

Appendix for *A general mathematical framework for representing soil organic matter dynamics*

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A Representation of illustrative models within the proposed framework

A.1 Henin’s model

The first published model of SOM decomposition based on differential equations was proposed by S. Henin and colleagues (Henin and Dupuis, 1945; Henin et al., 1959). The model contains a labile pool A and a stable pool B , which decomposed at annual rates α and β , respectively. The system of equations was originally expressed as

$$\begin{aligned}\frac{dA}{dt} &= m - \alpha A \\ \frac{dB}{dt} &= k\alpha A - \beta B,\end{aligned}\tag{A.1}$$

with annual organic matter inputs represented as m ; and k the ‘isohumic coefficient’, a transfer constant from the labile to the stable pool.

This linear system can be expressed as

$$\frac{d\mathbf{C}}{dt} = \mathbf{I} + \mathbf{A} \cdot \mathbf{C} = \begin{pmatrix} m \\ 0 \end{pmatrix} + \begin{pmatrix} -\alpha & 0 \\ k\alpha & -\beta \end{pmatrix} \cdot \begin{pmatrix} A \\ B \end{pmatrix}\tag{A.2}$$

Notice that this model corresponds to the LTI model structure. It is based on the principles of mass balance, substrate dependence, heterogeneity of decomposition rates, and organic matter transformations, but does not consider the effects of the environment on decomposition rates, and interactions among different types of organic matter.

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A.2 The ICBM model

The ICBM model, proposed by Andren and Katterer (1997), is similar to the model proposed by Henin, but includes the principle of environmental effects on decomposition. The two pools are called here young Y and old O , with decomposition rates k_1 and k_2 , respectively. The transfer coefficient from the young to the old pool is denoted here as ‘humification’ rate. The system of equations is expressed as

$$\begin{aligned}\frac{dY}{dt} &= i - rk_1Y \\ \frac{dO}{dt} &= hrk_1Y - rk_2O,\end{aligned}\tag{A.3}$$

which can be expressed within our framework as

$$\frac{d\mathbf{C}}{dt} = \mathbf{I} + \xi \cdot \mathbf{A} \cdot \mathbf{C} = \begin{pmatrix} i \\ 0 \end{pmatrix} + r \begin{pmatrix} -k_1 & 0 \\ hk_1 & -k_2 \end{pmatrix} \cdot \begin{pmatrix} Y \\ O \end{pmatrix}.\tag{A.4}$$

In this case the environmental effects term r is a constant.

Using the parameterization presented in Andren and Katterer (1997), where $k_1 = 0.8$ and $k_2 = 0.00605 \text{ yr}^{-1}$, the eigenvalues for different treatments were calculated as

Treatment	i	h	r	λ_1	λ_2
Bare fallow	0	0.130	1.32	-1.056	-0.00798
+N, + straw	0.285	0.125	1.00	-0.800	-0.00605
-N, + straw	0.248	0.125	1.22	-0.976	-0.00738
-N, - straw	0.057	0.125	1.17	-0.936	-0.00708
+N, - straw	0.091	0.250	1.10	-0.856	-0.00647
Farmyard manure	0.272	0.125	1.00	-0.880	-0.00665
Sewage sludge	0.296	0.34	0.97	-0.776	-0.00587

Notice that all eigenvalues in this model are negative, therefore the model is asymptotically stable.

A.3 The RothC model

The RothC model (Jenkinson and Rayner, 1977; Coleman and Jenkinson, 1999) can be described by the following set of differential equations

$$\begin{aligned}
\frac{dC_1}{dt} &= \gamma I - \xi(t)k_1C_1 \\
\frac{dC_2}{dt} &= (1 - \gamma)I - \xi(t)k_2C_2 \\
\frac{dC_3}{dt} &= \alpha_{1,3}\xi(t)k_1C_1 + \alpha_{2,3}\xi(t)k_2C_2 - \xi(t)k_3C_3 + \alpha_{3,3}\xi(t)k_3C_3 + \alpha_{4,3}\xi(t)k_4C_4 \\
\frac{dC_4}{dt} &= \alpha_{1,4}\xi(t)k_1C_1 + \alpha_{2,4}\xi(t)k_2C_2 + \alpha_{3,4}\xi(t)k_3C_3 - \xi(t)k_4C_4 + \alpha_{4,4}\xi(t)k_4C_4 \\
\frac{dC_5}{dt} &= 0
\end{aligned} \tag{A.5}$$

where C_1 represents the decomposable plant material (DPM) pool, C_2 the resistant plant material (RPM) pool, C_3 the microbial biomass (BIO) pool, C_4 the humified organic matter (HUM) pool, and C_5 the inert organic matter pool (IOM). This set of equations can be rewritten in the form

