Appendix B: 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)

Model Variants: Dynamic Quota of Inedible Producers and Attenuation of Light

In this appendix, we consider two key variations on the main model presented in the text (eqq. [1]). First, we allow the nutrient content (quota) of the inedible producer to respond dynamically. This variant preserved the key findings of the main model. Second, we allow light to attenuate with depth. This version revealed a richer understanding of cascade competition in these stoichiometrically explicit food webs.

Variant 1: Dynamic Quota of the Inedible Producer

The predictions of this model with the inedible producer, A_I, do not change qualitatively when A_I's nutrient quota changes dynamically. To illustrate, the balance equations for A_I, its dynamic nutrient quota, Q_I, and free resources, R, become

$$\frac{dA_I}{dt} = u_I\left(1 - \frac{k_{Q,I}}{Q_I}\right)\frac{L}{b_I + L}A_I - m_I A_I, \tag{B1a}$$

$$\frac{dQ_I}{dt} = v_I R - u_I\left(1 - \frac{k_{Q,I}}{Q_I}\right)\frac{L}{b_I + L}Q_I, \tag{B1b}$$

$$R = S - QA_E - \sum_j q_{G,j}G_j - Q_I A_I, \tag{B1c}$$

where $k_{Q,I}$ is the minimal nutrient quota, b_I is the half-saturation constant for light, and v_I is nutrient uptake rate of the inedible producer. In this case, once A_I invades, its nutrient quota remains at its realized minimum:

$$Q_I^* = \frac{u_I B_I}{u_I B_I - m_I}k_{Q,I}, \tag{B2}$$

where $B_I = L/(b_I + L)$. Otherwise, other qualitative predictions of this revised model (e.g., controls on nutrient content of edible producers, elimination of the superior carbon competitor via cascade competition) remain qualitatively identical to those arriving from analysis of the original model. More specifically, the minimal nutrient requirement of inedible producers, R_I^*, becomes

$$R_I^* = \frac{m_I}{v_I}Q_I^*, \tag{B3}$$

and the equilibrial quantities for the other food web components follow eqq. (A15) (substituting these new values for Q_I^* and R_I^*), except that now

$$A_I = \frac{S - R_I^* - Q^*A_E^* - q_{G,j}G_j^*}{Q_I^*}. \tag{B4}$$

Thus, even when nutrient quota of inedible producers becomes dynamic, inedible producers can still exert partial control on nutrient content of edible producers, and the cascade competition result between inedible producers and the superior carbon competitor, G_2, still remains.

Variation 2: Dynamic Quota of Inedible Producers with Attenuation of Light

A second variation to the food web model modifies the prediction of cascade competition. This second variation more realistically represents light as a unidirectionally supplied resource. If we allow light to attenuate with depth as a result of self-shading by producers and background sources, we can modify the light term for edible and inedible producers, $B_E = L/(b_E + L)$ and $B_I = L/(b_I + L)$, respectively, following Huisman and Weissing's (1995) derivation, where now

$$B_E = \frac{1}{z}\left(\int_{s=0}^{s=z} \frac{L(s)}{b_E + L(s)}\, ds\right) = \frac{\ln\left((b_E + L_{in})/\{b_E + L_{in}\exp[-kz(A_E + A_I) - k_{bg}z]\}\right)}{kz(A_E + A_I) + k_{bg}z}, \tag{B5a}$$

$$B_I = \frac{1}{z}\left(\int_{s=0}^{s=z} \frac{L(s)}{b_I + L(s)}\, ds\right) = \frac{\ln\left((b_I + L_{in})/\{b_I + L_{in}\exp[-kz(A_E + A_I) - k_{bg}z]\}\right)}{kz(A_E + A_I) + k_{bg}z}. \tag{B5b}$$

Both B_E and B_I terms have similar structure. The integral in the left-hand side of both equations tracks attenuation of incoming light, L_{in}, as it passes through a water column at depth s, $L(s)$, following Lambert-Beer's law:

$$L(s) = L_{in}\exp[-k(A_E + A_I)s - k_{bg}s], \tag{B6}$$

where k is the absorption coefficient of producer biomass per unit carbon (here assuming the same coefficient for inedible and edible producers) and k_{bg} captures background light extinction due to nonproducer sources. The $1/z$ term averages the light environment over the water column depth, z. This more realistic representation of light has some benefits and costs. Equation (B5) allows one to vary an ecosystem's light environment in three ways: by changing incident light supply, depth, and background light extinction (Huisman and Weissing 1995). However, this new system cannot be solved analytically, so we simulated it using a standard, adaptive-step numerical integrator (MathWorks 1999).

