon inputs are described below. All models consider one microbe feeding on one fast pool C and one slow pool C. We formulated the substrate uptake based on the argument in Tang et al. (2024), and added all microbial biomass from mortality to the slow pool C. In all model simulations, initial values of microbial biomass, fast and slow carbon pools are derived based on their respective steady-state-solutions under an annual carbon input of 350 gC m^{-2} year^{-1}. All the models are coded in Matlab, which are available at https://github.com/jinyun1tang/cue_paper.

Pirt model	
Fast pool C dynamics $\frac{dC_l}{dt} = (1-a)F_{npp} - C_B\left(\frac{V_l\,C_l/K_l}{1+C_l/K_l+C_S/K_S} + \frac{m_V}{Y_b}\frac{V_l\,C_l/K_l}{V_l\,C_l/K_l+V_S\,C_S/K_S}\right)$ $= (1-a)F_{npp} - C_B h_l\left(1+\frac{m_V}{hY_b}\right),$	(E1)
Slow pool C dynamics $\frac{dC_S}{dt} = aF_{npp} + \gamma_B C_B - C_B\left(\frac{V_S\,C_S/K_S}{1+C_l/K_l+C_S/K_S} + \frac{m_V}{Y_b}\frac{V_S\,C_S/K_S}{V_l\,C_l/K_l+V_S\,C_S/K_S}\right)$ $= aF_{npp} + \gamma_B C_B - C_B h_S\left(1+\frac{m_V}{hY_b}\right),$	(E2)
$h = h_l + h_S,$	(E3)
Specific microbial growth rate $\mu = Y_b h,$	(E4)
Microbial Biomass dynamics $\frac{dC_B}{dt} = (\mu - \gamma_B)C_B.$	(E5)

Compromise model	
Fast pool C dynamics $\frac{dC_l}{dt} = (1-a)F_{npp} - C_B\left(\frac{(V_l+m_V)C_l/K_l}{1+C_l/K_l+C_S/K_S}\right) = (1-a)F_{npp} - C_B h_l,$	(E6)
Slow pool C dynamics $\frac{dC_S}{dt} = aF_{npp} + \gamma_B C_B - C_B \frac{(V_S+m_V)C_S/K_S}{1+C_l/K_l+C_S/K_S} = aF_{npp} + \gamma_B C_B - C_B h_S,$	(E7)
$h = h_l + h_S,$	(E8)
Specific microbial growth rate $\mu = Y_b h - m_V$	(E9)
Microbial Biomass dynamics $\frac{dC_B}{dt} = (\mu - \gamma_B)C_B.$	(E10)
Modified Droop model	
Fast pool C dynamics $\frac{dC_l}{dt} = (1-a)F_{npp} - B_V \frac{qV_l C_l/K_l}{1+C_l/K_l+C_S/K_S} = (1-a)F_{npp} - B_V \theta h_l,$	(E11)
Slow pool C dynamics $\frac{dC_S}{dt} = aF_{npp} + \gamma_B B_C - B_V \frac{qV_S C_S/K_S}{1+C_l/K_l+C_S/K_S} = aF_{npp} + \gamma_B B_C - B_V \theta h_S,$	(E12)
$\theta = \frac{Q_{max}-Q}{Q_{max}-Q_{min}}, Q = \frac{B_X}{B_V}$	(E13)
$h = h_l + h_S,$	(E14)
Specific microbial growth rate $\mu = \mu_{max}\left(1 - \frac{Q_{min}}{Q}\right),$	(E15)
Specific microbial respiration rate $R = c_1 Q\mu + c_2(Q - Q_{min}),$	(E16)
Total microbial biomass dynamics $\frac{dB_X}{dt} = B_V(h\theta Y_b - R) - \gamma_B B_X,$	(E17)
Structural microbial biomass dynamics $\frac{dB_V}{dt} = (\mu - \gamma_B)B_V.$	(E18)
Variable-internal-store model	
Fast pool C dynamics	(E19)

