Multiple Nutrient Soil Food Web Analysis

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Model formulation

The model is based on a Lotka-Volterra population model between nodes wherein the amount of each element, k, is represented for each node in the food web, X. The biomass in each node is indexed in units of carbon, so we can use two equations to represent all of the elements in the food web: one for carbon and another for every other element.

$$\frac{dX_{C,i}}{dt} = \sum_j (a_{C,i,j} p_{C,i} F_{i,j}) - d_i C_i - E_{C,i} C_i - \sum_j M_{i,j} \tag{1}$$

$$\frac{dX_{k,i}}{dt} = \sum_j (a_{k,i,j} p_{k,i} F_{i,j} \frac{Q_{k,j}}{Q_{C,j}}) - d_i C_i \frac{Q_{k,i}}{Q_{C,i}} - E_{k,i} C_i \frac{Q_{k,i}}{Q_{C,i}} - \frac{Q_{k,i}}{Q_{C,i}} \sum_j M_{i,j} \tag{2}$$

In the above equations, $X_{k,i}$ is the biomass in element k. The model contains two ways that organisms mineralize elements that need to be chosen between. They can loose an element at a constant per capita rate $E_{k,i}$ or they can loose an element at a constant proportion of the food assimilated $p_{k,i}$. Both are used in the literature, the former in metabolic scaling models and the latter in existing soil food web models. We include both in our model so that the user can select which method is most appropriate for their application.

We assume fixed stoichiometry for each element, which means that the rate of change in carbon content to that of all the other elements remain the same over time. The model takes the percentage of each element present in the biomass of the animal $Q_{k,i}$. To simplify our notation, we will call the ratio of carbon to each element $\frac{Q_{C,i}}{Q_{k,i}} = \hat{Q}_{k,i}$. Because we typically take larger time steps, this means that we can assume the following equality:

$$\frac{X_{C,i}}{dt} = \hat{Q}_{k,i} \frac{X_{k,i}}{dt} \tag{3}$$

The consequence of this equality, is that we can calculate one parameter for each chemical element other than carbon by using the above equation. In soil food web models, this is

usually used to calculate the mineralization parameters $E_{k,i}$, which are usually reported as total mineralization or $E_{k,i}C_i$ in units of carbon or $\frac{E_{k,i}C_i}{\hat{Q}_{k,i}}$ in the units of element k.

Solving consumption rates

We can solve for the consumption rates using only the equations for carbon and then make modifications to this equation to balance demand for multiple elements. We define the consumption rates based on the availability of each food item and any preference weights set in the feeding preference matrix. We call these preferences w_{ij}. This leads to the following equation for each consumption rate.

$$F_{ij} = \frac{w_{ij}X_i}{\sum_{h=1}^{N} w_{ih}X_h} \sum_j^N F_{ij}$$

To solve the carbon equation, we use the full system of equations and assume that changes over time are zero or $\frac{dX_{C,i}}{dt} = 0$. We are solving for total consumption rate of each species, which is $\sum_j^N F_{ij}$.

Starting from equation (1), we solve the following matrix problem $Ax = b$, where x is a vector of total consumption rates for each species, A is a matrix of predation rates, and b is a vector of death rates and respiration rates.

$$A = \begin{pmatrix} a_{12}p_1 - \frac{w_{11}X_1}{\sum_{h=1}^{N} w_{1h}X_h} & \cdots & -\frac{w_{N1}X_1}{\sum_{h=1}^{N} w_{Nh}X_h} \\ \vdots & & \vdots \\ -\frac{w_{1N}X_N}{\sum_{h=1}^{N} w_{1h}X_h} & \cdots & a_{NN}p_N - \frac{w_{NN}X_N}{\sum_{h=1}^{N} w_{Nh}X_h} \end{pmatrix}$$

$$b = \begin{pmatrix} d_1X_1 + E_{C,1}X_1 \\ \vdots \\ d_NX_N + E_{C,N}X_N \end{pmatrix}$$

$$x = \begin{pmatrix} \sum_j^N F_{1j} \\ \vdots \\ \sum_j^N F_{Nj} \end{pmatrix}$$

Calculating mineralization rates

We can calculate mineralization rates using equations 1 to 3.