This model variant, coupled with dynamic representation of the inedible producers' nutrient quota, permits coexistence of the two grazers with both plants. Thus, it adds a more sophisticated view of cascade competition in this system. This result is seen along a light supply gradient at higher nutrient supply (fig. B1). As light supply increases, superior carbon competitor, G_2, first excludes inedible producer, A_I. Then, it coexists with both producers, and later it coexists with both producers and the superior nutrient competitor (grazer 1). With enough light, the inedible producer excludes grazer 2. The key intuition underlying this result is that, over a gradient of incident light supply (L_{in}), inedible producers lose some control over nutrient content (Q) and sequestered nutrient (QA_E) in edible producers and freely available resources, R. This reduced control occurs because inedible producers shade themselves. (This self-shading becomes evident after examining how light at the bottom of the system, L^*_{out}, decelerates with increasing incident light supply. This quantity L^*_{out} emerges from equation (B6) when $s = z$ and producers reach their equilibria; Huisman and Weissing 1995.) Still, enrichment with light continues to promote elimination of the superior carbon competitor (G_2) by the inedible producer via cascade competition. This exclusion still occurs because inedible producers exert some indirect control on nutrient content and sequestered nutrient of edible producers, and hence food quality, for grazer 2. Thus, although the revised model allows both grazers to coexist with the two producers, it still predicts strong influence of inedible producers over composition of grazer assemblages through indirect, stoichiometric pathways.

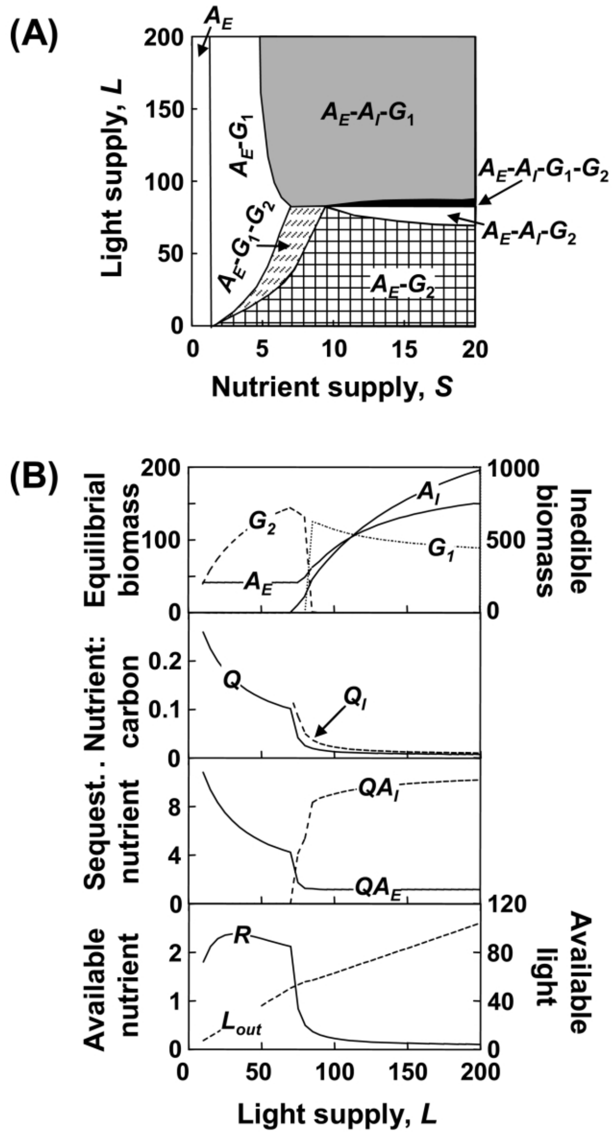

Figure B1: Results from a variation of the food web model that incorporated attenuation of light. *A*, At a narrow range of light supply and higher nutrient supply, this variant permits coexistence of the superior nutrient competitor (G_1), the superior carbon competitor (G_2), the edible producer (A_E), and the inedible producer (A_I), forming the A_E-A_I-G_1-G_2 configuration. This four-species coexistence state is wedged between exclusion of grazer 1 (i.e., the A_E-A_I-G_2 web) at low light and exclusion of grazer 2 (i.e., the A_E-A_I-G_1 web) at high light. *B*, Over a light supply gradient (keeping nutrient supply fixed at $S = 15$), this model variant predicts increasing biomass of both producers, decreasing nutrient : carbon content of both producers, decreasing nutrient sequestered in edible producers but increasing nutrient sequestered in inedible producers, first increasing then decreasing available nutrients, and increasing, but with decelerating increases, available light.