$\frac{dC_l}{dt} = (1-a)F_{npp} - B_V \frac{V_l C_l/K_l}{1+C_l/K_l+C_S/K_S} = (1-a)F_{npp} - B_V h_l,$	
Slow pool C dynamics $\frac{dC_S}{dt} = aF_{npp} + \gamma_B(B_C + B_V) - B_V \frac{V_S C_S/K_S}{1+C_l/K_l+C_S/K_S} = aF_{npp} + \gamma_B(B_C + B_V) - B_V h_S,$	(E20)
$h = h_l + h_S,$	(E21)
Reserve microbial biomass dynamics $\frac{dB_C}{dt} = (Y_S h - m_V)B_V - B_C v_E - \gamma_B B_C,$	(E22)
Structural microbial biomass dynamics $\frac{dB_V}{dt} = (\mu - \gamma_B)B_V,$	(E23)
Specific microbial growth rate $\mu = Y_{RV} v_E B_C/B_V.$	(E24)
sDEB model	
Fast pool C dynamics $\frac{dC_l}{dt} = (1-a)F_{npp} - B_V \frac{V_l C_l/K_l}{1+C_l/K_l+C_S/K_S} = (1-a)F_{npp} - B_V h_l,$	(E25)
Slow pool C dynamics $\frac{dC_S}{dt} = aF_{npp} + \gamma_B(B_C + B_V) - B_V \frac{V_S C_S/K_S}{1+C_l/K_l+C_S/K_S} = aF_{npp} + \gamma_B(B_C + B_V) - B_V h_S,$	(E26)
$h = h_l + h_S, x = B_C/B_V$	(E27)
Specific microbial growth rate $\mu = \frac{Y_{RV} v_E x - m_V}{1+Y_{RV} x},$	(E28)
Reserve microbial biomass dynamics $\frac{dB_C}{dt} = Y_S B_V h - (v_E - \mu)B_C - \gamma_B B_C,$	(E29)
Structural microbial biomass dynamics $\frac{dB_V}{dt} = (\mu - \gamma_B)B_V.$	(E30)
mDEB model	
Fast pool C dynamics $\frac{dC_l}{dt} = (1-a)F_{npp} - B_V \frac{V_l C_l/K_l}{1+C_l/K_l+C_S/K_S} = (1-a)F_{npp} - B_V h_l,$	(E31)
Slow pool C dynamics	(E32)

$\frac{dC_S}{dt} = aF_{npp} + \gamma_B(B_C + B_V) - B_V \frac{V_S C_S/K_S}{1+C_l/K_l+C_S/K_S} = aF_{npp} + \gamma_B(B_C + B_V) - B_V h_S,$	
$h = h_l + h_S,$	(E33)
Specific microbial growth rate $\mu = Y_{RV} v_E\, B_C/B_V - m_V,$	(E34)
Reserve microbial biomass dynamics $\frac{dB_C}{dt} = Y_S B_V h - v_E B_C - \gamma_B B_C,$	(E35)
Structural microbial biomass dynamics $\frac{dB_V}{dt} = (\mu - \gamma_B) B_V.$	(E36)

F. Temperature dependence

Following Tang and Riley (2015) and Tang et al. (2021), we parameterize the temperature sensitivity with three different functions. V_l, V_S and v_E are parameterized using Eyring's transition state theory, so that

$v(T) = v(T_0)\left(\frac{T}{T_0}\right)\exp\left(-\frac{\Delta H_V}{R_g}\left(\frac{1}{T} - \frac{1}{T_0}\right)\right).$	(F1)

where dummy variable v can be V_l, V_S or v_E, T_0 is reference temperature, and ΔH_V is enthalpy of activation.

In order to represent the temperature-induced conformation change in proteins, V_l, V_S and v_E are further multiplied by f_{act} that is defined by

$f_{act}(T) = \frac{1+exp\left(-\Delta G/R_g T_0\right)}{1+exp\left(-\Delta G/R_g T\right)},$	(F2)

with

$\Delta G = -n(\Delta H^* - 18.1T + \Delta C_P[(T - 373.6) - Tln(T/385.2)]),$	(F3)
$\Delta C_P = -46.0 + 30(1 - 1.54n^{-0.268})N_{CH},$	(F4)

where n is the average number of amino acid residues in the proteins, N_{CH} is the average number of non-polar hydrogen atoms per amino acid residue, ΔH^* is the enthalpy change at the convergence temperature for enthalpy set at 373.6 K.

