Appendix A: from S. R. Hall et al., "Inedible Producers in Food Webs: Controls on Stoichiometric Food Quality and Composition of Grazers" (Am. Nat., vol. 167, no. 5, p. 000)

Analysis of Food Web Model: Equilibria, Thresholds, Stability, and Assembly Rules

In this appendix, we provide analytical results to support the description of the food web model (eqq. [1]) presented in the text. This model considers interactions between edible and inedible producers (A_E and A_I, respectively) and two grazers (G_1 and G_2). Simultaneously, it tracks the nutrient : carbon ratio of the edible producer (Q), nutrient sequestered in edible producers (i.e., the product of Q and A_E, denoted as QA_E), and available nutrient resources (R) over gradients of nutrient (S) and light (L) supply. For compactness, we write the Monod function for light as $B_E = L/(b_E + L)$ and $B_I = L/(b_I + L)$ for edible and inedible producers, respectively. These functions B_E and B_I increase with light supply, from 0 to an asymptote of 1. They can be thought of as the degree to which producers are limited by light (Hall 2004). Some of these results, particularly those concerning the food chain and grazer coexistence, have been presented in detail elsewhere for a similar model (Hall 2004). Thus, they are presented summarily here. Two tables accompany this appendix. Table A1 summarizes the variables, parameters, and synthetic quantities, while table A2 describes qualitative response of the food web components to increases in nutrient and light supply in the original model (eqq. [1]).

Food Chain: Edible Producer with One Grazer

A food chain consisting of the edible producer and a single grazer can arise if there is sufficient nutrient sequestered in edible producers to support the grazer. The edible producer (A_E) alone can invade and persist in a system when nutrient (S) and light (L) supply both exceed the A_E's minimal resource requirements (denoted R_E^*, following Tilman 1982; Grover 1997), that is, $S > R_E^*$. If so, the edible-producer-only equilibrium emerges, where:

$$Q^* = \frac{u_E B_E}{u_E B_E - m_E} k_Q, \tag{A1a}$$

$$A_E^* = \frac{S}{Q^*} - \frac{m_E}{v}, \tag{A1b}$$

$$R^* = \frac{m_E}{v} Q^* = R_E^*, \tag{A1c}$$

$$QA_E^* = S - R_E^*. \tag{A1d}$$

The equilibrial quantities Q^* and A_E^* were solved from the ordinary differential equation system (eqq. [1]), R^* follows from the algebraic mass balance constraint (eq. [1e]), and QA_E^* is simply the product of Q^* and A_E^*. At this equilibrium, available nutrients (R_E^*) and nutrient content of edible producers (Q^*) decrease with decreasing light limitation (B_E) but remain constant as nutrient supply (S) increases. Higher nutrient enrichment (S) yields higher biomass (A_E^*) and nutrient sequestered (QA_E^*) in edible producers.

It should not surprise students of resource competition theory that the A_E-only equilibrium is stable in systems without grazers. Using the familiar Routh-Hurwitz (RH) criteria (Kot 2001), this stability emerges upon examination of the associated Jacobian matrix ($\mathbf{J}$); for this model,

$$\mathbf{J} = \begin{bmatrix} 0 & u_{\mathrm{E}}B_{\mathrm{E}}\left(\dfrac{k_{\mathrm{Q}}}{Q^*}\right)A_{\mathrm{E}}^* \\ -vQ^* & -(u_{\mathrm{E}}B_{\mathrm{E}} + vA_{\mathrm{E}}^*) \end{bmatrix}. \tag{A2}$$

The RH criteria demand that the trace of this two-dimensional matrix be less than 0 and that the determinant be positive. Clearly, both criteria are met here (just based on signs of the elements of $\mathbf{J}$), so this equilibrium is stable when feasible.