$$\begin{aligned}
\frac{d\mathbf{C}}{dt} &= \mathbf{I} + \xi(t) \cdot \mathbf{A} \cdot \mathbf{C} \\
\frac{d\mathbf{C}}{dt} &= I \begin{pmatrix} \gamma \\ 1 - \gamma \\ 0 \\ 0 \\ 0 \end{pmatrix} + \xi(t) \begin{pmatrix} -k_1 & 0 & 0 & 0 & 0 \\ 0 & -k_2 & 0 & 0 & 0 \\ \alpha_{1,3}k_1 & \alpha_{2,3}k_2 & -k_3(1 - \alpha_{3,3}) & \alpha_{4,3}k_4 & 0 \\ \alpha_{1,4}k_1 & \alpha_{2,4}k_2 & \alpha_{3,4}k_3 & -k_4(1 - \alpha_{4,4}) & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} C_1 \\ C_2 \\ C_3 \\ C_4 \\ C_5 \end{pmatrix} \\
\frac{d\mathbf{C}}{dt} &= I \begin{pmatrix} \gamma \\ 1 - \gamma \\ 0 \\ 0 \\ 0 \end{pmatrix} + \xi(t) \begin{pmatrix} -k_1 & 0 & 0 & 0 & 0 \\ 0 & -k_2 & 0 & 0 & 0 \\ a_{1,3} & a_{2,3} & -k_3 + a_{3,3} & a_{4,3} & 0 \\ a_{1,4} & a_{2,4} & a_{3,4} & -k_4 + a_{4,4} & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} C_1 \\ C_2 \\ C_3 \\ C_4 \\ C_5 \end{pmatrix},
\end{aligned} \tag{A.6}$$

where $\xi(t) = f(T) \cdot f(W)$; i.e. a time-dependent rate modifying scalar that is the product of a function that depends on temperature and a function that depends on soil moisture.

The value of the transfer coefficients is determined by a function of soil texture. For the microbial biomass pool, transfer coefficients are calculated as

$$a_{3,j} = k_{3,j} \frac{0.46}{x + 1} \tag{A.7}$$

where x is a value that determines the proportion of decomposed material that is respired as CO_2 and is given by

$$x = 1.67(1.85 + 1.60 \exp(-0.0786 pClay)) \tag{A.8}$$

where $pClay$ is percent clay in mineral soil (Jenkinson and Rayner, 1977). Similarly, the transfer coefficients for the humified pool are given by

$$a_{4,j} = k_{4,j} \frac{0.54}{x + 1}. \tag{A.9}$$

The partitioning coefficient for the litter inputs is calculated from the ratio of decomposable plant material to resistant plant material DR as

$$\gamma = \frac{DR}{DR + 1}. \quad (\text{A.10})$$

With parameters substituted as follows (Jenkinson and Rayner, 1977; Coleman and Jenkinson, 1999): $k_1 = 10$, $k_2 = 0.3$, $k_3 = 0.66$, $k_4 = 0.02$, $k_5 = 0$, $pClay = 23.4$, $DR = 1.44$, $I = 1.7$, $\xi(t) = 1$; the eigenvalues are: $\lambda : \{0, -0.0174, -0.3, -0.593, -10.0\}$. Notice that the inert pool has $k_5 = 0$ and therefore one of the eigenvalues is equal to zero.

A.4 The Century model

The Century model (Parton et al., 1987) can be described by the following set of differential equations

$$\begin{aligned} \frac{dC_1}{dt} &= I \cdot F_m - \xi(t)C_1k_1e^{-3.0L_s} \\ \frac{dC_2}{dt} &= I \cdot F_s - \xi(t)C_2k_2 \\ \frac{dC_3}{dt} &= C_1\alpha_{31}\xi(t)k_1e^{-3.0L_s} + C_2\alpha_{32}\xi(t)k_2 + C_4\alpha_{34}\xi(t)k_4 + C_5\alpha_{35}\xi(t)k_5 - C_3\xi(t)k_3f(Tx) \\ \frac{dC_4}{dt} &= C_1\alpha_{41}\xi(t)k_1e^{-3.0L_s} + C_3\alpha_{43}\xi(t)k_3f(Tx) - C_4\xi(t)k_4 \\ \frac{dC_5}{dt} &= C_3\alpha_{53}\xi(t)k_3f(Tx) + C_4\alpha_{54}\xi(t)k_4 - C_5\xi(t)k_5 \end{aligned} \quad (\text{A.11})$$

where $C_1 \dots C_5$ represent the pools: structural litter, metabolic litter, active SOM, slow SOM, and passive SOM, respectively. F_m and F_s are fractions in which incoming litter is partitioned between structural and metabolic litter, L_s the fraction of structural material that is lignin, and $f(Tx)$ is a function of soil texture that modifies decomposition rates of the active SOM pool.

This system of equations can also be expressed as

$$\begin{aligned} \frac{d\mathbf{C}}{dt} &= \mathbf{I} + \xi(t) \cdot \mathbf{A} \cdot \mathbf{C} \\ &= \mathbf{I} \begin{pmatrix} F_m \\ F_s \\ 0 \\ 0 \\ 0 \end{pmatrix} + \xi(t) \begin{pmatrix} -k_1e^{-3L_s} & 0 & 0 & 0 & 0 \\ 0 & -k_2 & 0 & 0 & 0 \\ \alpha_{31}k_1e^{-3L_s} & \alpha_{32}k_2 & -k_3f(Tx) & \alpha_{34}k_4 & \alpha_{35}k_5 \\ \alpha_{41}k_1e^{-3L_s} & 0 & \alpha_{43}k_3f(Tx) & -k_4 & 0 \\ 0 & 0 & \alpha_{53}k_3f(Tx) & \alpha_{54}k_4 & -k_5 \end{pmatrix} \begin{pmatrix} C_1 \\ C_2 \\ C_3 \\ C_4 \\ C_5 \end{pmatrix}. \end{aligned} \quad (\text{A.12})$$

In Century, the environmental rate modifier is also a function of temperature and moisture of the form $\xi(t) = f(T) \cdot f(W)$. This modifier is commonly called DEFAC.