K_l, K_S, m_V and γ_B are parameterized using the Arrhenius function, which is

$\varsigma(T) = \varsigma(T_0)\exp\left(-\frac{\Delta H_\varsigma}{R_g}\left(\frac{1}{T} - \frac{1}{T_0}\right)\right),$	(F5)

where dummy variable ς can be K_l, K_S or m_V, T_0 is reference temperature, and ΔH_ς is enthalpy of activation.

G. Nomenclature

Table G1. Definition of symbols used in the models in sections

Symbol	Unit	Definition
a	None	Fraction of input carbon allocated to slow pool carbon
c_1	None	Scaling parameter for growth respiration
c_2	year^{-1}	Scaling parameter for maintenance respiration
f_{act}	None	Fraction of proteins in active states
h	year^{-1}	Total specific substrate uptake
h_l	year^{-1}	Specific fast carbon uptake rate
h_S	year^{-1}	Specific slow carbon uptake rate
j_A	year^{-1}	Specific substrate uptake rate without the carbon quota limiter for mDroop model; specific substrate uptake rate for VIS model, sDEB model and mDEB model
m_V	year^{-1}	Specific maintenance respiration rate for VIS model, sDEB model and mDEB model
n	None	Average number of amino acid residues in the proteins
q	year^{-1}	Specific substrate uptake rate
t	year	Time
x	None	Reserve biomass density
v_E	year^{-1}	Specific reserve mobilization rate in the VIS model and DEB models
B_C	gC m^{-3}	Reserve biomass C for VIS model, sDEB model and mDEB model
B_X	gC m^{-3}	Total biomass C for mDroop model; Reserve biomass C for VIS model, sDEB model and mDEB model
B_V	gC m^{-3}	Structural biomass C
C_B	gC m^{-3}	Total microbial biomass for Pirt model and Compromise model
C_l	gC m^{-3}	Fast pool C

C_S	gC m^{-3}	Slow pool C
ΔC_P	J mol^{-1} K^{-1}	Heat capacity
F_{npp}	gC m^{-3} year^{-1}	Soil carbon input
ΔG	J mol^{-1}	Gibbs free energy for computing f_{act}
ΔH_V	J mol^{-1}	Enthalpy of activation
ΔH^*	J mol^{-1}	Enthalpy change at the convergence temperature for enthalpy set at 373.6 K.
N_{CH}	None	Average number of non-polar hydrogen atoms per amnio acid residue
Q	None	Carbon quota
Q_{min}	None	Minimum carbon quota
Q_{max}	None	Maximum carbon quota
R	year^{-1}	Specific respiration
R_g	J mol^{-1} K^{-1}	Universal gas constant
T	K	Temperature
T_0	K	Temperature
Y_B	None	Total biomass yield
Y_b	None	Biomass yield for Pirt model and compromise model
Y_{RV}	None	Structural biomass yield from reserve biomass
Y_S	None	Reserve biomass yield from substrate assimilation
Y_V	None	Structural biomass yield
μ	year^{-1}	Specific growth rate
μ_{max}	year^{-1}	Maximum specific growth rate
θ	None	Normalized carbon quota for mDroop model
γ_B	year^{-1}	Specific microbial mortality

