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Appendix 2. Equilibria, trophic indices, and stability of tri-trophic model with dynamic stoichiometry of plants.

In this second Appendix, we detail a tri-trophic model in which variation in nutrient enrichment and traits of plants and herbivore can shape the plant's nutrient content. The bi-trophic case has been considered before by Hall (2004). It is worth noting that, in this model, there are no freely available nutrients (i.e. $R^* = 0$). Also, we describe nutrients sequestered in plants (QP^*), which is the total amount of nutrient per unit habitat. This quantity is not represented by its own equation, but is simply the product of nutrient content per unit carbon (Q^*) times amount of carbon per unit habitat (P^*). Sequestered nutrient provides useful information about the bi-trophic and tri-trophic systems, since it can correspond to the herbivore's nutrient demands. Since most of the results for this model closely resemble those from the model with static stoichiometry of the producer (Appendix 1), we describe results more briefly here.

Equilibria

A herbivore can first invade and persist with the plant when nutrient supply (S) exceeds the herbivores (H)'s minimal sequestered nutrient requirement, QP_H^*. The requirement is the smallest amount of nutrients locked in plant (P) tissues that can support herbivores. Once exceeded, a two-species equilibrium emerges:

$$Q_{2,NL}^* P_{2,NL}^* = \frac{mq_H}{ea} = QP_H^* \tag{B1a}$$

$$H_{2,NL}^* = \left(S - QP_H^* \right) \big/ q_H \tag{B1b}$$

$$Q_{2,NL}^* = \left(\frac{r}{r - aH_{2,NL}^*} \right) k_Q \tag{B1c}$$

$$P_{2,NL}^* = QP_H^* \big/ Q_{2,NL}^* \tag{B1d}$$

where both nutrient content of plant and herbivore biomass increase with enrichment (Table B1). Plant biomass decreases with enrichment until a certain level:

$$S = QP_H^* + \left(\frac{r}{a} \right) \left(q_H - k_Q \left(1 + \frac{s}{am} \right) \right) \tag{B2}$$

after which point the P-H equilibrium switches to a carbon-limited region, where now:

$$P_{2,CL}^* = (m + \sigma) \big/ (ea) \tag{B3a}$$

$$H_{2,CL}^* = \frac{1}{2} \left(\frac{r}{a} + \frac{S}{q_H} - \sqrt{4 \left(\frac{k_Q}{q_H} \right) \left(\frac{r}{a} \right) P_{2,CL}^* + \left(\frac{r}{a} - \frac{S}{q_H} \right)^2} \right) \tag{B3b}$$

$$Q_{2,CL}^{*} = \frac{1}{2}\left(\frac{S}{P_{2,CL}^{*}} - \frac{q_H r}{aP_{2,CL}^{*}} \right) + \sqrt{ \frac{4k_Q q_H r}{aP_{2,CL}^{*}} + \left(\frac{q_H r}{aP_{2,CL}^{*}} - \frac{S}{P_{2,CL}^{*}} \right)^2 } \qquad (B3c)$$

In this portion of the plant-herbivore only equilibrium, plant biomass is fixed at the producer's minimal carbon requirement, but herbivore biomass, nutrient quota, and sequestered nutrient increase with S (Table B1).

Before the herbivore in the plant-herbivore only equilibrium becomes carbon-limited, it could also support a carnivore if nutrient enrichment exceeds:

$$S = QP_H^{*} + q_H m_C / (a_C e_C) \qquad (B4)$$

or the minimal nutrient requirement of the herbivore plus the nutrients contained in the carnivores's own minimal requirement for herbivores, $m_C / e_C a_C$. If satisfied, a new equilibrium emerges with a nutrient-limited herbivore:

$$H_{3,NL}^{*} = \frac{m_C}{e_C a_C} \qquad (B5a)$$

$$Q_{3,NL}^{*} = k_Q \left(\frac{r}{r - aH_{3,NL}^{*}} \right) \qquad (B5b)$$

$$C_{3,NL}^{*} = \frac{S - q_H H_{3,NL}^{*} - QP_H^{*}}{q_C + a_C QP_H^{*} / m} \qquad (B5c)$$

$$P_{3,NL}^{*} = \left(\frac{q_H}{Q_{3,NL}^{*}} \right) \left(\frac{a_C \left(S - QP_H^{*} + mq_C \right)}{eaq_C + q_H} \right) \qquad (B5d)$$

which requires that the ratio of nutrient uptake rate (r) to herbivore attack rate (a) exceed the biomass of herbivores ($H_{3,NL}^{*}$), or $r/a > H_{3,NL}^{*}$. At this equilibrium, herbivore biomass remains fixed at the carnivore's minimal carbon requirement. Additionally, nutrient quota of plants remains fixed. Both carnivore and plant biomass increase with nutrient enrichment, as does the total amount of nutrient sequestered in plants ($Q_{3,NL}^{*} P_{3,NL}^{*}$; Eq. B10; Table B1).