A grazer G_j can invade this edible-producer-only equilibrium if sequestered nutrient exceeds the grazer's minimal sequestered nutrient requirement ($QA_{\mathrm{E},j}^*$) plus the edible producer's minimal available resource requirement (R_{E}^*), where

$$QA_{\mathrm{E},j}^* = \frac{d_j q_{\mathrm{G},j}}{e_{\mathrm{R},j} f_j}. \tag{A3}$$

This minimal nutrient requirement of the grazer depends solely on grazer traits and is a key component driving the outcomes of grazer competition. Once $S > QA_{\mathrm{E},j}^* + R_{\mathrm{E}}^*$ (which is threshold a of fig. 1), the grazer can invade but remains limited by nutrients sequestered in edible producers. The associated equilibrium is

$$Q^* = \frac{1}{2}\left\{ \frac{v}{u_{\mathrm{E}}B_{\mathrm{E}}}\left(S - QA_j^* + \frac{q_j m_{\mathrm{E}}}{f_j}\right) + k_{\mathrm{Q}} + \frac{q_j v}{f_j} + \sqrt{\frac{4vk_{\mathrm{Q}}}{f_j} + \left[\frac{v}{u_{\mathrm{E}}B_{\mathrm{E}}}\left(S - QA_j^* + \frac{q_j m_{\mathrm{E}}}{f_j}\right) + k_{\mathrm{Q}} + \frac{q_j v}{f_j}\right]^2} \right\}, \tag{A4a}$$

$$QA_{\mathrm{E}}^* = QA_{\mathrm{E},j}^*, \tag{A4b}$$

$$A_{\mathrm{E}}^* = \frac{QA_{\mathrm{E},j}^*}{Q^*}, \tag{A4c}$$

$$G_j^* = \frac{1}{f_j}\left[u_{\mathrm{E}}B_{\mathrm{E}}\left(1 - \frac{1}{Q^*}\right) - m_{\mathrm{E}} \right], \tag{A4d}$$

$$R^* = S - QA_{\mathrm{E},j}^* - q_{\mathrm{G},j}G_j^*. \tag{A4e}$$

At this equilibrium, nutrients sequestered in edible producers (QA_{E}^*) remain fixed at G_j's minimal requirement, yet the edible producer's nutrient : carbon ratio (Q^*) increases and biomass (A_{E}^*) decreases over an enrichment gradient (S).

Stability analysis of this food chain reveals the stabilizing effects of nutrient-limited grazing. The Jacobian matrix ($\mathbf{J}$) associated with equilibrium (eq. [A4]) is

$$\mathbf{J} = \begin{bmatrix} 0 & u_{\mathrm{E}}B_{\mathrm{E}}\left(\dfrac{k_{\mathrm{Q}}}{Q^*}\right)A_{\mathrm{E}}^* & -f_j A_{\mathrm{E}}^* \\ -vQ^* & -(u_{\mathrm{E}}B_{\mathrm{E}} + vA_{\mathrm{E}}^*) & -q_{\mathrm{G},j}v \\ e_{\mathrm{R},j}f_j\left(\dfrac{Q^*}{q_{\mathrm{G},j}}\right)G_j^* & A_{\mathrm{E}}^*G_j^*\left(\dfrac{e_{\mathrm{R},j}f_j}{q_{\mathrm{G},j}}\right) & 0 \end{bmatrix}. \tag{A5}$$

A Jacobian matrix with this structure has a characteristic polynomial $\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3$, where the λ's are the eigenvalues and the A_n are the coefficients. The RH requirements for these coefficients are $A_1 > 0$, $A_3 > 0$, and $A_1 A_2 - A_3 > 0$. The first criterion is met because $A_1 = -j_{22} > 0$ (where j_{nk} are the elements of $\mathbf{J}$). The second criterion requires that $A_3 = j_{13}(j_{22}j_{31} - j_{21}j_{32}) - j_{12}j_{23}j_{31} > 0$, which can be shown with some simple algebra to be met always. One can also show with more tedious algebra that the third criterion is always met (because instability occurs only if A_{E}^* is negative).