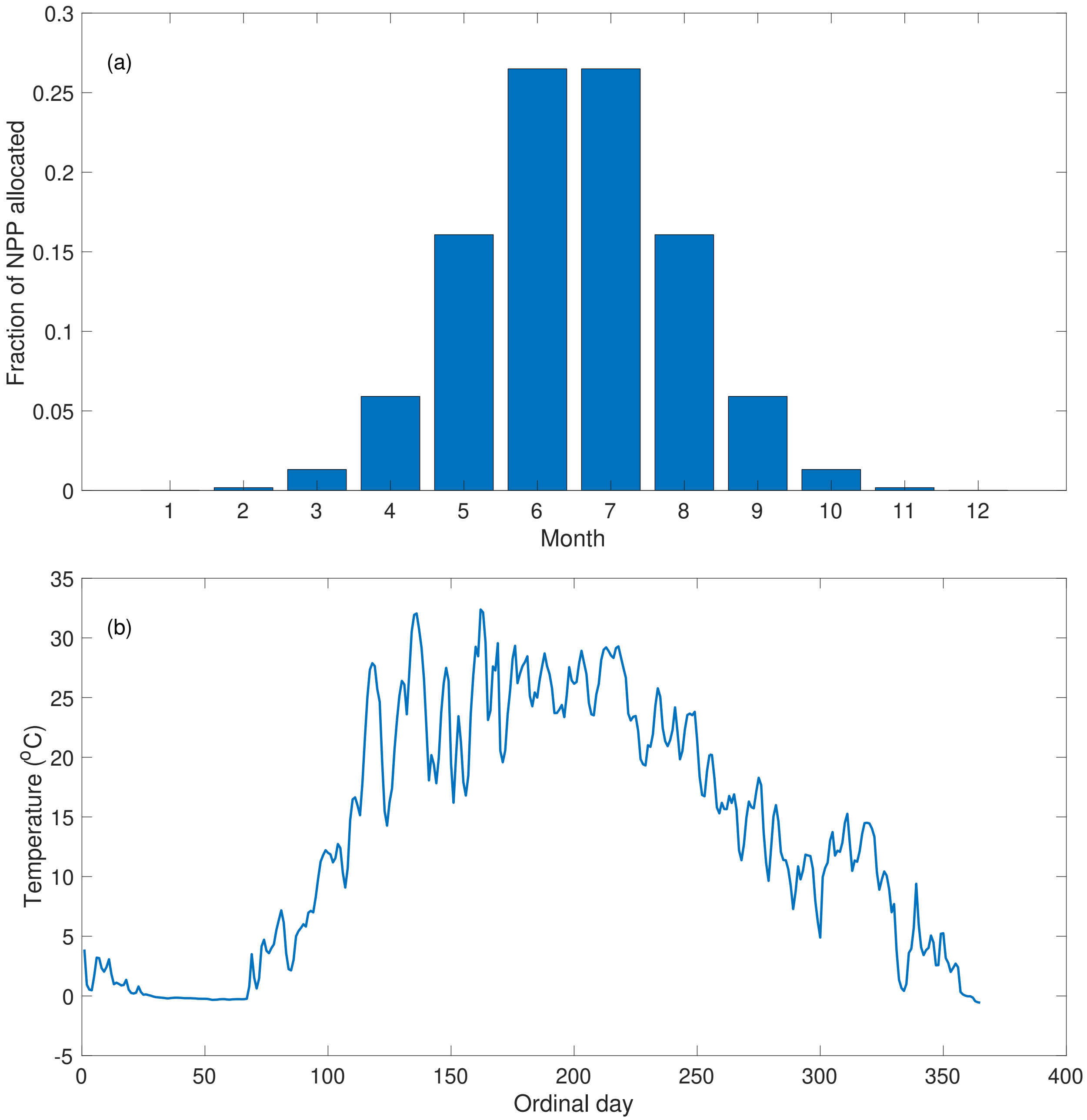

Figure S1. Forcing for the day-to-day varying temperature simulations: (a) monthly allocation of carbon input for each year; (b) daily temperature taken at the 5 cm soil depth from a simulation for a US Midwest corn-field by the EcoSIM model (https://github.com/jinyun1tang/EcoSIM/tree/main/examples/run_dir/dryland).