If the herbivore in the two-level system is carbon-limited, the carnivore can invade if:

$$S > q_H H_{3,CL}^{*} + Q_{3,CL}^{*} P_{2,CL}^{*} \qquad (B6)$$

which says that nutrient supply must exceed the nutrient sequestered in the carnivore's minimal requirement for carbon in herbivores ($H_{3,CL}^{*}$) plus the nutrient sequestered in producers at the herbivore's minimal carbon requirement ($P_{2,CL}^{*}$), given the nutrient quota of those producers in the three-level system ($Q_{3,CL}^{*}$). The tri-trophic interior equilibrium that contains these terms for carbon-limited herbivores ($H_{3,CL}^{*}$) and quota ($Q_{3,CL}^{*}$) becomes :

$$H_{3,CL}^{*} = H_{3,NL}^{*} \qquad (B7a)$$

$$Q_{3,CL}^{*} = Q_{3,NL}^{*} \qquad (B7b)$$

$$C_{3,CL}^{*} = \frac{ea \left(S - q_H H_{3,CL}^{*} - Q_{3,CL}^{*} P_{2,CL}^{*} \right)}{eaq_C + a_C Q_{3,CL}^{*}} \qquad (B7c)$$

$$P_{3,CL}^{*} = \frac{a_C \left(S - q_H H_{3,CL}^{*} \right) - eaq_C P_{2,CL}^{*}}{eaq_C + a_C Q_{3,CL}^{*}} . \tag{B7d}$$

Note that both herbivore biomass and nutrient quota do not differ from those values in tri-trophic case with a nutrient-limited herbivore (Eq. B5a and B5b, respectively). Instead, biomass of carnivores and plants continues to increase with enrichment, but just at a different slope.

Over a nutrient enrichment gradient, the carnivore can invade the plant-herbivore system via two scenarios. In the first, the herbivore is limited by nutrients and remains so with further enrichment. This occurs when nutrient content of the plant, $Q_{3,NL}^{*}$, is relatively small:

$$Q_{3,NL}^{*} < q_H \, m / (m + \sigma) \tag{B8}$$

(which is a condition that closely resembles the one for the static case, Eq. A4). The herbivore feeding on relatively nutrient-poor plants always stays nutrient-limited in this tri-trophic system because the threshold at which it would switch to carbon limitation,

$$S = q_H H_{3,NL}^{*} - \frac{mq_C}{a_C} + \frac{\sigma Q_{3,NL}^{*} \left(q_C / a_C + q_H / (ae) \right)}{Q_{3,NL}^{*} + 1} \tag{B9}$$

occurs at a lower level than required for the carnivore to invade (Eq. B4). The other scenario involves a more nutrient rich plant (i.e. one with nutrient:carbon ratio that exceeds the right hand side of Eq. B8). In this case, the carnivore invades when the herbivore in the two-dimensional system is carbon-limited. That herbivore remains carbon-limited with further enrichment until a resource limitation threshold for herbivores in tri-trophic chains (Eq. B9) is crossed. After this point, the herbivore actually becomes nutrient-limited again. As with the static case, there is no scenario in which a herbivore is nutrient limited when the carnivore invades and then becomes carbon limited.

As with the static stoichiometry model, it seems counter-intuitive at first glance that production of herbivores could should switch from carbon limitation to nutrient limitation with enrichment in the three species chain. To understand this result, one must appreciate that the minimal nutrient demands of herbivore in the presence of predators ($QP_{H,3}^{*}$) increases from the minimal nutrient requirement without predators, QP_{H}^{*} in the two-species chain (Eq. B1a) to:

$$QP_{H,3}^{*} = Q_{3,NL}^{*} P_{3,NL}^{*} = q_H \left(\frac{S - q_H H_{3,NL}^{*} + m \, q_C / a_C}{q_H + ea \, q_C / a_C} \right) \tag{B10}$$

This requirement increases because of mortality imposed by the carnivore: the herbivore must eat more sequestered nutrient to compensate for this higher mortality rate. (A parallel phenomenon occurs for plants and their nutrient requirements when they are grazed; Grover 1997). Although nutrients sequestered in plants do increase with enrichment when the herbivore is carbon-limited, they do not increase steeply enough. Thus, eventually production of herbivores in the tri-trophic system becomes nutrient limited.

