

Stoichiometrically Explicit Competition between Grazers: Species Replacement, Coexistence, and Priority Effects along Resource Supply Gradients

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Submitted December 9, 2003; Accepted April 15, 2004;
Electronically published June 24, 2004

Online enhancements: appendixes.

ABSTRACT: Assuming key trade-offs among interactors, several models (resource ratio, keystone predation, intraguild predation) predict changes in species composition over resource supply gradients. Ecological stoichiometry could also predict compositional shifts of grazers over gradients of nutrient and light supply through a mechanism involving (mis)matches between elemental body composition of grazers and plants. This hypothesis is explored here using a suite of two-grazer, one-plant models that incorporate three key components: plant production depends on light and nutrients, nutrient content of plants can vary, and homeostatic grazers can be carbon or nutrient limited. The results from this suite closely resemble the classical resource ratio model describing plant competition for two resources. Here, the models predict shifts of grazer composition along resource supply gradients if species trade off competitive abilities for plant carbon and nutrients. Given this trade-off, superior nutrient competitors should dominate low nutrient environments, and superior carbon competitors should dominate high nutrient environments. At intermediate nutrient supply, species can coexist at a stable equilibrium, or alternative stable states emerge, depending on how grazers impact their resources. These results depend on food web architecture, however. For instance, predators can alter or reduce possibilities for stoichiometry-mediated coexistence of grazers.

Keywords: competition, coexistence, ecological stoichiometry, priority effects, resource ratio, trade-offs.

Ecologists continue to explore mechanisms that predict and explain changes in species composition along envi-

ronmental gradients. At least three major models predict such shifts. Resource ratio (Tilman 1982; Huisman and Weissing 1995; Grover 1997), keystone predation (Grover 1994; Holt et al. 1994; Leibold 1996), and intraguild predation (Holt and Polis 1997) models each assume key trade-offs among species interactors. For instance, species may differ in ability to compete for resources, such as light and nutrients, ability to resist predation, and ability to eat resource competitors. These trade-offs govern species interactions and determine which species should dominate at various points along gradients of resource supply. They can also permit local coexistence of species at intermediate resource supply or ratio.

Developments in ecological stoichiometry suggest that a fourth model could also explain shifts in species composition over gradients of resource supply, especially in plankton communities. Stoichiometric research to date (Sterner and Elser 2002) suggests that the relative supply of light and nutrients to ecosystems might drive changes in grazer composition through elemental food quality mechanisms. These mechanisms involve three main components. First, light and nutrient supply to (lake) ecosystems may drive variation in phosphorus content of producers (light:nutrient hypothesis; Urabe and Sterner 1996; Sterner et al. 1997; Hessen et al. 2002). Second, grazers are much less plastic in their body composition than are plants (Andersen and Hessen 1991; DeMott et al. 1998), and variation of producer nutrient content can impact growth and population dynamics of grazers (Sterner 1993; Urabe and Sterner 1996; Elser et al. 2001). The magnitude of this impact, however, depends on the size of the mismatch between nutrient content of plants and grazers. In nature, these mismatches may be large because phytoplankton often contain much less nutrients than do zooplankton grazers (Elser et al. 2000). Third, differences in body composition among grazer species may be large as well (Andersen and Hessen 1991; Hall et al., in press). When plants contain low nutrients, grazing by taxa with high nutrient content may become nutrient lim-

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ited and inefficient. However, at least for phosphorus, the benefit of high nutrient content may lie in a maximal growth rate advantage over lower nutrient grazers when food quality is good (Elser et al. 1996; Main et al. 1997).

When combined, these three components suggest that grazers that vary in body composition may perform differently along gradients of resource supply. In ecosystems with low nutrient supply relative to light supply, poor food quality may prevent high phosphorus grazers (e.g., *Daphnia*) from dominating grazer assemblages. In these environments, species with lower phosphorus demands may instead dominate. In contrast, ecosystems with high nutrient supply relative to light supply are presumed to produce nutrient-rich food for grazers. In these environments, phosphorus-rich grazers could dominate assemblages because of their growth rate advantage over less phosphorus-rich species.