$$\sum_j (a_{C,i,j} p_{C,i} F_{i,j}) - d_i C_i - E_{C,i} C_i - \sum_j M_{i,j} = \hat{Q}_{k,i} \left(\sum_j \left(\frac{a_{k,i,j} p_{k,i} F_{i,j}}{\hat{Q}_{k,i}} \right) - \frac{d_i C_i}{\hat{Q}_{k,i}} - \frac{E_{k,i} C_i}{\hat{Q}_{k,i}} - \frac{1}{\hat{Q}_{k,i}} \sum_j M_{i,j} \right) \tag{4}$$

$$\sum_j (a_{C,i} p_{C,i} F_{i,j}) - d_i C_i - E_{C,i} C_i - \sum_j M_{i,j} = \hat{Q}_{k,i} \sum_j \left(\frac{a_{k,i} p_{k,i} F_{i,j}}{\hat{Q}_{k,j}} \right) - d_i C_i - E_{k,i} C_i - \sum_j M_{i,j} \tag{5}$$

We can cancel terms for death rate and predation, since these represent losses of all elements at the proportion that they exist in the biomass.

$$E_{k,i} C_i = E_{C,i} C_i + \hat{Q}_{k,i} \sum_j \left(\frac{a_{k,i,j} p_{k,i} F_{i,j}}{\hat{Q}_{k,j}} \right) - \sum_j (a_{C,i,j} p_{C,i} F_{i,j}) \tag{6}$$

Then we can combine the terms that sum across all other species j and factor out the feeding rate.

$$E_{k,i} C_i = E_{C,i} C_i + \sum_j \left(\frac{\hat{Q}_{k,i}}{\hat{Q}_{k,j}} a_{k,i} p_{k,i} - a_{C,i} p_{C,i} \right) F_{i,j} \tag{7}$$

This equation provides an easy interpretation of how mineralization is determined. The amount of element k mineralized is $\frac{E_{k,i} C_i}{\hat{Q}_{k,i}}$ in its own units, but because the nutrient stoichiometry is fixed, we can express it in units of carbon to make it easier to compare across multiple chemical elements. This value $E_{k,i} C_i$ is equal to the amount of carbon mineralized $E_{C,i} C_i$ plus the additional gain or loss of the element k from the food, considering assimilation and production efficiency. So, when the second term is positive, there is relatively more of element k mineralized than carbon. When it is negative, there is relatively less.

The term in the parenthetical has an important interpretation. When it is negative for food source j, then eating that food leads to a nutrient deficiency. When it is positive, eating that food leads to a nutrient surplus. For the purposes of further modelling, we define this term using calographic letter $\mathfrak{a}$.

Overall, we can solve for mineralization rates using the following, simplified equation:

$$E_{k,i} C_i = E_{C,i} C_i + \sum_j \mathfrak{a}_{k,i,j} F_{i,j} \tag{8}$$

Using dietary changes to meet nutrient demands

For many species included in food web models, we need to adhere to the constraint that mineralizaiton is greater than zero or some minimum value. Mathematically, this means the following:

$$E_{k,i}C_i \geq 0 \tag{9}$$

$$E_{C,i}C_i \geq -\sum_j \mathfrak{a}_{k,i,j}F_{i,j} \tag{10}$$

To ensure that this constraint is met, we can modify the feeding rates on each food source until the RHS of the equation is less than the amount of carbon mineralized.

We want to modify the feeding rates so that they are as close as possible to the actual food availability. To do this, we define $b_{i,j}$ as the proportion of the total available food in the biomass of source j and $f_{i,j}$ as the proportion of the overall diet $F_{i,T}$ that is composed of food j. This allows us to modify the above equation to be:

$$E_{C,i}C_i \geq -\sum_j \mathfrak{a}_{k,i,j}f_{i,j}F_{i,T} \tag{11}$$

With this notation, we can define the following quadratic program:

$$
\begin{aligned}
\min_{f_{i,j}} \quad & \sum_j^N (b_{i,j} - f_{i,j})^2 \\
\text{subject to} \quad & \sum_j f_{i,j} = 1 \\
& -f_{i,j} \geq -L_{i,j} \forall i \in 1 : N \\
& \sum_j \mathfrak{a}_{k,i,j}f_{i,j}F_{i,T} \geq -E_{C,i}C_i
\end{aligned} \tag{12}
$$

In the above program, we minimize the differences between the abundance of the food in the environment and the diet, while ensuring food consumption rate remains the same, that any user-defined dietary limits $L_{i,j}$ are met, and that mineralization rate remains positive. The function **quadprog::solve.QP** only accepts equalities or greater than or equal to expressions, so the program is written with several negative values to fit that notation.

The quadratic program does not always have a solution because it is possible that shifting diets can improve nutrient intake, but not enough to meet demand. In these cases, the program will fail but the organism should shift it's diet somewhat to minimize nutrient deficiency.