Because nutrient content of edible producers Q^* continues to increase with nutrient enrichment S, the grazer eventually becomes limited by carbon (A_{E}), not nutrient (QA_{E}^*), sequestered in edible producers. This transition occurs when

$$Q^* = \frac{q_{G,j}}{e_{R,j}}\left(e_{C,j} - \frac{r_j}{f_j A_E^*}\right), \tag{A6}$$

where Q^* and A_E^* follow equation (A4). Once this threshold is passed (corresponding in fig. 1 to b for grazer 1 and e for grazer 2), the equilibrium switches to

$$A_E^* = \frac{d_j + r_j}{e_{C,j}f_j} = A_{E,j}^*, \tag{A7a}$$

$$Q^* = \frac{\left[(u_E B_E/v) + A_{E,j}^*\right]^{-1}}{2}$$

$$\times \left\{\left[S + \frac{u_E B_E}{v}k_Q + \frac{q_{G,j}}{f_j}(u_E B_E - m_E)\right] - \sqrt{4u_E B_E \frac{k_Q q_{G,j}}{f}\left(\frac{u_E B_E}{v} + A_{E,j}^*\right) + \left[S + \frac{u_E B_E}{v}k_Q + \frac{q_{G,j}}{f_j}(u_E B_E - m_E)\right]^2}\right\}, \tag{A7b}$$

$$G_j^* = \frac{1}{2}\left[\left(\frac{S}{q_{G,j}} + \frac{k_Q}{q_{G,j}}\frac{u_E B_E}{v} + \frac{u_E B_E - m_E}{f_j}\right) - \sqrt{4u_E B_E \frac{k_Q}{q_{G,j}}\left(\frac{u_E B_E}{v} + A_{E,j}^*\right) + \left(\frac{S}{q_{G,j}} + \frac{k_Q}{q_{G,j}}\frac{u_E B_E}{v} + \frac{u_E B_E - m_E}{f_j}\right)^2}\right], \tag{A7c}$$

$$QA_E^* = Q^* A_{E,j}^*, \tag{A7d}$$

$$R^* = S - QA_{E,j}^* - q_{G,j}G_j^*. \tag{A7e}$$

Once the grazer becomes limited by the carbon sequestered in edible producers, producer biomass remains fixed at grazer j's minimal carbon requirement, $A_{E,j}^*$. This minimal requirement is also a function of grazer traits alone and becomes critical to understanding grazer competition. Meanwhile, at the carbon-limited portion of the edible producer–one grazer equilibrium, nutrient : carbon ratio (Q^*) and sequestered nutrient (QA_E^*) continue to increase with enrichment. Because of these increases, another grazer may potentially invade this equilibrium and either displace or coexist with the grazer.

Stability analysis of this portion of the chain with the edible producer and one grazer employs a Jacobian matrix with a structure very similar to that for the nutrient-limited case (eq. [A5]). However, the third row changes to $j_{31} = e_{C,j}f_j G_j^*$ and $j_{32} = 0$. With this structure, the coefficients of the characteristic polynomial are $A_1 = -j_{22}$, $A_2 = -j_{12}j_{21} - j_{13}j_{31}$, and $A_3 = j_{13}j_{22}j_{31} - j_{12}j_{23}j_{31}$. On the basis of signs of the associated $\mathbf{J}$ alone, it becomes clear that the three coefficients are all positive. While not as transparent, the third criterion ($A_1 A_2 - A_3 > 0$) reveals that this equilibrium becomes unstable once

$$G_j^* > \frac{Q^*(u_E B_E + vA_E^*)}{e_{C,j}f_j q_{G,j}}. \tag{A8}$$

Thus, at some high level of nutrient supply (S), this model will oscillate once equation (A8) is met.