A suite of simple models shows that these stoichiometric mechanisms predict shifts in grazer composition and coexistence or alternative stable states over gradients of resource (nutrient and light) supply. These outcomes closely resemble those of resource ratio models (Tilman 1982; Grover 1997), although here they apply to a higher (grazer) trophic level. Like in resource ratio models, the outcomes hinge on a trade-off for abilities to compete for two resources: plant carbon and sequestered nutrient. However, these two resources are packaged within the same species (the plant). I also explore how competition among grazers within a regional species pool can reduce variation in plant stoichiometry over broad resource gradients and how predators can alter competitive outcomes.

Theory

The model suites all use Lotka-Volterra-like predator-prey models as a basic structure. However, these models all contain three important components of stoichiometric theory (Andersen 1997; Loladze et al. 2000, 2004; Muller et al. 2001). First, primary production depends on light and a nutrient (indirectly, via nutrient content). Second, nutrient content of the producer varies (following the variable stores/Droop formulation), but otherwise grazers readily eat the plant. Third, grazers have fixed nutrient content and can switch from nutrient to carbon limitation. The base model is a variation on a similar model of stoichiometrically explicit grazer competition (Loladze et al. 2004). Here, the Type I functional response of the grazers simplifies the model dynamics and yields analytically tractable insights. Using this model, I also consider competition in a regional species regional pool. Later, I change or relax two main assumptions in this model (involving respiration rate and dynamics of nutrient content of

plants), and I include predation as a factor potentially impacting grazer competition.

Base Model and Regional Species Pools

In the base model, two grazers eat a single producer following a system of ordinary differential and algebraic equations (see also tables 1, 2):

$$\frac{dA}{dt} = u \left(1 - \frac{k_Q}{Q} \right) \left(\frac{L}{b + L} \right) A - A \sum_j f_j G_j, \quad (1a)$$

$$\frac{dG_j}{dt} = e_j \min \left(1, \frac{Q}{q_j} \right) f_j A G_j - d_j G_j, \quad (1b)$$

$$Q = \frac{S - \sum_j q_j G_j}{A}, \quad (1c)$$

where $\min(\dots)$ indicates the minimum of the arguments. The autotroph producer (A) balance equation (eq. [1a]) combines the net effect of primary production and grazing. Producer productivity is a multiplicative function of both nutrients and light (Huisman and Weissing 1995) multiplied by a maximal growth rate (u). Nutrient uptake follows the variable stores formulation (Grover 1997), producer nutrient content (Q) varies, and per capita productivity increases monotonically as Q exceeds a minimal nutrient content, k_Q . I also assume that producers can consume all available nutrients in an ecosystem. In equation (1c), producers use all ecosystem nutrients (S) not already contained in j grazers ($\sum q_j G_j$; see also Loladze et al. 2000, 2004; Muller et al. 2001). This unrealistic assumption simplifies the analysis because it algebraically represents Q , but a modified version loosens this assumption below. This structure (eq. [1c]) implicitly includes nutrient recycling and follows a mass balance constraint (Grover 1997). Producers use incident light (L) in a Monod fashion, in which b is the half-saturation constant. Below, the more compact substitution $\beta \equiv L/(b + L)$ reflects the degree of light saturation of plant growth. More complex representations of the light component exist (see "Discussion"), but this form maintains analytical tractability. Additionally, producers lose biomass through herbivory by grazers (G_j) that feed according to a Type I functional response at rate f_j .