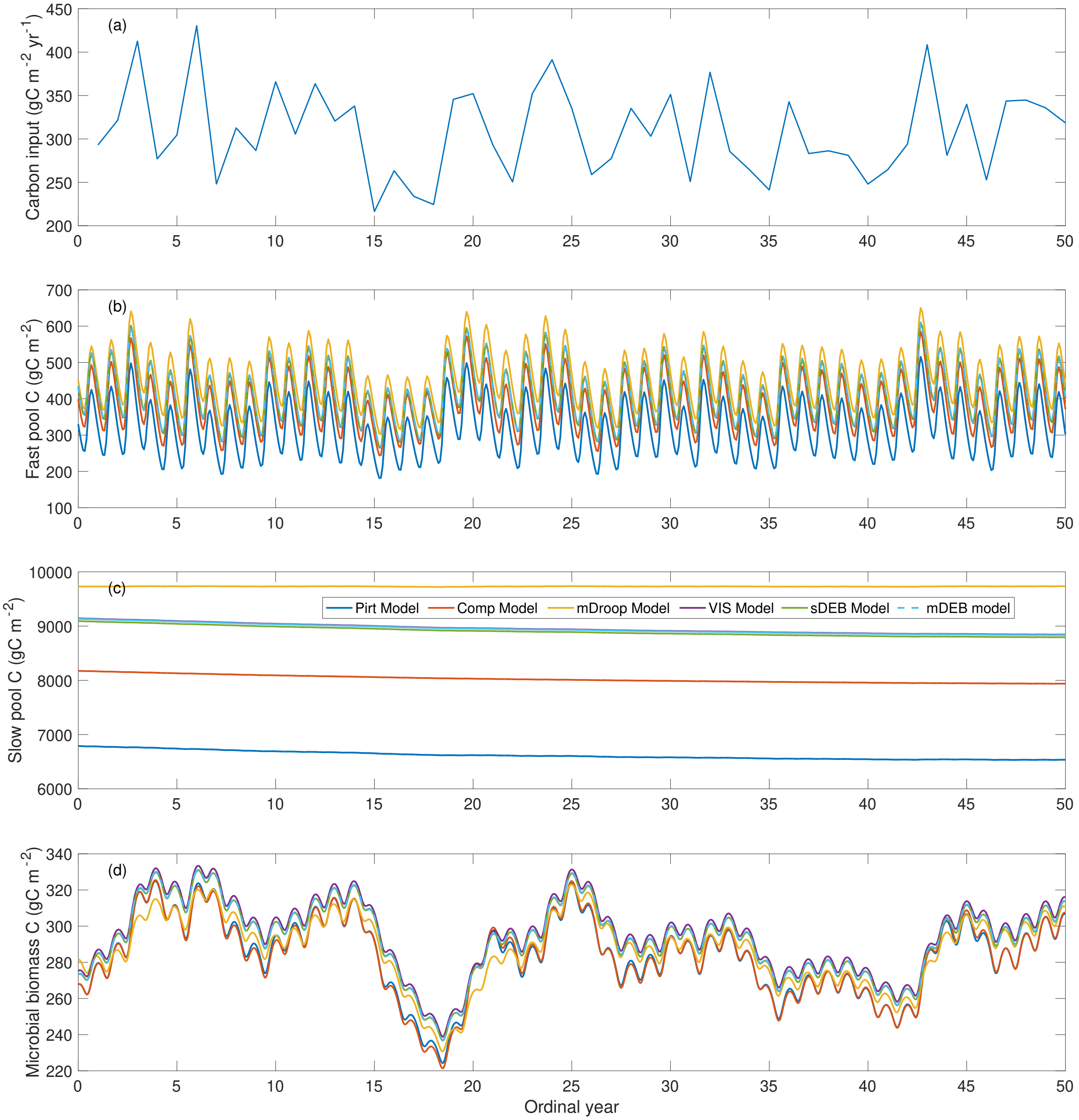

Figure S2 Simulation results from the six models under constant temperature: (a) Annual carbon input; (b) Fast pool C; (c) Slow pool C; and (d) Total microbial biomass C. In panels (b), (c) and (d), results by VIS model, sDEB model and mDEB model overlap each other. In panel (d), results by the Pirt model and Compromise model overlap each other. For the carbon input in each year, it is distributed to each month using the fraction in Figure S1a, which is then averaged by the total number of days in each month to obtain daily carbon input.

