Biodiversity and Stoichiometry:
Models and Analyses

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Facts: About 27,000 species a year, which boils down to 3 species an hour lost forever.

In the tropics ecosystem destruction is so severe that some 60,000 plant species, roughly one-quarter of the world’s remaining total, could be lost within 25 years.

The earth has an estimate of some 14 million species.

Globally, each day we depend on over 40,000 species of plants, animals, fungi, and microbes.
We incorporate *stoichiometric principles* into standard predator-prey models to analyze competition between consumers on autotrophic resources. The models tracks two essential elements, carbon and phosphorus, in each species. We show that a stable equilibrium is possible with two competitors on a single biotic resource. In general, we speculate that if each resource containing the same $n$ essential and limiting nutrients, then $m$ resources together can sustain $n \times m$ consumers in the form of stable coexistence.
Take home message: In general, intraspecific competitions promote diversity (Kuang, Fagan and Loladze 2003, Biodiversity, habitat area, resource growth rate and interference competition, *Bulletin of Mathematical Biology, 65*, 497-518) and interspecific competitions decrease diversity. Ecological stoichiometry provides a mechanism that generates both intra- and inter-specific competitions. On balance, stoichiometry is a powerful diversity generating mechanism.
1 Introduction

The most basic question in the study of biodiversity is what mechanisms sustain the vast diversity of species. In other words, why can so many species coexist on so few resources (Hutchinson 1961. The paradox of the plankton. *Am. Nat.* 95, 137-45.)?
A biotic resource (hereafter, prey), consists of multiple abiotic resources that are essential to its consumer. All known organisms require carbon (C), oxygen (O), hydrogen (H), nitrogen (N), and phosphorus (P) and other elements.

Consumer species share the requirement for the same nutrients, they can differ in their chemical composition. Autotrophic resources (i.e. plants and algae) are known to exhibit highly variable intraspecific chemical composition.

**Can such “chemical heterogeneity” within and among species enhance biodiversity by providing previously unrecognized mechanisms for coexistence?**
The challenge of developing a mechanistic and predictive theory of biological systems is daunting. However, there has been important progress in understanding and modeling ecological systems in recent years via the development of the theory of ecological stoichiometry (Sterner and Elser 2002). Ecological stoichiometry is the study of the balance of energy and multiple chemical resources (usually elements) in ecological interactions.

Ecological stoichiometry has been most fruitfully deployed in study of competition for multiple abiotic resources (Tilman 1982, Smith 1983, Grover 1997) and of plant-herbivore interactions in food webs (Sterner and Hessen 1994, Elser and Urabe 1999, empirical studies).
Recent advances in stoichiometric theory have revived and expanded the stoichiometric concepts embodied in Lotka’s (1925) pioneering work. Andersen (1997) developed detailed, mechanistic physio-ecological models that feature explicit stoichiometric constraints. Aided by differential equation models, Nisbet et al. (1991) addressed the key issue that nutrients stored in consumer biomass are temporarily unavailable for growth of resource species.

2 Formulation of models

If we let $P_p$, $P_z$ and $P_f$ be the phosphorous in autotroph, phosphorous in herbivore, and the free phosphorous respectively, then $P_t = P_p + P_z + P_f$. Let $x = x(t)$ be the autotroph density, $y = y(t)$ be the herbivore density and $Q = Q(t)$ be the autotroph’s cell quota for $P$, then $P_p = Qx$ and $P_z = \theta y$. Hence

$$P_t = P_f + Qx + \theta y.$$ (2.1)

In the following, we let $q$ be the autotroph’s minimal cell quota for $P$, $\mu_m$ be the autotroph’s true maximal growth rate, $D$ be its death rate and $f(x)$ be the herbivore’s ingestion rate (functional response). We use
a variable-internal-stores model which is based on the Droop equation
that relates growth rate to the internal cell quota (Droop, 1973, 1974).
We then have the following equation for the autotroph growth

$$\frac{dx}{dt} = \mu_m \left(1 - \frac{q}{Q}\right)x - Dx - f(x)y.$$  \hspace{1cm} (2.2)
Let $e$ be the herbivore’s yield constant which measures the conversion rate of ingested autotroph into its own biomass when the autotroph is $P$ rich (when $Q \geq \theta$) and $d$ be the specific loss rate of herbivore that includes metabolic losses and death. If the autotroph is $P$ poor (when $Q < \theta$), then the conversion rate suffers a reduction and it becomes $eQ/\theta$. This approach follows the Liebig’s (1840) minimum principle and is used in Loladze et al.’s (2000) model formulation.