In the grazer balance equations (eq. [1b]), growth rate of grazer j is the net sum of production from feeding and density-independent losses (d_j , which could equal the sum of respiration, r_j , and death, δ_j). In this base model, it is physiologically most realistic to ignore respiration to prevent a nutrient-limited grazer from respiring nutrient

Table 1: Variables and parameters used in competition models

Variables/parameters	Units	Definition	Value ^a
State variables:			
A	$\mu\text{g C L}^{-1}$	Edible autotroph (producer, plant) biomass	...
G_j	$\mu\text{g C L}^{-1}$	Grazer biomass, sp. j	...
Q	$\mu\text{g P } (\mu\text{g C})^{-1}$	Nutrient content, plant	...
R	$\mu\text{g P L}^{-1}$	Available nutrient	...
t	days	Time	...
Parameters:			
b	$\mu\text{mol photons m}^{-2} \text{ s}^{-1}$	Half-saturation constant for plant, light	36^b
δ_j	day^{-1}	Death rate, grazer sp. j	.07, .05 ^c
d_j	day^{-1}	Combined loss rate of grazer j ($\delta_j + r_j$)	.15, .10 ^c
e_j	...	Transfer efficiency of grazer j	.80, .80 ^d
f_j	$\text{day}^{-1} (\mu\text{g C/L})^{-1}$	Grazing rate, grazer sp. j	.004, .004 ^e
h	$\mu\text{g P L}^{-1}$	Saturation constant for edible plant	1.4 ^f
k_Q	$\mu\text{g P } (\mu\text{g C})^{-1}$	Minimum nutrient content, edible plant	.004 ^f
L	$\mu\text{mol photons m}^{-2} \text{ s}^{-1}$	Incident light intensity	50–1,000
q_j	$\mu\text{g P } (\mu\text{g C})^{-1}$	Nutrient content, grazer sp. j	.04, .08 ^g
r_j	day^{-1}	Respiration rate, grazer sp. j	.08, .07
S	$\mu\text{g P L}^{-1}$	Total nutrient supply	0–30
u	day^{-1}	Maximum specific production rate	1.0 ^f
v_{\max}	$\mu\text{g P } \mu\text{g C}^{-1} \text{ day}^{-1}$	Maximum specific nutrient uptake rate	.027 ^f
Substitutions/compound parameters:			
A_j^*	$\mu\text{g C/L}$	Minimal carbon requirement, grazer sp. j	...
β	...	Degree of light saturation, $L/(b + L)$...
λ_j	...	Predation : other loss rates, CLG sp. j (eq. [13])	...
η_j	...	Predation : other loss rates, NLG sp. j (eq. [13])	...
QA_j^*	$\mu\text{g P/L}$	Minimal nutrient requirement, grazer sp. j	...

Note: Respiration rate was implicitly 0 in the base model (E. Muller, personal communication). CLG = carbon-limited grazer; NLG = nutrient-limited grazer.

^a Default values: parameters for sp. 1 are followed by those for sp. 2.

^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.

(hence, $r_j = 0$, and d_j is only death rate). Grazer production depends on its feeding rate (f_j) but also on the efficiency at which it converts producer biomass into its own. This efficiency reflects the relative imbalance between Q and (homeostatic) nutrient content of the grazer, q_j (Loladze et al. 2000; this representation is modified below). Nutrient-rich plants yield a carbon-limited grazer and maximal conversion efficiency (at e_j) when $Q > q_j$, while nutrient-poor plants generate nutrient limitation when $Q < q_j$ and lower efficiency to $e_j q_j$.

Single-Grazer Case. I first examine behavior of the single-grazer plant system. This system depends on the grazer's niche, that is, how it responds to and impacts its resources, as captured by nullclines and impact vectors, respectively (Leibold 1995; Grover 1997), and a system nutritional con-

straint. The plant provides two niche dimensions for the grazer. In plant-sequestered nutrient (QA)-carbon (A) phase space, the grazer's nullcline becomes

$$A = \frac{d}{ef}, \quad QA = \frac{dq}{ef}. \quad (2)$$

This elbow-shaped grazer nullcline has two legs (eq. [2]; fig. 1A). In the vertical section, the grazer is carbon limited. In traditional models, this section would typically intersect the A -axis. However, here the grazer nullcline bends horizontally in A - QA space as the grazer becomes nutrient limited (fig. 1A). At the intersection of both segments, the grazer is perfectly colimited by A and QA because the plant just meets the minimal sequestered carbon (A^*) and nutrient (QA^*) requirements of the grazer. These two key