A.5 The exoenzyme model of Schimel and Weintraub

A model that explicitly represents microbial exoenzyme production and its control on soil organic carbon decomposition was proposed by Schimel and Weintraub (2003). The model contains four state variables: Soil organic carbon S , dissolved organic carbon D , microbial biomass M , and exoenzymes E . Three versions of the model were proposed in the original paper, which we describe below.

A.5.1 Decomposition as first order on enzyme concentrations

The model can be represented as a system of differential equations as

$$\begin{aligned}\frac{dS}{dt} &= -K_d E \\ \frac{dD}{dt} &= K_d E + K_t K_r M - D \\ \frac{dM}{dt} &= D - K_e D - K_m M \\ \frac{dE}{dt} &= K_e D - K_l E\end{aligned}\tag{A.13}$$

where K_e , K_d , K_t , K_r , K_m , and K_l are first rate constants. The version of the model we present here contains some mathematical simplification by aggregating constants into a single one, but in essence it is the same model.

Notice that this model (A.13) only incorporates the output component of the soil carbon balance so external inputs of organic matter are ignored. Within our general framework, the exoenzyme model can be described as

$$\frac{d\mathbf{C}}{dt} = \mathbf{T} \cdot \mathbf{O} = \begin{pmatrix} -1 & 0 & 0 & 0 \\ 1 & -1 & \frac{K_t K_r}{K_m} & 0 \\ 0 & 1 - K_e & -1 & 0 \\ 0 & K_e & 0 & -1 \end{pmatrix} \begin{pmatrix} K_d E \\ D \\ K_m M \\ K_l E \end{pmatrix}\tag{A.14}$$

or

$$\frac{d\mathbf{C}}{dt} = \mathbf{T} \cdot \mathbf{N}(\mathbf{C}) \cdot \mathbf{C} = \begin{pmatrix} -1 & 0 & 0 & 0 \\ 1 & -1 & \frac{K_t K_r}{K_m} & 0 \\ 0 & 1 - K_e & -1 & 0 \\ 0 & K_e & 0 & -1 \end{pmatrix} \begin{pmatrix} K_d E & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & K_m & 0 \\ 0 & 0 & 0 & K_l \end{pmatrix} \begin{pmatrix} 1 \\ D \\ M \\ E \end{pmatrix}.\tag{A.15}$$

This matrix representation of the exoenzyme model allow us to see important properties of the model not necessarily obvious in the original representation (Schimel and Weintraub, 2003). First, the model assumes no dependence on substrate concentrations for decomposition as shown by the value of 1 in the first element of the vector of states of equation (A.15). Second, the 1 elements of the matrix of equation (A.14) represent the assumption of this model that the entire amount of C from the decomposed substrate is transferred to the

DOC pool and subsequently is taken up by the microbes. Third, proportion of this DOC taken up by the microbes is immediately used to produce exoenzymes according to the parameter K_e . Fourth, a proportion of the total losses from the microbial biomass pool is transferred to the exoenzyme pool; this proportion is given by the term $(K_r K_t M)/(K_e D + R + K_t M)$.

The Jacobian matrix for this model is given by

$$\frac{\partial}{\partial \mathbf{C}} (\mathbf{T} \cdot \mathbf{O}) = \begin{pmatrix} 0 & 0 & 0 & -K_d \\ 0 & -1 & K_r K_t & K_d \\ 0 & 1 - K_e & -K_m & 0 \\ 0 & K_e & 0 & -K_l \end{pmatrix}. \quad (\text{A.16})$$

Notice the zero in the first entry, which is the result of the lack of substrate dependence of the S pool for decomposition. This is problematic because it implies that even if the S pool is depleted, decomposition will still occur as long as there is enzyme, leading to unrealistic negative values of the S pool. Further, if the system is driven by inputs to the S pool, C may accumulate indefinitely in the system.

Using the set of parameters provided in Schimel and Weintraub (2003), we found the following set of eigenvalues of the matrix of equation (A.16)

$$\begin{aligned} \lambda_1 &= 0 \\ \lambda_2 &= -1.0177 - 7.0 \times 10^{-24}i \\ \lambda_3 &= 0.0002 + 8.0 \times 10^{-25}i \\ \lambda_4 &= -0.2076 + 1.0 \times 10^{-23}i \end{aligned}$$

Notice that $\lambda_3 > 0$, therefore this system is unstable and violates the principle of mass balance.

A.5.2 Decomposition as a Reverse Michaelis-Menten process

The most commonly used version of this model includes a ‘Reverse Michaelis-Menten’ (RMM) form for the decomposition term that accounts for the enzyme limitation of decomposition. The model can be expressed in matrix form as

$$\frac{d\mathbf{C}}{dt} = \mathbf{T} \cdot \mathbf{N}(\mathbf{C}) \cdot \mathbf{C} = \begin{pmatrix} -1 & 0 & 0 & 0 \\ 1 & -1 & \frac{K_t K_r}{K_m} & 0 \\ 0 & 1 - K_e & -1 & 0 \\ 0 & K_e & 0 & -1 \end{pmatrix} \begin{pmatrix} \frac{K_d E}{K_{es} + E} & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & K_m & 0 \\ 0 & 0 & 0 & K_l \end{pmatrix} \begin{pmatrix} 1 \\ D \\ M \\ E \end{pmatrix}. \quad (\text{A.17})$$

This version of the model also ignores the principle of substrate dependence of decomposition and therefore produces eigenvalues of the Jacobian with positive real part.