We have the following growth equation for herbivore

$$\frac{dy}{dt} = e \min \left(1, \frac{Q}{\theta} \right) f(x) y - dy. \quad (2.3)$$
Finally, we need an equation governing the dynamics of $Q$, the autotroph’s cell quota for $P$. We assume that $Q$’s recruitment comes proportionally from the free phosphorous ($\alpha P_f$) and its depletion due to the cell growth is $\mu_m(Q - q)$. This results in the following simple equation

\[
\frac{dQ}{dt} = \alpha P_f - \mu_m(Q - q) .
\]

(2.4)

Since $Q(0) \geq q$, mathematically, it is easy to see that this ensures that $Q(t) \geq q$ for all $t > 0$. 

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Since the cell metabolic process operates in a much faster pace than the
growth of total biomass of either species, the quasi steady state argument
allow us to approximate \( Q(t) \) by the solution of

\[
\alpha P_f - \mu_m(Q - q) = 0. \tag{2.5}
\]

We have the following mechanistically formulated stoichiometric autotroph-
herbivore model when \( P \) is the only limiting element:

\[
\frac{dx}{dt} = (\mu_m - D)x \left[ 1 - \frac{x + \mu_m \alpha^{-1}}{[(\mu_m - D)/\mu_m][\mu_m \alpha^{-1} + (P_t - \theta y)/q]} \right] - f(x)y.
\]

\[
\frac{dy}{dt} = e \min \left( 1, \frac{Q}{\theta} \right) f(x)y - dy. \tag{2.6}
\]
we assume now that in addition to $P$, carbon $C$ is also a potential limiting factor. If only $C$ is limiting the autotroph’s growth, then the traditional autotroph equation can be used.

$$\frac{dx}{dt} = bx \left(1 - \frac{x}{K}\right) - f(x)y$$

(2.7)

where $b = \mu_m - D$ is the net autotroph growth rate. Applying Leipig’s minimum principle, we obtain the following autotroph-herbivore model with two limiting elements

$$\frac{dx}{dt} = bx \left[1 - \max\left(\frac{x}{K}, \frac{x + \mu_m \alpha^{-1}/\mu_m}{[(\mu_m - D)/\mu_m][\mu_m \alpha^{-1} + (P_t - \theta y)/q]}\right)\right] - f(x)y.$$  

$$\frac{dy}{dt} = e \min\left(1, \frac{Q}{\theta}\right)f(x)y - dy.$$  

(2.8)
If we, in addition, assume that the natural autotroph death rate $D$ is far less than its true maximal growth rate, then we can approximate the value of $(\mu_m - D)/\mu_m$ by 1. Together with the assumption $\alpha$ tends to $\infty$, the above model becomes

$$
\frac{dx}{dt} = bx[1 - \max\left(\frac{x}{K}, \frac{x}{\left(P_t - \theta y\right)/q}\right)] - f(x)y. \tag{2.9}
$$

$$
\frac{dy}{dt} = e \min\left(1, \frac{Q}{\theta}\right)f(x)y - dy.
$$

As $\alpha$ tends to $\infty$, we see that

$$Q \quad \text{tends to} \quad (P_t - \theta y)/x.$$

The above model is exactly the same as the LKE (Loladze, Kuang and Elser: Stoichiometry in producer-grazer systems: linking energy flow and element cycling, Bull. Math. Biol., 62, 1137-1162(2000)) model:

$$\begin{align*}
\frac{dx}{dt} &= bx \left(1 - \frac{x}{\min(K, (P_t - \theta y)/q)} \right) - f(x)y, \\
\frac{dy}{dt} &= e \min \left(1, \frac{(P_t - \theta y)/x}{\theta} \right) f(x)y - dy.
\end{align*}$$

(2.10)
Light-based plant growth:

Following Huisman & Weissing (1994): the light-based plant growth rate is

$$\mu_L = \frac{1}{z_m} \int_0^{z_m} p(I(z)) x dz, \quad (2.11)$$

where $z$ is the depth of the water column, which runs from $z = 0$ at the top of the water column to $z = z_m$ at the bottom of the water column, and $p(I)$ is the specific production rate as a function of light intensity $I$. The light intensity $I$ is a function of depth, according to Lambert-Beer’s law:
\[ I(z) = I_{\text{in}}e^{-kxz-K_{\text{bg}}z}. \] (2.12)

Suppose

\[ p(I) = \frac{\mu_{\text{max}}I}{K_I + I}, \] (2.13)

where \( K_I \) is the half-saturation constant of light-limited growth. This yields

\[ \mu_L = \frac{\mu_{\text{max}}x}{(kx + K_{\text{bg}})z_m} \ln \left( \frac{K_I + I_{\text{in}}}{K_I + I_{\text{out}}} \right), \] (2.14)

with

\[ I_{\text{out}} = I_{\text{in}}e^{-kxz_m-K_{\text{bg}}z_m}. \] (2.15)
This model is supported by lab experiments of light-limited phytoplankton
(Huisman 1999; Huisman et al. 1999) growth.