It is useful to start describing the results of the model using assembly rules. Assembly rules precisely describe conditions under which, in this case, the food chain could be built through invasions of an edible producer and a grazer. Following Grover (1997), we state these in terms of the available resource concentration of the food chains/webs. Here, for the food chain, the assembly rule is

$$R_E^* < R_{j,NL}^* \text{ or } R_E^* < R_{j,CL}^*, \tag{A9}$$

depending on whether the grazer is nutrient limited (left) or carbon limited (right), where R_E^* is the minimal

resource requirement of the edible producer (eq. [A1c]), $R^*_{j,\mathrm{NL}}$ is the equilibrial free resource concentration when grazer j is nutrient limited (eq. [A4e]), and $R^*_{j,\mathrm{CL}}$ is that when grazer j is carbon limited (eq. [A7e]).

Grazer Coexistence Web: Edible Producer with Both Grazers

As we have shown elsewhere (Hall 2004), two grazers can potentially coexist with a single, edible producer. This requires that the two grazers experience a trade-off in their minimal carbon ($A^*_{\mathrm{E},j}$) and nutrient ($QA^*_{\mathrm{E},j}$) requirements. Here we will assume that grazer 1 is a superior nutrient competitor to grazer 2 (i.e., $QA^*_{\mathrm{E},1} < QA^*_{\mathrm{E},2}$), while grazer 2 is a superior carbon competitor to grazer 1 (i.e., $A^*_{\mathrm{E},2} < A^*_{\mathrm{E},1}$). Given this trade-off architecture, coexistence of the two grazers can occur at intermediate nutrient supply, where

$$S > QA^*_2 + R^*_{\mathrm{Co}} - \frac{q_{\mathrm{G},2}}{f_2}\left(\frac{vR^*_{\mathrm{Co}}}{Q^*_{\mathrm{Co}}} - m_{\mathrm{E}}\right), \tag{A10a}$$

$$S < QA^*_2 + R^*_{\mathrm{Co}} + \frac{q_{\mathrm{G},1}}{f_2}\left(\frac{vR^*_{\mathrm{Co}}}{Q^*_{\mathrm{Co}}} - m_{\mathrm{E}}\right). \tag{A10b}$$

The quantity R^*_{Co} equals the available nutrient concentration at the coexistence equilibrium, defined below (eq. [A11]). The lower threshold (eq. [A10a]) permits grazer 2 to invade a chain with the edible producer and grazer 1 if grazer 1 is carbon limited; it corresponds to $\hat{S}_{\mathrm{G2,in}}$ and threshold c of figures 1 and 2. The upper threshold demarks where grazer 2, although still nutrient limited, competitively displaces grazer 1; it corresponds to $\hat{S}_{\mathrm{G1,out}}$ and threshold d in the same figures. Assuming that these criteria are met, a potential one-producer–two-grazers coexistence equilibrium emerges:

$$A^*_{\mathrm{E}} = A^*_{\mathrm{E},1}, \tag{A11a}$$

$$QA^*_{\mathrm{E}} = QA^*_{\mathrm{E},2}, \tag{A11b}$$

$$Q^* = \frac{QA^*_{\mathrm{E},2}}{A^*_{\mathrm{E},1}}, \tag{A11c}$$

$$R^*_{\mathrm{Co}} = \frac{uB_{\mathrm{E}}}{v}\left(\frac{QA^*_{\mathrm{E},2}}{A^*_{\mathrm{E},1}} - k_{\mathrm{Q}}\right), \tag{A11d}$$

$$G^*_1 = \frac{1}{f_2 q_{\mathrm{G},1} - f_1 q_{\mathrm{G},2}}\left[-f_2(S - QA^*_2 - R^*_{\mathrm{Co}}) + q_{\mathrm{G},2}\left(\frac{vR^*_{\mathrm{Co}}}{Q^*_{\mathrm{Co}}} - m_{\mathrm{E}}\right)\right], \tag{A11e}$$

$$G^*_2 = \frac{1}{f_2 q_{\mathrm{G},1} - f_1 q_{\mathrm{G},2}}\left[f_1(S - QA^*_2 - R^*_{\mathrm{Co}}) + q_{\mathrm{G},1}\left(\frac{vR^*_{\mathrm{Co}}}{Q^*_{\mathrm{Co}}} - m_{\mathrm{E}}\right)\right]. \tag{A11f}$$