A.5.3 Decomposition as RMM with substrate dependence

An improved version of the model does include substrate dependence of decomposition and therefore values of the eigenvalues of the Jacobian with negative real parts.

$$\frac{d\mathbf{C}}{dt} = \mathbf{T} \cdot \mathbf{N}(\mathbf{C}) \cdot \mathbf{C} = \begin{pmatrix} -1 & 0 & 0 & 0 \\ 1 & -1 & \frac{K_i K_r}{K_m} & 0 \\ 0 & 1 - K_e & -1 & 0 \\ 0 & K_e & 0 & -1 \end{pmatrix} \begin{pmatrix} \frac{K_d E}{K_{es} + E} & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & K_m & 0 \\ 0 & 0 & 0 & K_l \end{pmatrix} \begin{pmatrix} S \\ D \\ M \\ E \end{pmatrix}. \quad (\text{A.18})$$

A.6 The BACWAVE model

One of the earliest models of soil organic matter decomposition presenting oscillatory behavior was proposed by Zelenev et al. (2000). The model consist of a microbial biomass X and a substrate pool S , and the system of equations is given by

$$\begin{aligned} \frac{dX}{dt} &= \mu_{max} X \frac{S}{K_S \cdot \theta + S} - D_{max} X \frac{K_d}{K_d + S/\theta} \\ \frac{dS}{dt} &= \frac{-X}{Y} \frac{\mu_{max} S}{K_S \cdot \theta + S} + K_r X D_{max} \frac{K_d}{K_d + S/\theta} + BFG + Exu(t), \end{aligned} \quad (\text{A.19})$$

where all other terms represent constants, except $Exu(t)$, which is a time-dependent exudation rate. For details about the ecological meaning of all terms see Zelenev et al. (2000).

This model can be represented within our theoretical framework as

$$\frac{d\mathbf{C}}{dt} = \mathbf{I}(t) + \mathbf{T} \cdot \mathbf{O} = \begin{pmatrix} 0 \\ BFG + Exu(t) \end{pmatrix} + \begin{pmatrix} -1 & Y \\ K_r & -1 \end{pmatrix} \begin{pmatrix} D_{max} X \frac{K_d}{K_d + S/\theta} \\ \frac{X}{Y} \frac{\mu_{max} S}{K_S \cdot \theta + S} \end{pmatrix} \quad (\text{A.20})$$

or as

$$\begin{aligned} \frac{d\mathbf{C}}{dt} &= \mathbf{I}(t) + \mathbf{T} \cdot \mathbf{N}(\mathbf{C}) \cdot \mathbf{C} \\ &= \begin{pmatrix} 0 \\ BFG + Exu(t) \end{pmatrix} + \begin{pmatrix} -1 & Y \\ K_r & -1 \end{pmatrix} \begin{pmatrix} D_{max} \frac{K_d}{K_d + S/\theta} & 0 \\ 0 & \frac{X}{Y} \frac{\mu_{max}}{K_S \cdot \theta + S} \end{pmatrix} \begin{pmatrix} X \\ S \end{pmatrix}. \end{aligned} \quad (\text{A.21})$$

With parameter values as reported in Zelenev et al. (2000): $D_{max} = 0.26$, $Y = 0.44$, $k_s = 3.0$, $\theta = 0.23$, $Exu_T = 0.8$, $BGF = 0.15$, $k_d = 14.5$, $k_r = 0.4$, $Exu_{max} = 8$, $u_{max} = 0.063$; the eigenvalues of the model are given by

$$\begin{aligned}\lambda_1 &= -0.495 - 0.237i, \\ \lambda_2 &= -0.495 + 0.237i.\end{aligned}$$

These eigenvalues lead to oscillatory behavior in the model, which is characterized by a damping ratio $\zeta = 0.91$.

A.7 The microbial model of Allison, Wallenstein, and Bradford (AWB)

A microbial explicit model that includes a DOC pool was proposed by Allison et al. (2010). This model represent the dynamics of a microbial biomass B , enzyme E , soil organic carbon S , and dissolved organic carbon D pools. Using the notation in Li et al. (2014), the model is described by the system

$$\begin{aligned}\frac{dB}{dt} &= V_M \exp\left(\frac{-E_a}{\Re \cdot (T + 273)}\right) \frac{B \cdot D}{(K m_{us} T + K m_{u0}) + D} (\epsilon_0 + \epsilon_s T) - r_B B - r_E B \\ \frac{dE}{dt} &= r_E \cdot B - r_L \cdot E \\ \frac{dS}{dt} &= I_S + a_{BS} \cdot r_B \cdot B - V_m \exp\left(\frac{-E_a}{\Re(T + 273)}\right) \frac{E \cdot S}{(K m_s T + K m_0) + S}\end{aligned}\tag{A.22}$$

$$\begin{aligned}\frac{dD}{dt} &= I_D + r_B(1 - a_{BS})B + V_m \exp\left(\frac{-E_a}{\Re(T + 273)}\right) \frac{E \cdot S}{(K m_s T + K m_0) + S} \\ &\quad + r_L E - V_M \exp\left(\frac{-E_a}{\Re \cdot (T + 273)}\right) \frac{B \cdot D}{(K m_{us} T + K_{u0}) + D}.\end{aligned}$$