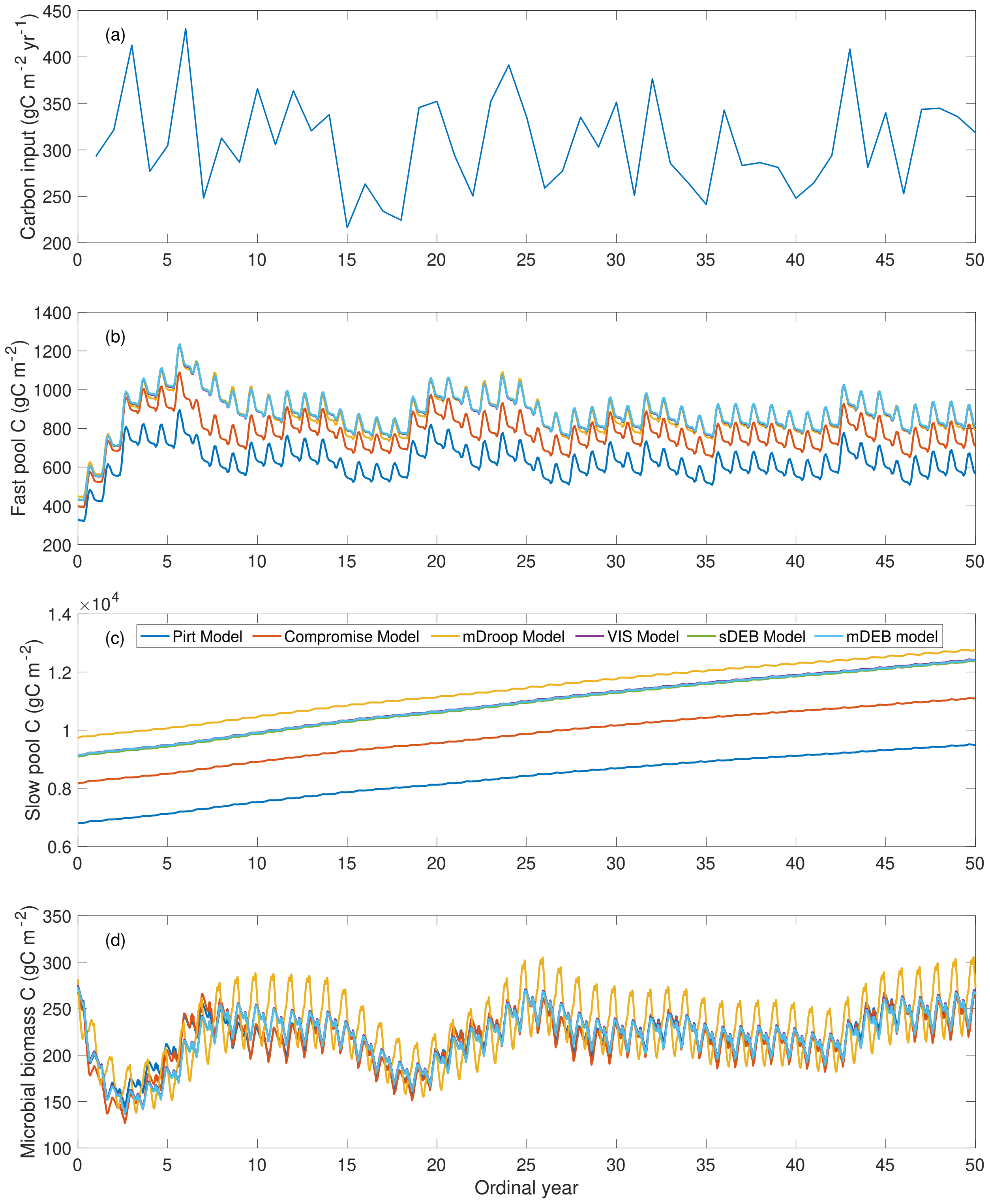

Figure S3. Simulation results from the six models under day-to-day varying temperature: (a) Annual carbon input; (b) Fast pool C; (c) Slow pool C; and (d) Total microbial biomass C. In panes (b), (c) and (d), results by VIS model, sDEB model and mDEB model overlap each other. For the carbon input in each year, it is distributed to each month using the fraction in Figure S1a, which is then averaged by the total number of days in each month to obtain daily carbon input.

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