Here edible-producer carbon is set by the minimal requirement of the inferior carbon competitor (grazer 1, G_1), while sequestered nutrient is set by the minimal requirement of the inferior nutrient competitor (G_2). Importantly, at this equilibrium, grazer 1 decreases, while grazer 2 increases with nutrient enrichment (S). In addition, the resources available at this equilibrium (R^*_{Co}) increase as light (L) increases (because $\partial B_{\mathrm{E}}/\delta L > 0$ and $\partial R^*_{\mathrm{Co}}/\delta B_{\mathrm{E}} > 0$), but this increase slows with increasing light (because $\partial B^2_{\mathrm{E}}/\delta^2 L < 0$; see fig. 2$B$).

Stability analysis of this grazer coexistence equilibrium in Hall (2004) also revealed another stipulation for stable coexistence of the two grazers. Coexistence requires that

$$\frac{f_2}{f_1} > \frac{q_{\mathrm{G},2}}{q_{\mathrm{G},1}}. \tag{A12}$$

To understand the statement, one must realize that feeding rate f_j is the effect of grazer G_j on producer carbon (A_{E}), while nutrient content $q_{\mathrm{G},j}$ is its effect on sequestered nutrient (QA_{E}). Thus, equation (A12) requires that

each competitor has greater effect on the resource most limiting its own growth (Hall 2004). If this condition is not met, the interior equilibrium (eq. [A11]) becomes a saddle, and priority effects/alternative stable states emerge. Assuming that equation (A12) is met, the assembly rules for this three-species community become

$$R_E^* < R_{2,NL}^* < R_{Co}^* < R_{1,CL}^*. \tag{A13}$$

Here the available nutrient concentration at equilibrium is intermediate between those of the two grazers.

Food Web with Inedible Producers but Only One Grazer

A first condition required to build a food web with an inedible producer is that the inedible producer (A_I) is an inferior competitor to the edible producer (A_E) for available nutrients (R). This means that $R_E^* < R_I^*$, where R_E^* is the minimal resource requirement of A_E (eq. [A1c]) and the minimum requirements of A_I are

$$R_I^* = \frac{m_I}{uB_I}. \tag{A14}$$

As shown in figure 2B, this quantity is a decreasing, concave-up function of light supply, L (because $\partial B_I^{-1}/\delta L < 0$ but $\partial (B_I^{-1})^2/\delta^2 L < 0$). The inedible producer can coexist with the edible producer and one grazer at an equilibrium:

$$R^* = R_I^*, \tag{A15a}$$

$$Q^* = k_Q + \frac{vR_I^*}{u_E B_E}, \tag{A15b}$$

$$G_j^* = \frac{1}{f_j}\left(\frac{vR_I^*}{Q^*} - m_E\right), \tag{A15c}$$

$$A_E^* = \frac{QA_{E,j}^*}{Q^*} \text{ or } A_E^* = A_{E,j}^*, \tag{A15d}$$

$$QA_E^* = QA_{E,j}^* \text{ or } QA_E^* = Q^*A_{E,j}^*, \tag{A15e}$$

$$A_I = \frac{S - R_I^* - Q^*A_E^* - q_{G,j}G_j^*}{q_I}. \tag{A15f}$$

Here available resources are termed solely by the traits of the inedible producer and do not increase with enrichment (S). The nutrient : carbon ratio of the edible producer is set by this minimal requirement and the ratio of nutrient uptake of available resources (vR_I^*) to maximal growth rate of the edible producer allowed by the light supply ($u_E B_E$). Thus, inedible producers and light both control nutrient : carbon ratio of food for grazers; grazers may be nutrient or carbon limited by this food. Regardless of the type of limitation for grazers, inedible producers lock biomass of grazers at a level (eq. [A15c]) that does not respond to nutrient enrichment (but does increase with light). However, carbon (A_E) and nutrient sequestered in edible producers (QA_E) do depend on the identity of the limiting resource for the grazers. When grazer j is nutrient limited, sequestered nutrient in edible producers, QA_E, is set by the minimal requirements of the grazer ($QA_{E,j}^*$) while producer carbon, A_E, is determined by the ratio of $QA_{E,j}^*$ and Q^* (left-hand portions of eqq. [A15d], [A15e]). On the other hand, if grazer j is carbon limited at the equilibrium, producer carbon is locked at the grazer's minimal requirement ($A_{E,j}^*$) and sequestered nutrient is determined by this minimal requirement and Q^* (right-hand portions of eqq. [A15d], [A15e]). Finally, all nutrients of the system (S) that exceed the inedible producer's minimal requirement (R_I^*) but are not locked in tissues of edible producers ($Q^*A_E^*$) and grazers ($g_{G,j}G_j^*$) are shunted into biomass of the inedible producer (eq. [A15f]).

It is worth noting that regardless of which resource limits grazers, the biomass of grazers increases as light supply diminishes in systems with inedible producers. This result seems counterintuitive at first. In fact, it superficially resembles surprising results from stoichiometrically explicit food chain experiments (Urabe and Sterner 1996; Sterner et al. 1998) and an associated food chain model (Loladze et al. 2000). In those examples,

the surprising result (higher grazer biomass at low light) emerges through the effects of light on elemental food quality (where lower light yields higher nutrient : carbon ratio of edible producers and hence more efficient grazing by nutrient-limited herbivores). Here, in the web with one grazer and two producers, the result emerges from interplay between food web components. Thus, observation of higher grazer biomass at lower light in nature could indeed emerge from stoichiometric effects in food chains (Urabe and Sterner 1996; Sterner et al. 1998; Loladze et al. 2000) or purely through food web interactions.

The resource supply required for invasion by the inedible producers becomes obvious from the equation describing the equilibrial biomass of inedible producers, A_I^*. Specifically, nutrient supply S must exceed $R_I^* + Q^* A_E^* + q_{G,j} G_j^*$, where the equilibrial quantities are described above (eqq. [A15]). If the grazer is nutrient limited when coexisting with the edible producer alone, nutrient content Q^* and sequestered carbon A_E^* of edible producers in this invasion criterion follow that for the nutrient-limited grazer (left-hand portions of eqq. [A15d], [A15e]). If the grazer is carbon limited, Q^* and A_E^* switch accordingly (to the right-hand portions of eqq. [A15d], [A15e]). (Strictly speaking, this invasion criterion is necessarily accurate only if the edible producer–grazer j equilibrium is stable; Grover 1997.) However, once the inedible producer invades and reaches its equilibrial biomass, the grazer may switch from being carbon limited to being nutrient limited. This fact underscores the importance of inedible producers in stoichiometrically explicit food webs. This result can be stated precisely with assembly rules (Grover 1997); the grazer is nutrient limited at the one-grazer–two-producer equilibrium if

$$R_E^* < R_I^* < R_{j,NL}^* \tag{A16a}$$

but carbon limited at this equilibrium if

$$R_E^* < R_{j,NL}^* < R_I^*, \tag{A16b}$$

where $R_{j,NL}^*$ is the available nutrient concentration in the edible producer–grazer j chain with a nutrient-limited grazer (following eq [A4e]).