In matrix form

$$\begin{aligned}\frac{d\mathbf{C}}{dt} &= \mathbf{I} + \mathbf{T} \cdot \mathbf{O} \\ &= \begin{pmatrix} 0 \\ 0 \\ I_S \\ I_D \end{pmatrix} + \begin{pmatrix} -1 & 0 & 0 & (\epsilon_0 + \epsilon_s T) \\ r_E/(r_B + r_E) & -1 & 0 & 0 \\ a_{BS} \cdot r_B/(r_B + r_E) & 0 & -1 & 0 \\ r_B(1 - a_{BS})/(r_B + r_E) & 1 & 1 & -1 \end{pmatrix} \\ &\quad \cdot \begin{pmatrix} (r_B + r_E)B \\ r_L E \\ V_m \exp\left(\frac{-E_a}{\Re(T+273)}\right) \frac{E \cdot S}{(K m_s T + K m_0) + S} \\ V_M \exp\left(\frac{-E_a}{\Re \cdot (T+273)}\right) \frac{B \cdot D}{(K m_{us} T + K m_{u0}) + D} \end{pmatrix},\end{aligned}\tag{A.23}$$

or as

$$\begin{aligned}
\frac{d\mathbf{C}}{dt} &= \mathbf{I} + \mathbf{T} \cdot \mathbf{N}(\mathbf{C}) \cdot \mathbf{C} \\
&= \begin{pmatrix} 0 \\ 0 \\ I_S \\ I_D \end{pmatrix} + \begin{pmatrix} -1 & 0 & 0 & (\epsilon_0 + \epsilon_s T) \\ r_E/(r_B + r_E) & -1 & 0 & 0 \\ a_{BS} \cdot r_B/(r_B + r_E) & 0 & -1 & 0 \\ r_B(1 - a_{BS})/(r_B + r_E) & 1 & 1 & -1 \end{pmatrix} \\
&\cdot \begin{pmatrix} (r_B + r_E) & 0 & 0 & 0 \\ 0 & r_L & 0 & 0 \\ 0 & 0 & V_m \exp\left(\frac{-E_a}{\Re(T+273)}\right) \frac{E}{(K m_s T + K m_0) + S} & 0 \\ 0 & 0 & 0 & V_M \exp\left(\frac{-E_a}{\Re(T+273)}\right) \frac{B}{(K_{U_s} T + K_{U_0}) + D} \end{pmatrix} \cdot \begin{pmatrix} B \\ E \\ S \\ D \end{pmatrix}.
\end{aligned} \tag{A.24}$$

A.8 The Microbial-Enzyme-Mediated Decomposition model MEND

Wang et al. (2013) proposed a microbial explicit model that consists of seven pools, P : particulate organic carbon, M : mineral associated carbon, Q : adsorbed phase of DOC, B : microbial biomass, D : dissolved organic carbon, EP : enzymes for the decomposition of P , and EM : enzymes for the decomposition of M . The model can be expressed as the following system of equations. Details about the parameters can be found in Wang et al. (2013).

$$\begin{aligned}
\frac{dP}{dt} &= I_P + (1 - g_D)(1 - P_{EP} - P_{EM})m_R \cdot B - \frac{V_P \cdot EP \cdot P}{K_P + P} \\
\frac{dM}{dt} &= (1 - f_D) \frac{V_P \cdot EP \cdot P}{K_P + P} - \frac{V_M \cdot EM \cdot M}{K_M + M} \\
\frac{dQ}{dt} &= K_{ads} \left(1 - \frac{Q}{Q_{\max}}\right) D - K_{des} \frac{Q}{Q_{\max}} \\
\frac{dB}{dt} &= \frac{V_D + m_R}{E_C} \frac{D \cdot B}{K_D + D} - \left(\frac{1}{E_C} - 1\right) \frac{B \cdot D (V_D + m_R)}{K_D + D} - B \cdot m_R \tag{A.25} \\
\frac{dD}{dt} &= I_D + f_D \frac{V_P \cdot EP \cdot P}{K_P + P} + g_D(1 - P_{EP} - P_{EM})m_R \cdot B + \frac{V_M \cdot EM \cdot M}{K_M + M} \\
&\quad + r_{EP} \cdot EP + r_{EM} \cdot EM - D \left(\frac{V_D + m_R}{E_C} \frac{B}{K_D + D} + \frac{K_{ads}(Q_{\max} - Q)}{Q_{\max}} \right) + K_{des} \frac{Q}{Q_{\max}} \\
\frac{dEP}{dt} &= P_{EP} \cdot m_R \cdot B - r_{EP} \cdot EP \\
\frac{dEM}{dt} &= P_{EM} \cdot m_R \cdot B - r_{EM} \cdot EM
\end{aligned}$$