Here, we benefit from representing all nutrient deficiencies in units of carbon. This allows us to maximize the nutrient content of the diet across all nutrients. We justify this, because the organism response to any dietary limitation not addressed by diet will be to increase their metabolic losses. This means that the best strategy is to get all elements as close to matching as possible rather than get lots of one element at the expense of another. **A core assumption here is that all elements included in this model are essential.**

Given this assumption, we can write the following linear program:

$$
\begin{aligned}
\max_{f_{i,j}} \quad & \sum_k \sum_j^N \mathfrak{a}_{k,i,j} f_{i,j} F_{i,T} \\
\text{subject to} \quad & \sum_j f_{i,j} = 1 \\
& -f_{i,j} \geq -L_{i,j} \forall i \in 1 : N
\end{aligned}
\tag{13}
$$

The objective function in the above program sums the mineralization across all elements after calculating the net mineralization of each element in units of carbon. By dealing in carbon, all elements are compared in the same currency and therefore can be summed.

Deficiencies unaddressed by diet

In many cases, nutrient deficiency may not be addressed by diet alone because there is only 1 dietary option or all options have insufficient nutrient content. In these cases, the organism is limited by the nutrient in shortest supply by Liebig's Law of the Minimum and must reduce their growth to match this supply rate.

We can calculate this reduction in growth by calculating the amount of extra carbon that needs to be mineralized. We can decide to either (1) increase per capita respiration or (2) decrease production efficiency. **So far we will only use the former, but we can add functionality for the latter later. At equilibrium, the difference is trivial because neither biomass nor consumption rate change.**

Using the equation for the element in shortest supply, which is identified as the one where $E_{k,i}$ is smallest, we can calculate a new $E_{C,i}$ using equation (8):

$$
E_{k,i} C_i \geq 0 \quad \forall k
\tag{14}
$$

If we already know that the mineralization rate is less than zero, we can calculate the case where mineralization rate is zero for the element in shortest supply.

$$
E_{C,i} C_i + \sum_j \mathfrak{a}_{k,i,j} F_{i,j} = 0
\tag{15}
$$

However, the consumption rate $F_{i,j}$ will change as a function of $E_{C,i}$ because higher respiration requires more consumption to hold the biomass at equilibrium. Therefore to isolate the term $E_{C,i}$, we need to solve $F_{i,j}$ simultaneously. To do this, we return to our matrix problem above and add one version of equation (15) for every species that needs to increase its respiration rate. To make the changes more transparent, we introduce a new term into the equation $\hat{E}_{C,i}$, which is the rate of overflow respiration caused by nutrient limitation. Treating this term separately makes the solution easier and makes the result easier to interpret and use.

Returning to our matrix problem $Ax = b$, we can add equations to solve for this new value of $\hat{E}_{C,i}$. Assume that there are M species indexed by m that require an increased respiration rate. We can write a new version of this problem $\hat{A}\hat{x} = \hat{b}$ with M new equations. The example matricies below place the terms for these new equations in the middle of the matrix, but note that they always sit in the column or row corresponding to the species requiring respiration correction. This could be species 1 or N.

$$
\hat{A} = \begin{pmatrix}
a_{12}p_1 - \frac{w_{11}X_1}{\sum_{h=1}^{N} w_{1h}X_h} & \cdots & -\frac{w_{N1}X_1}{\sum_{h=1}^{N} w_{Nh}X_h} & \cdots & 0 \\
\vdots & & \vdots & -X_m & 0 \\
\vdots & & \vdots & \vdots & \vdots \\
\vdots & & \vdots & 0 & -X_M \\
-\frac{w_{1N}X_N}{\sum_{h=1}^{N} w_{1h}X_h} & \cdots & a_{NN}p_N - \frac{w_{NN}X_N}{\sum_{h=1}^{N} w_{Nh}X_h} & \cdots & 0 \\
\cdots & \sum_{j}^{N} \mathfrak{a}_{k,m,j}\frac{w_{mj}X_m}{\sum_{h=1}^{N} w_{mh}X_h} & \cdots & X_m & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots \\
\cdots & \sum_{j}^{N} \mathfrak{a}_{k,M,j}\frac{w_{Mj}X_M}{\sum_{h=1}^{N} w_{Mh}X_h} & \cdots & 0 & X_M
\end{pmatrix}
$$

$$
\hat{b} = \begin{pmatrix}
d_1 X_1 + E_{C,1}X_1 \\
\vdots \\
d_N X_N + E_{C,N}X_N \\
-E_{C,m}X_m \\
\vdots \\
-E_{C,M}X_M
\end{pmatrix}
$$

$$
\hat{x} = \begin{pmatrix}
\sum_{j}^{N} F_{1j} \\
\vdots \\
\sum_{j}^{N} F_{Nj} \\
\hat{E}_{C,m} \\
\vdots \\
\hat{E}_{C,M}
\end{pmatrix}
$$