The following is a light and P limited predator-prey model. Here
\( \mu = \mu_{\max}, I_i = I_{in}, \beta = \alpha^{-1} \) and \( K_b = K_{bg}. \)

\[
\frac{dx}{dt} = \mu_x \min\left(1, \frac{1}{(kx + K_b)z_m} \ln\left(\frac{H + I_i}{H + I_i \exp(-kxz_m - K_bz_m)}\right)\right) - \frac{cxy}{a + x},
\]

\[
\frac{dy}{dt} = e \min\left(1, \frac{P_t - \theta y + \mu q \beta}{\theta (x + \mu \beta)}\right) - \frac{cxy}{a + x} - dy.
\]
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_t$</td>
<td>0.025</td>
<td>(mg P)/l</td>
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<tr>
<td>$e$</td>
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<td></td>
</tr>
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<td>$\mu$</td>
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<td>day⁻¹</td>
</tr>
<tr>
<td>$d$</td>
<td>0.25</td>
<td>day⁻¹</td>
</tr>
<tr>
<td>$\theta$</td>
<td>0.03</td>
<td>(mg P)/(mg C)</td>
</tr>
<tr>
<td>$q$</td>
<td>0.0038</td>
<td>(mg P)/(mg C)</td>
</tr>
<tr>
<td>$c$</td>
<td>0.81</td>
<td>day⁻¹</td>
</tr>
<tr>
<td>$a$</td>
<td>0.25</td>
<td>(mg C)/l</td>
</tr>
<tr>
<td>$D$</td>
<td>0.54</td>
<td>day⁻¹</td>
</tr>
<tr>
<td>$\alpha$</td>
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<td>day⁻¹</td>
</tr>
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</tr>
<tr>
<td>$K_b$</td>
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</tr>
<tr>
<td>$k$</td>
<td>0.3</td>
<td>m²/mg C</td>
</tr>
</tbody>
</table>
Figure 2.1: A bifurcation diagram for the dynamics of the full (with light intensity consideration) model.
Figure 2.2: Phase plane of the four types of dynamics of the new full (with light intensity consideration) model.
Figure 2.3: Comparison of the four types of dynamics of the new full (with light intensity consideration) model with LKE model.
Figure 2.4: Another comparison of isoclines of the new full (with light intensity consideration) model with LKE model
3 Single resource (with C, P) model with two consumers

Let us start with a conventional model, which describes a system of two consumers feeding on one biotic resource.

\[\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - f_1(x) y_1 - f_2(x) y_2\]
\[\frac{dy_1}{dt} = e_1 f_1(x) y_1 - d_1 y_1\]
\[\frac{dy_2}{dt} = e_2 f_2(x) y_2 - d_2 y_2\]  
(3.1)
3.1 Stoichiometry Based Model Assumptions

(A1): Phosphorus to carbon ratio (P:C) in the resource never falls below a minimum $q$ (mg P/mg C); the two consumers maintain a constant P:C ratio, $s_1$ and $s_2$ (mg P/mg C), respectively.

(A2): The system is closed for phosphorus, with a total of P milligrams of phosphorus per liter (mg P/l). In the spirit of Liebig’s Law of the Minimum, the combination of light and phosphorus limits the carrying capacity of the resource to

$$\min \left( K, \frac{P - s_1y_1 - s_2y_2}{q} \right). \quad (3.2)$$
(A3): The growth efficiency under both good and bad resource quality conditions is:

\[
e_i \min \left( 1, \frac{(P - s_1 y_1 - s_2 y_2)}{s_i} / x \right). \tag{3.3}
\]
Here is our model (LKE style) incorporating stoichiometry constraints.

\[
\frac{dx}{dt} = rx \left( 1 - \frac{x}{\min(K, (P - s_1y_1 - s_2y_2)/q)} \right) - f_1(x)y_1 - f_2(x)y_2 \\
= F(x, y_1, y_2)
\]

\[
\frac{dy_1}{dt} = e_1 \min \left( 1, \frac{(P - s_1y_1 - s_2y_2)}{xs_1} \right) f_1(x)y_1 - d_1y_1 = G_1(x, y_1, y_2)
\]

\[
\frac{dy_2}{dt} = e_2 \min \left( 1, \frac{(P - s_1y_1 - s_2y_2)}{xs_2} \right) f_2(x)y_2 - d_2y_2 = G_2(x, y_1, y_2)
\]

(3.4)
The following theorem provides an analytical result on the boundedness and invariance of solutions of model.