Stability analysis of this web (eqq. [A15]), assuming that the grazer is nutrient limited, follows from the associated Jacobian matrix (**J**) again, where

$$\mathbf{J} = \begin{bmatrix} 0 & u_E B_E \left(\dfrac{k_Q}{Q^*} \right) A_E^* & 0 & -f A_E^* \\ -v Q^* & -(u_E B_E + v A_E^*) & -q_I v & -q_G v \\ -u B_I Q^* A_I^* & -u B_I A_E^* A_I^* & -u B_I (q_I A_I^* - R_{Co}^*) - m_I & -u B_I q_G G^* \\ \dfrac{e_R f G^* Q^*}{q_G} & \dfrac{e_R f G^* A_E^*}{q_G} & 0 & 0 \end{bmatrix}. \tag{A17}$$

Note that here and below we have dropped the subscript "j" for compactness. A four-dimensional matrix such as this one (eq. [A17]) yields a characteristic polynomial with four coefficients: $\lambda^4 + A_1 \lambda^3 + A_2 \lambda^2 + A_3 \lambda + A_4$. Given this characteristic polynomial, the RH criteria for stability are $A_1 > 0$, $A_3 > 0$, $A_4 > 0$, and $A_1 A_2 A_3 > A_3^2 + A_1^2 A_4$. Coefficient A_1, which equals $-(j_{22} + j_{33})$, is always positive. Coefficients A_3 and A_4 simplify to, respectively,

$$\frac{e_R f A_E^* G^*}{q_G Q^*} [f Q^* (u B_I q_I A_I + u_E B_E) + u_E B_E v q_G k_Q], \tag{A18a}$$

$$(u B_I A_I^*)(u_E B_E A_E^*)(e_R f^2 G^*) \left(\frac{q_I}{q_G} \right); \tag{A18b}$$

both of these expressions are positive. The last requirement ($A_1 A_2 A_3 > A_3^2 + A_1^2 A_4$) proves too complex for transparent analytical understanding. It may place restrictions on stability that the other conditions have not. The Jacobian matrix that corresponds to the model with a carbon-limited grazer is similar to equation (A17), except that $j_{41} = e f G^*$, while $j_{42} = 0$. In this case, it remains true that A_1, A_3, and A_4 exceed 0, while the fourth criterion defies analytical transparency.

As described in the "Model" section of the text, two grazers cannot coexist with the inedible producer in this model. Either the inedible producer displaces the superior carbon competitor (here, grazer 2) from the grazer coexistence equilibrium or grazer 2 can displace the inedible producer at intermediate resource supply (i.e., meeting eq. [A10]). In terms of assembly rules, this implies that the minimal resource requirement of the inedible producer is less than that produced by the web with one producer and two grazers, $R_I^* < R_{Co}^*$ in the former case, while $R_{Co}^* < R_I^*$ in the latter. Because both available nutrient (R^*) quantities respond to light supply differently (fig. 2B), the rank ordering can switch as light supply increases from low to high levels.

Table A1
Variables and parameters used in the stoichiometrically explicit food web model