Trophic indices

One can calculate response of the trophic indices for plants and herbivores following the same methods used for the static stoichiometry case. That is, many of the responses of the indices to change in parameters can be calculated from the individual response of the numerator (biomass in the three-level system) and the response of the denominator (biomass in the two level system) to a change in a parameter and the quotient rule from calculus (i.e. Eq. A12). The results (Table 2, A1) closely match those for the static stoichiometry case. As with that first model, response of plant biomass in tri-

trophic chains with nutrient-limited herbivores ($P_{3,NL}^*$) to increases in nutrient:carbon ratio of herbivores (q_H) depends upon enrichment (S). Below a certain level of enrichment,

$$S = q_H H_{3,NL}^* \left(\frac{a_C}{m q_C} Q P_H^* + 2 \right) - m q_C / a_C \tag{B11}$$

plant biomass decreases with q_H; above this threshold, it increases (Table B1). As for the static stoichiometry model, this switch in sign of $P_{3,NL}^*$ affects response of the plant trophic index to q_H when different resources limit herbivores in bi-trophic and tri-trophic chains (Table 2).

Stability

Elsewhere, we already shown that bi-trophic system is always stable, regardless of the resource limiting herbivore growth (Hall 2004). For tri-trophic systems with carbon-limited herbivores, the Jacobian matrix for a carbon-limited herbivore (J_{CL}) is:

$$J_{CL} = \begin{bmatrix} aH^* - r & -aP^* - \dfrac{k_Q q_H r}{(Q^*)^2} & -\dfrac{k_Q q_C r}{(Q^*)^2} \\ aeH^* & 0 & -a_C H^* \\ 0 & e_C a_C C^* & 0 \end{bmatrix} \tag{B12}$$

where we have dropped subscripts denoting trophic level and resource limitation status. Meanwhile, the Jacobian matrix for a nutrient-limited herbivore (J_{NL}) is:

$$J_{NL} = \begin{bmatrix} aH^* - r & -aP^* - \dfrac{k_Q q_H r}{(Q^*)^2} & -\dfrac{k_Q q_C r}{(Q^*)^2} \\ 0 & -eaH^* & -H^* \left(\dfrac{e a q_C}{q_H} + a_C \right) \\ 0 & e_C a_C C^* & 0 \end{bmatrix} \tag{B13}$$

Stability analysis of the three-dimensional models depends upon the three Routh-Hurwitz criteria $A_1 > 0$, $A_3 > 0$, and $A_1 A_2 - A_3 > 0$, where A_1, A_2, and A_3 are the coefficients of the Jacobian matrix' characteristic polynomial. In the Jacobian matrix for the carbon-limited herbivore (J_{CL}), the first criterion ($A_1 > 0$) is always met. The second criterion ($A_3 > 0$) is always met (because $Q^* > -ea q_C / a_C$). The third criterion is met as long as:

$$P_{3,CL}^* > \frac{r}{a} \left(\frac{k_Q}{Q_{3,CL}^*} \right) \left(a_C e_C C_{3,CL}^* - \frac{r q_H}{Q_{3,CL}^*} \right) \tag{B15}$$

which is met as long as the three-level is feasible. When herbivores are nutrient-limited, one can show that the model is stable based on the signs of the associated Jacobian matrix (J_{NL}). The first Routh-Hurwitz criterion is met since $J_{11} < 0$, implying that $A_1 = -(J_{11} + J_{22}) > 0$. The second criterion is met since $A_3 = J_{11} J_{23} J_{32} > 0$ always. The third criterion ($A_1 A_2 - A_3 > 0$) is met since $-J_{11} J_{22} (J_{11} + J_{22}) + J_{22} J_{23} J_{32} > 0$ always. Hence, the three-level food chain model with a nutrient or carbon limited herbivore is stable.

Table B1. Signs of partial derivatives of equilibrial biomass of plants (P_j^*) and herbivores (H_j^*) derived from the model with dynamic stoichiometric of the producer, where "+" indicates increase in the equilibrium with an increase in the parameter, "–" indicates a decrease in the equilibrium, and "0" indicates no change. Responses of nutrient quota (Q) are presented in the main text (Table 2).

Resource[a]	Quantity[b]	Nutrient supply, S	Maximum efficiency, e	Min. plant nutr:C, k_Q	Grazer nutr:C, q_H
Carbon	P_2^*	0	–	0	0
	H_2^*	+	+	0	0
	P_3^*	+	–	–	–
	H_3^*	0	0	0	0
Nutrient	P_2^*	–	–	–	+
	H_2^*	+	+	0	–
	P_3^*	+	–	–	–,+ [c]
	H_3^*	0	0	0	0

[a] "Carbon" means that carbon limits herbivores; "nutrient" indicates nutrient limitation.

[b] Subscript refers to number of trophic levels ("2" for bi-level, "3" for tri-level).

[c] This sign changes as nutrient enrichment crosses the particular threshold (Eq. B11).