**Theorem 3.1** Let \( k = \min(K, P/q) \). Then, solutions with initial conditions in

\[
\Delta \equiv \{(x, y_1, y_2) \mid 0 < x < k, y_1 > 0, y_2 > 0, qx + s_1 y + s_2 y < P\}
\]

remain there for all forward times.
Figure 3.5: A bifurcation diagram for the dynamics of the one resource-two consumers model.
3.2 Equilibria

If the following system has a positive solution

\[ F(x, y_1, y_2) = G_1(x, y_1, y_2) = G_2(x, y_1, y_2) = 0, \]  \hspace{1cm} (3.6)

then system has an internal (positive) equilibrium. Let us denote such an equilibrium as \((x^*, y^*_1, y^*_2)\).

If

\[ \frac{(P - s_1y_1^* - s_2y_2^*)}{x^*} > s_i, \quad i = 1, 2 \]  \hspace{1cm} (3.7)

then the quality of the resource is good for both consumers, the signs in
the ecosystem matrix are

\[
\begin{pmatrix}
  +/ & - & - & - \\
  + & 0 & 0 \\
  + & 0 & 0 \\
\end{pmatrix},
\]

meaning that a conventional predator-prey type interaction exists between the competitors and the resource. In this case, \( f_i(x^*) = d_i/e_i, i = 1, 2 \), an almost impossible situation.
If
\[
(P - s_1y_1^* - s_2y_2^*)/x^* < s_i, \quad i = 1, 2
\] (3.9)
then the quality of the resource is bad for both consumers, and the signs of the ecosystem matrix are
\[
\begin{pmatrix}
+/- & - & - & - \\
- & - & - & - \\
- & - & - & -
\end{pmatrix}.
\] (3.10)

This means that all species compete with each other and the consumers endure self-limitation.
In this case,

\[
A \equiv P - s_1 y_1^* - s_2 y_2^* = \frac{d_1 s_1 x^*}{e_1 f_1(x^*)} = \frac{d_2 s_2 x^*}{e_2 f_2(x^*)}
\]

and

\[
B \equiv r x^* \left( 1 - \frac{x^*}{\min(K, (d_2 s_2 x^*)/(q e_2 f_2(x^*)))} \right) = f_1(x^*) y_1^* + f_2(x^*) y_2^*.
\]

This case is highly likely to happen with the value of \( x^* \) determined by

\[
\frac{d_1 s_1 x^*}{e_1 f_1(x^*)} = \frac{d_2 s_2 x^*}{e_2 f_2(x^*)},
\]

(3.11)

and the values of \( y_1^* \) and \( y_2^* \) given by

\[
y_1^* = \frac{f_2(x^*) P - f_2(x^*) A - s_2 B}{s_1 f_2(x^*) - s_2 f_1(x^*)}, \quad y_2^* = \frac{f_1(x^*) A + s_1 B - f_1(x^*) P}{s_1 f_2(x^*) - s_2 f_1(x^*)}.
\]

(3.12)
It is straightforward to find that condition (3.9) is equivalent to

\[ d_i < e_i f_i(x^*), \quad i = 1, 2, \]  

(3.13)

which is to say that if the resource at density, \( x^* \), would have been of good quality, then the growth rate of each consumer would have exceeded its death rate. At this equilibrium both consumers are limited by the quality (i.e. phosphorus content) of the resource.
stable coexistence!

Fig. 1
Fig. 2
An intermediate scenario can also occur, where the quality is bad for one consumer, but good for the other. The coexistence of all species at a stable positive equilibrium is possible as well in this case. (One example of parameter values for such a case is $r = 1.4, c_1 = 0.63, c_2 = 0.6, a_1 = 0.45, a_2 = 0.36, e_1 = 0.85, e_2 = 0.8, P = 0.036, q = 0.003, s_1 = 0.038, s_2 = 0.025, d_1 = 0.1, d_2 = 0.12$.