To simplify the matrix representation, we introduce the following variables:

$$\begin{aligned}
P_E &= P_{EP} + P_{EM} \\
F_R &= B \cdot \left(\frac{1}{E_C} - 1 \right) \frac{D(V_D + m_R)}{K_D + D} \\
F_E &= B \cdot m_R \\
O_B &= F_R + F_E \\
F_U &= D \cdot \frac{V_D + m_R}{E_C} \frac{B}{K_D + D} \\
F_A &= D \cdot \frac{K_{ads}(Q_{\max} - Q)}{Q_{\max}} \\
O_D &= F_U + F_A,
\end{aligned}$$

so we can define the fractions of the decomposed microbial biomass that is allocated to enzyme production f_E , the fraction of the total DOC that is allocated to microbial uptake f_U , and the fraction of total DOC that is adsorbed f_A as

$$\begin{aligned}
f_E &= \frac{F_E}{O_B}, \\
f_U &= \frac{F_U}{O_D}, \\
f_A &= \frac{F_A}{O_D}.
\end{aligned}$$

The system of equations can then be represented as

$$\begin{aligned}
\frac{d\mathbf{C}}{dt} &= \mathbf{I} + \mathbf{T} \cdot \mathbf{O} \\
&= \begin{pmatrix} I_P \\ 0 \\ 0 \\ 0 \\ I_D \\ 0 \\ 0 \end{pmatrix} + \begin{pmatrix} -1 & 0 & 0 & (1 - g_D)(1 - P_E)f_E & 0 & 0 & 0 \\ 1 - f_D & -1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & 0 & f_A & 0 & 0 \\ 0 & 0 & 0 & -1 & f_U & 0 & 0 \\ f_D & 1 & 1 & g_D(1 - P_E)f_E & -1 & 1 & 1 \\ 0 & 0 & 0 & P_{EP}f_E & 0 & -1 & 0 \\ 0 & 0 & 0 & P_{EM}f_E & 0 & 0 & -1 \end{pmatrix} \\
&\cdot \begin{pmatrix} \frac{V_P \cdot EP \cdot P}{K_E + P} \\ \frac{V_M \cdot EM \cdot M}{K_M + M} \\ \frac{K_{des} Q}{Q_{\max}} \\ O_B \\ O_D \\ r_{EP} \cdot EP \\ r_{EM} \cdot EM \end{pmatrix}, \tag{A.26}
\end{aligned}$$

or alternatively as

$$\begin{aligned}
\frac{d\mathbf{C}}{dt} &= \mathbf{I} + \mathbf{T}(\mathbf{C}) \cdot \mathbf{N}(\mathbf{C}) \cdot \mathbf{C} \\
&= \begin{pmatrix} I_P \\ 0 \\ 0 \\ 0 \\ I_D \\ 0 \\ 0 \end{pmatrix} + \begin{pmatrix} -1 & 0 & 0 & (1-g_D)(1-P_E)f_E & 0 & 0 & 0 \\ 1-f_D & -1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & 0 & f_A & 0 & 0 \\ 0 & 0 & 0 & -1 & f_U & 0 & 0 \\ f_D & 1 & 1 & g_D(1-P_E)f_E & -1 & 1 & 1 \\ 0 & 0 & 0 & P_{EP}f_E & 0 & -1 & 0 \\ 0 & 0 & 0 & P_{EM}f_E & 0 & 0 & -1 \end{pmatrix} \\
&\cdot \begin{pmatrix} \frac{V_P \cdot EP}{K_P + P} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{V_M \cdot EM}{K_M + M} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{K_{des}}{Q_{max}} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \frac{O_B}{B} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{O_D}{D} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & r_{EP} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & r_{EM} \end{pmatrix} \cdot \begin{pmatrix} P \\ M \\ Q \\ B \\ D \\ EP \\ EM \end{pmatrix}. \quad (\text{A.27})
\end{aligned}$$

A.9 Microbial models of Fontaine and Barot

Fontaine and Barot (2005) proposed a family of models representing aggregated microbial populations and their effects on carbon and nitrogen cycling.

A.9.1 Model 1

This model can be expressed as a system of equations of the form

$$\begin{aligned}
\frac{dC_s}{dt} &= -AC_{ds} \\
\frac{dC_{ds}}{dt} &= (A-r)C_{ds} + \phi_l
\end{aligned} \quad (\text{A.28})$$

This model is linear therefore can be represented in the form $\mathbf{I} + \mathbf{AC}$ as

$$\frac{d\mathbf{C}}{dt} = \begin{pmatrix} 0 \\ \phi_l \end{pmatrix} + \begin{pmatrix} 0 & -A \\ 0 & A-r \end{pmatrix} \begin{pmatrix} C_s \\ C_{ds} \end{pmatrix}. \quad (\text{A.29})$$

Outputs from the C_s pool are not proportional to the size of this pool, instead they are proportional to the size of C_{ds} . Notice that this model leads to one eigenvalue with value zero.

A.9.2 Model 2

The system of equation is given by

$$\begin{aligned}\frac{dC_s}{dt} &= (s - A)C_{ds} \\ \frac{dC_{ds}}{dt} &= (A - r - s)C_{ds} + \phi_l,\end{aligned}\tag{A.30}$$

and the linear matrix form is given by

$$\frac{dC}{dt} = \begin{pmatrix} 0 \\ \phi_l \end{pmatrix} + \begin{pmatrix} 0 & s - A \\ 0 & A - r - s \end{pmatrix} \begin{pmatrix} C_s \\ C_{ds} \end{pmatrix}.\tag{A.31}$$

This model also presents one eigenvalue equal to zero.