Variables, parameters	Unit	Definition	Value[a]
State variables:			
A_E	mg C m^{-3}	Edible autotroph (producer) biomass	…
A_I	mg C m^{-3}	Inedible autotroph (producer) biomass	…
G_j	mg C m^{-3}	Grazer biomass, sp. j	…
Q	mg P (mg C)$^{-1}$	Nutrient content, edible producer	…
Q_I	mg P (mg C)$^{-1}$	Nutrient content, inedible producer	…
R	mg P m^{-3}	Available nutrient	…
t	days	Time	…
Parameters:			
b_E, b_I	μmol photons m^{-2} s^{-1}	Half-saturation constant for light for edible and inedible producers, respectively	36, 100[b]
d_j	day^{-1}	Death rate, grazer sp. j	.07, .05[c]
$e_{C,j}$		Transfer efficiency of carbon, grazer j	.60, .60[d]
$e_{R,j}$		Transfer efficiency of nutrient, grazer j	.60, .60[d]
f_j	day^{-1} (mg C m^{-3})$^{-1}$	Grazing rate, grazer sp. j	.004, .004[e]
k	m^2 (mg C)$^{-1}$	Attenuation coefficient of producer biomass	.0003
k_{bg}	m^{-1}	Background light attenuation coefficient	.25
k_Q	mg P (mg C)$^{-1}$	Minimum nutrient content, edible producer	.004[f]
$k_{Q,I}$	mg P (mg C)$^{-1}$	Minimum nutrient content, inedible producer	.004[f]
L, L_{in}	μmol photons m^{-2} s^{-1}	Incident light intensity	50–1000
q_j	mg P (mg C)$^{-1}$	Nutrient content, grazer sp. j	.04, .08[g]
q_I	mg P (mg C)$^{-1}$	Nutrient content, inedible producer	.04, .08[g]
r_j	day^{-1}	Respiration rate, grazer sp. j	.08, .07
S	mg P m^{-3}	Total nutrient supply	0–20
u_E	day^{-1}	Maximum production rate, edible producer	1.0[f]
u_I	mg C mg P^{-1} day^{-1}	Maximum production rate, inedible producer	.25
v	mg P mg C^{-1} day^{-1}	Nutrient uptake rate, edible producer	.027[f]
v_I	mg P mg C^{-1} day^{-1}	Nutrient uptake rate, inedible producer	.01
z	m	Water column depth	.25
Synthetic quantities:			
$A_{E,j}^*$	mg C m^{-3}	Minimum sequestered carbon requirement, grazer j	…
B_E		Degree of light limitation, edible producer	…
B_I		Degree of light limitation, inedible producer	…
$QA_{E,j}^*$	mg P m^{-3}	Minimum sequestered nutrient requirement, grazer j	…
R_E^*	mg P m^{-3}	Minimum available nutrient requirement, edible producer	…
R_I^*	mg P m^{-3}	Minimum available nutrient requirement, inedible producer	…
R_{Co}^*	mg P m^{-3}	Available nutrient at grazer coexistence	…

[a] Default values. When two values are given, value for sp. 1 is followed by that for sp. 2. Ellipses = not applicable.
[b] Diehl 2002.
[c] Muller et al. 2001.
[d] Loladze et al. 2000.
[e] Slightly less than Grover 2002.
[f] Andersen 1997.
[g] Higher than Andersen 1997.

Table A2
Qualitative response of food web components in the base model
(eqq. [1]) to increases in light (L) and nutrient (S) supply

Architecture, resource[a]	A_E^*	Q^*	QA_E^*	G_j^{*}[b]	A_I^*	R^*
A_E alone (A1):						
$\quad L$	+	−	+	NA	NA	−
$\quad S$	+	0	+	NA	NA	0
A_E-$G_{j,NL}$ (A4):						
$\quad L$	+	−	0	−	NA	−
$\quad S$	−	+	0	+	NA	+
A_E-$G_{j,CL}$ (A7):						
$\quad L$	0	−	−	−	NA	−
$\quad S$	0	+	+	+	NA	+
A_E-G_1-G_2 (A11):						
$\quad L$	0	0	0	−, +	NA	+
$\quad S$	0	0	0	−, +	NA	0
A_E-A_I-$G_{j,NL}$ (A15):						
$\quad L$	+	−	0	−	+	−
$\quad S$	0	0	0	0	+	0
A_E-A_I-$G_{j,CL}$ (A15):						
$\quad L$	0	−	−	−	+	−
$\quad S$	0	0	0	0	+	0

Note: Response determined from calculation of partial derivatives of the corresponding equilibria. See table A1 for definitions of column headings. Plus sign = positive increase, minus sign = negative response, 0 = no response, and NA = not applicable.

[a] "NL" corresponds to cases in which grazers are limited by sequestered nutrients in edible producers; "CL" corresponds to limitation by sequestered carbon. Equations in parentheses refer to the appropriate equilibria.

[b] In the grazer coexistence (A_E-G_1-G_2) case, the first sign corresponds to the superior nutrient competitor (G_1), while the second indicates response of the superior carbon competitor (G_2).

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