For general functions $f_i(x)$ satisfying, there can be many nonnegative equilibria on the boundary surfaces ($x - y_i$ surface, $i = 1, 2$) of $\Delta$ (Loladze, Kuang and Elser, 2000). The stability of these equilibria and positive equilibria (if any) can be routinely studied via Routh-Hurwitz criteria when specific functions $f_i(x), i = 1, 2$ are given.
Light intensity represented by $K$ (mg C)/L

species densities, (mg C)/L

prey

consumer 1

consumer 2

stable coexistence

Fig. 3

Light intensity represented by $K$ (mg C)/L
Figure 3.6: Another bifurcation diagram for the dynamics of the one resource-two consumers model.
Fig. 5

Nullclines:
- Green: prey
- Red: consumer 1
- Blue: consumer 2

Trajectory

Species densities, (mg C)/L vs. Light intensity represented by K (mg C)/L.
Nullclines:
consumer 1
consumer 2

Fig. 6
We discuss the following system that models $k$ consumers exploiting one biotic resource consisting of $n + 1$ essential chemical elements (carbon, which represents pure energy, is an implicit limiting nutrient limited by
the carrying capacity $K$):

$$x' = bx \left[ 1 - \frac{x}{\min(K, (N_1 - \sum_{i=1}^{k} s_{1i}y_i)/q_1, \ldots, (N_n - \sum_{i=1}^{k} s_{ni}y_i)/q_n)} \right]$$

$$- \sum_{i=1}^{m} f_i(x) y_i$$

$$y_i' = e_i \min \left( 1, \frac{(N_1 - \sum_{i=1}^{k} s_{1i}y_i)}{x s_{1i}}, \ldots, \frac{(N_n - \sum_{i=1}^{k} s_{ni}y_i)}{x s_{ni}} \right) f_i(x) y_i - d_i y_i$$

(4.1)

$N_i$ is the total amount of $i$-th nutrient in the system, $q_i$ is the resource’s minimal $i$-th nutrient content, $s_{ij}$ is the $j$-th consumer’s constant (homeostatic) $i$-th nutrient content.
Our experience suggests that the ultimate dynamics of the model (4.1) will depend on both model parameters and initial population densities. We assume below that \( m = n + 1 \geq 3 \). To see the possibility of stable coexistence at a positive steady state, we consider a possible scenario that at such a steady state, say \( E_1 = (x^*, y_1^*, ..., y_m^*) \), the first two consumers are limited by 1st (non-carbon) nutrient, and the \( j \)-th consumer is limited by \((j - 1)\)-th nutrient, where \( j = 3, ..., m \). In this case, \( x^* \), if exist, is given by

\[
A \equiv \frac{d_1 s_{11} x^*}{e_1 f_1(x^*)} = \frac{d_2 s_{12} x^*}{e_2 f_2(x^*)}.
\]
The $y_i^*$s are given by

$$\sum_{i=1}^k s_{1i}y_i^* = N_1 - A,$$

$$\sum_{i=1}^k s_{(j-1)i}y_i^* = N_{j-1} - \frac{d_j s_{(j-1)j}x^*}{e_j f_j(x^*)}, j = 3, ..., n + 1$$

$$\sum_{i=1}^m \left(\frac{f_i(x^*)}{x^*}\right)y_i^* = b \left[1 - \frac{x^*}{\min\{K, \frac{A}{q_1}, \frac{d_i s_{(i-1)i}x^*}{q_i e_i f_i(x^*)}, i = 2, ..., n\}}\right].$$

Given the independent nature of parameters $s_{ij}$ and values $f_i(x^*)/x^*$, it is certainly conceivable that such a positive steady state can be realized by suitable choices of parameters and the functions $f_i(x)$. 

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Figure 4.7: Three consumers coexisting on a single resource (with C, P and N).
Figure 4.8: Three consumers coexisting (in an oscillatory way) on a single resource (with C, P and N).
Bifurcation diagram for a stoichiometric one plant–two herbivores model

Figure 4.9: A bifurcation diagram for the dynamics of the one resource-three consumers (with C, P and N) model.
a: Coexistence of four consumers on two resources (with stoichiometry)

b: Coexistence of only two consumers on two resources (without stoichiometry)

Figure 4.10: Four consumers coexisting on a single resource (with C and P).
Our experience suggests that the ultimate dynamics of model (4.1) will depend on both model parameters and initial population densities. We can speculate that if one biotic resource provides \( n \) essential chemical elements for competing consumers, it may support up to \( n \) different competitors at a stable equilibrium.
The formulation of a plausible and tractable mathematical version of model (4.1) with more than one biotic resource is challenging. This difficulty stems from the competition among resource species, which forces one either to consider free pools of essential elements (i.e., not bound in any biomass) and model their uptake, or to find some other way to distribute each essential element among all resource species. A mathematically easier case can be imagined in a patchy habitat, where specialist consumers in each patch exploit a distinct biotic resource that provides $n$ essential chemical elements. Then, $m$ distinct biotic resources can support up to $m \times n$ consumer species at a stable equilibrium.