Both model 1 and 2 seem quite unrealistic because they accumulate carbon in the decomposer biomass C_{ds} exponentially independent of the amount of substrate. Even worse, if the substrate is completely depleted the decomposers can continue growing. These models do not comply with the principle of mass balance.

A.9.3 Model 3

This model includes a nitrogen pool. The system of equations is given by

$$\begin{aligned}\frac{dC_s}{dt} &= (s - A)C_{ds} \\ \frac{dC_f}{dt} &= \phi_l - \phi_d \\ \frac{dC_{ds}}{dt} &= (A - s - r)C_{ds} + \phi_d \\ \frac{dN}{dt} &= \phi_i - \phi_o - \phi_{up} + \phi_{IMs}\end{aligned}\tag{A.32}$$

The inputs ϕ_i and outputs ϕ_o of mineral nitrogen as well as plant uptake ϕ_{up} are considered constant, therefore we define $\phi = \phi_i - \phi_o - \phi_{up}$. The immobilization-mineralization flux is given by $\phi_{IMs} = \alpha r C_{ds} + (\beta - \alpha)\phi_d$. Under C limitation conditions the decomposition flux is given by $\phi_d = k C_f$. Again, this is a linear model that can be expressed as

$$\frac{d(C, N)}{dt} = \begin{pmatrix} 0 \\ \phi_l \\ 0 \\ \phi \end{pmatrix} + \begin{pmatrix} s - A & 0 & 0 & 0 \\ 0 & -k & 0 & 0 \\ 0 & k & A - s - r & 0 \\ 0 & k(\beta - \alpha) & \alpha r & 0 \end{pmatrix} \begin{pmatrix} C_s \\ C_f \\ C_{ds} \\ N \end{pmatrix}.\tag{A.33}$$

If the system is N-limited, then $\phi_d = (iN + \alpha r C_{ds})/(\alpha - \beta)$, and the system of equations is defined as

$$\begin{aligned}
\frac{dC_s}{dt} &= (s - A)C_{ds} \\
\frac{dC_f}{dt} &= \phi_l - \frac{iN}{\alpha - \beta} - \frac{\alpha r C_{ds}}{\alpha - \beta} \\
\frac{dC_{ds}}{dt} &= C_{ds} \left((A - s - r) + \frac{\alpha r}{\alpha - \beta} \right) + \frac{iN}{\alpha - \beta} \\
\frac{dN}{dt} &= \phi - iN
\end{aligned} \tag{A.34}$$

which in matrix form can be expressed as

$$\frac{d(C, N)}{dt} = \begin{pmatrix} 0 \\ \phi_l \\ 0 \\ \phi \end{pmatrix} + \begin{pmatrix} s - A & 0 & 0 & 0 \\ 0 & 0 & \frac{-\alpha r}{\alpha - \beta} & \frac{-i}{\alpha - \beta} \\ 0 & 0 & (A - s - r) + \frac{\alpha r}{\alpha - \beta} & \frac{i}{\alpha - \beta} \\ 0 & 0 & 0 & -i \end{pmatrix} \begin{pmatrix} C_s \\ C_f \\ C_{ds} \\ N \end{pmatrix}. \tag{A.35}$$

This model also presents one eigenvalue equal to zero, and if $A < s$ the system is unstable and violates the principle of mass balance.

A.9.4 Model 4

Again, there are two versions of the model, one under carbon limitation and another under nitrogen limitation. The system of equations for the version of C-limitation is given by

$$\begin{aligned}
\frac{dC_s}{dt} &= (s - A)C_{ds} + sC_{df} \\
\frac{dC_f}{dt} &= \phi_l - C_f(y + u) \\
\frac{dC_{ds}}{dt} &= C_{ds}(A - s - r) + yC_f \\
\frac{dC_{df}}{dt} &= uC_f - (s + r)C_{df} \\
\frac{dN}{dt} &= \phi + \alpha r C_{ds} + C_f(\beta - \alpha)(y + u) + \alpha r C_{df}
\end{aligned} \tag{A.36}$$

which in matrix form looks like

$$\frac{d(C, N)}{dt} = \begin{pmatrix} 0 \\ \phi_l \\ 0 \\ 0 \\ \phi \end{pmatrix} + \begin{pmatrix} s - A & 0 & 0 & s & 0 \\ 0 & y + u & 0 & 0 & 0 \\ 0 & y & (A - s - r) & 0 & 0 \\ 0 & u & 0 & -(s + r) & 0 \\ 0 & (\beta - \alpha)(y + u) & \alpha r & \alpha r & 0 \end{pmatrix} \begin{pmatrix} C_s \\ C_f \\ C_{ds} \\ C_{df} \\ N \end{pmatrix}. \tag{A.37}$$

Now, under N-limitation the system of equations is given by

$$\begin{aligned}
\frac{dC_s}{dt} &= (s - A)C_{ds} + sC_{df} \\
\frac{dC_f}{dt} &= \phi_l - \frac{2iN}{\alpha - \beta} - \frac{\alpha r C_{ds}}{\alpha - \beta} - \frac{\alpha r C_{df}}{\alpha - \beta} \\
\frac{dC_{ds}}{dt} &= C_{ds} \left(\frac{\alpha r}{\alpha - \beta} + (A - s - r) \right) + \frac{iN}{\alpha - \beta} \\
\frac{dC_{df}}{dt} &= C_{df} \left(\frac{\alpha r}{\alpha - \beta} - (s + r) \right) + \frac{iN}{\alpha - \beta} \\
\frac{dN}{dt} &= \phi - 2iN
\end{aligned} \tag{A.38}$$

which in matrix form looks like

$$\frac{d(C, N)}{dt} = \begin{pmatrix} 0 \\ \phi_l \\ 0 \\ 0 \\ \phi \end{pmatrix} + \begin{pmatrix} s - A & 0 & 0 & s & 0 \\ 0 & 0 & \frac{-\alpha r}{\alpha - \beta} & \frac{-\alpha r}{\alpha - \beta} & \frac{-2i}{\alpha - \beta} \\ 0 & 0 & \frac{\alpha r(A - s - r)}{\alpha - \beta} & 0 & \frac{i}{\alpha - \beta} \\ 0 & 0 & 0 & \frac{\alpha r}{\alpha - \beta} - (s + r) & \frac{i}{\alpha - \beta} \\ 0 & 0 & 0 & 0 & -2i \end{pmatrix} \begin{pmatrix} C_s \\ C_f \\ C_{ds} \\ C_{df} \\ N \end{pmatrix}. \tag{A.39}$$

A particular case of this model is proposed by Fontaine and Barot (2005) under the assumption that the SOM decomposers are C-limited and the FOM decomposers are N-limited.

$$\begin{aligned}
\frac{dC_s}{dt} &= (s - A)C_{ds} + sC_{df} \\
\frac{dC_f}{dt} &= \phi_l - yC_f - \frac{iN}{\alpha - \beta} - \frac{\alpha r C_{df}}{\alpha - \beta} \\
\frac{dC_{ds}}{dt} &= (A - s - r)C_{ds} + yC_f \\
\frac{dC_{df}}{dt} &= \frac{iN}{\alpha - \beta} + C_{df} \left(\frac{\alpha r}{\alpha - \beta} - (s + r) \right) \\
\frac{dN}{dt} &= \phi + \alpha r C_{ds} + (\beta - \alpha)yC_f - iN
\end{aligned} \tag{A.40}$$

which in matrix form looks like

$$\frac{d(C, N)}{dt} = \begin{pmatrix} 0 \\ \phi_l \\ 0 \\ 0 \\ \phi \end{pmatrix} + \begin{pmatrix} s - A & 0 & 0 & s & 0 \\ 0 & -y & 0 & \frac{-\alpha r}{\alpha - \beta} & \frac{-i}{\alpha - \beta} \\ 0 & y & (A - s - r) & 0 & 0 \\ 0 & 0 & 0 & \frac{\alpha r}{\alpha - \beta} - (s + r) & \frac{i}{\alpha - \beta} \\ 0 & (\beta - \alpha)y & \alpha r & 0 & -i \end{pmatrix} \begin{pmatrix} C_s \\ C_f \\ C_{ds} \\ C_{df} \\ N \end{pmatrix}. \tag{A.41}$$

From all models, this last model is the only one in it is possible that all eigenvalues of the matrix have real negative part, therefore the system can be stable and reach steady-state, but this depends on the actual combination of parameter values.

Literature cited

- Allison, S. D., Wallenstein, M. D., and Bradford, M. A. (2010). Soil-carbon response to warming dependent on microbial physiology. *Nature Geosci*, 3(5):336–340. 10.1038/ngeo846.
- Andren, O. and Katterer, T. (1997). Icbm: The introductory carbon balance model for exploration of soil carbon balances. *Ecological Applications*, 7(4):1226–1236.
- Coleman, K. and Jenkinson, D. (1999). Rothc-26.3 a model for the turnover of carbon in soil: model description and windows user guide (modified 2008). Technical report, IACR Rothamsted.
- Fontaine, S. and Barot, S. (2005). Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. *Ecology Letters*, 8(10):1075–1087.
- Henin, S. and Dupuis, M. (1945). Essai de bilan de la matière organique du sol. *Annales Agronomique*, 15:17–29.
- Henin, S., Monnier, G., and Turc, L. (1959). Un aspect de la dynamique des matières organiques du soi. *Comptes rendus hebdomadaires des séances de l'Académie des sciences*, 248(1):138–141.
- Jenkinson, D. S. and Rayner, J. H. (1977). The turnover of soil organic matter in some of the rothamsted classical experiments. *Soil Science*, 123(5):298–305.
- Li, J., Wang, G., Allison, S., Mayes, M., and Luo, Y. (2014). Soil carbon sensitivity to temperature and carbon use efficiency compared across microbial-ecosystem models of varying complexity. *Biogeochemistry*, 119:67–84.
- Parton, W. J., Schimel, D. S., Cole, C. V., and Ojima, D. S. (1987). Analysis of factors controlling soil organic matter levels in great plains grasslands1. *Soil Sci. Soc. Am. J.*, 51(5):1173–1179.
- Schimel, J. P. and Weintraub, M. N. (2003). The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. *Soil Biology and Biochemistry*, 35(4):549–563.
- Wang, G., Post, W. M., and Mayes, M. A. (2013). Development of microbial-enzyme-mediated decomposition model parameters through steady-state and dynamic analyses. *Ecological Applications*, 23(1):255–272.

Zelenev, V., van Bruggen, A., and Semenov, A. (2000). “BACWAVE”, a spatial-temporal model for traveling waves of bacterial populations in response to a moving carbon source in soil. *Microbial Ecology*, 40(3):260–272.