Table 2: Some assumptions of the suite of stoichiometrically explicit competition models

Assumptions	Results for model structure
System closed to nutrients and migrants but is open to carbon and light	Obviates a nutrient ODE; allows mass balance constraint construction
Nutrients are instantaneously recycled from dead plants and grazers	Obviates a detrital ODE
Grazer nutrient content is fixed	Constant parameter for grazer nutrient content
Producers use all available phosphorus in the ecosystem	Represent changes in producer nutrient content with an algebraic equation rather than an ODE (relaxed in modification 3)
System nutrients and biomass are mixed homogeneously	ODEs are a reasonable formulation; mass action is acceptable for grazing
Extinction of light in the water column is negligible	Simple Monod term instead of Huisman and Weissing (1995) formulation; no depth or background extinction
Light-nutrient kinetics are interactive-essential	Multiplicative Droop \times Monod specific production (i.e., no minimum function as in Loladze et al. 2000, 2004)
Parameters and environment do not change in time	Autonomous ODE construction

quantities, determined solely by grazer traits, are analogous to R^* traits in classical resource competition theory (Tilman 1982; Grover 1997). Furthermore, they become crucial in grazer competition below. The second niche component involves the grazer's impact on its resources (carbon and nutrient packaged in the plant). The grazer's per capita impact on A is its feeding rate (f), while its per capita impact on QA is q (eqq. [1]). Thus, the slope of the impact vector on Q is q/f (fig. 1B). These vectors weigh critically on outcomes of grazer competition.

The system nutritional constraint (SNC) provides important information about the grazer equilibrium. The SNC arises from the plant nullcline, which is

$$QA = A \left(\frac{k_Q u \beta}{u \beta - f G} \right). \quad (3)$$

When solved for QA , this nullcline cannot locate equilibria in A - QA space because it must be evaluated and plotted with an equilibrated solution of G . Nonetheless, its intersection with the grazer nullcline in A - QA space indicates nutrient or carbon limitation of the grazer (fig. 1A). Furthermore, its slope reflects the plant's nutrient : carbon ratio at equilibrium. The SNC is a system property because it depends not only on plant biomass and traits but also on grazer biomass and traits and resource supply.

If the SNC intersects the nutrient-limited leg of the grazer nullcline, a nutrient-limited, single-grazer equilibrium emerges:

$$A^* = \frac{1}{k_Q} \left[QA^* + u \beta \left(\frac{d}{e} \right) (QA^* - S) \right], \quad (4a)$$

$$G^* = \frac{1}{q_j} (S - QA^*), \quad (4b)$$

$$Q^* = \left\{ \frac{1}{k_Q} \left[\frac{f}{q u \beta} (QA^* - S) + 1 \right] \right\}^{-1}. \quad (4c)$$

This single-grazer equilibrium is feasible ($A^* > 0$, $G^* > 0$) when nutrient supply, S , exceeds QA^* , the minimal sequestered nutrient requirement of the nutrient-limited grazer (fig. 1C). At this equilibrium, plant biomass (A^*) decreases, and grazer biomass (G^*) and plant nutrient content (Q^*) increase with increasing nutrient supply (fig. 1D). Additionally, A^* increases, but Q^* decreases with increasing degree of light saturation, β (eqq. [4]).

Once a resource limitation threshold is reached, the grazer becomes carbon limited because nutrient content of plants equals that of the grazer ($Q^* = q$). This threshold occurs at

$$S = QA^* + \frac{u \beta (q - k_Q)}{f}, \quad (5)$$

which is a positive function of the degree of β (fig. 1C). Past this threshold, the SNC intersects with the vertical section of the grazer nullcline (fig. 1A). Thus, a carbon-limited, single-grazer equilibrium arises:

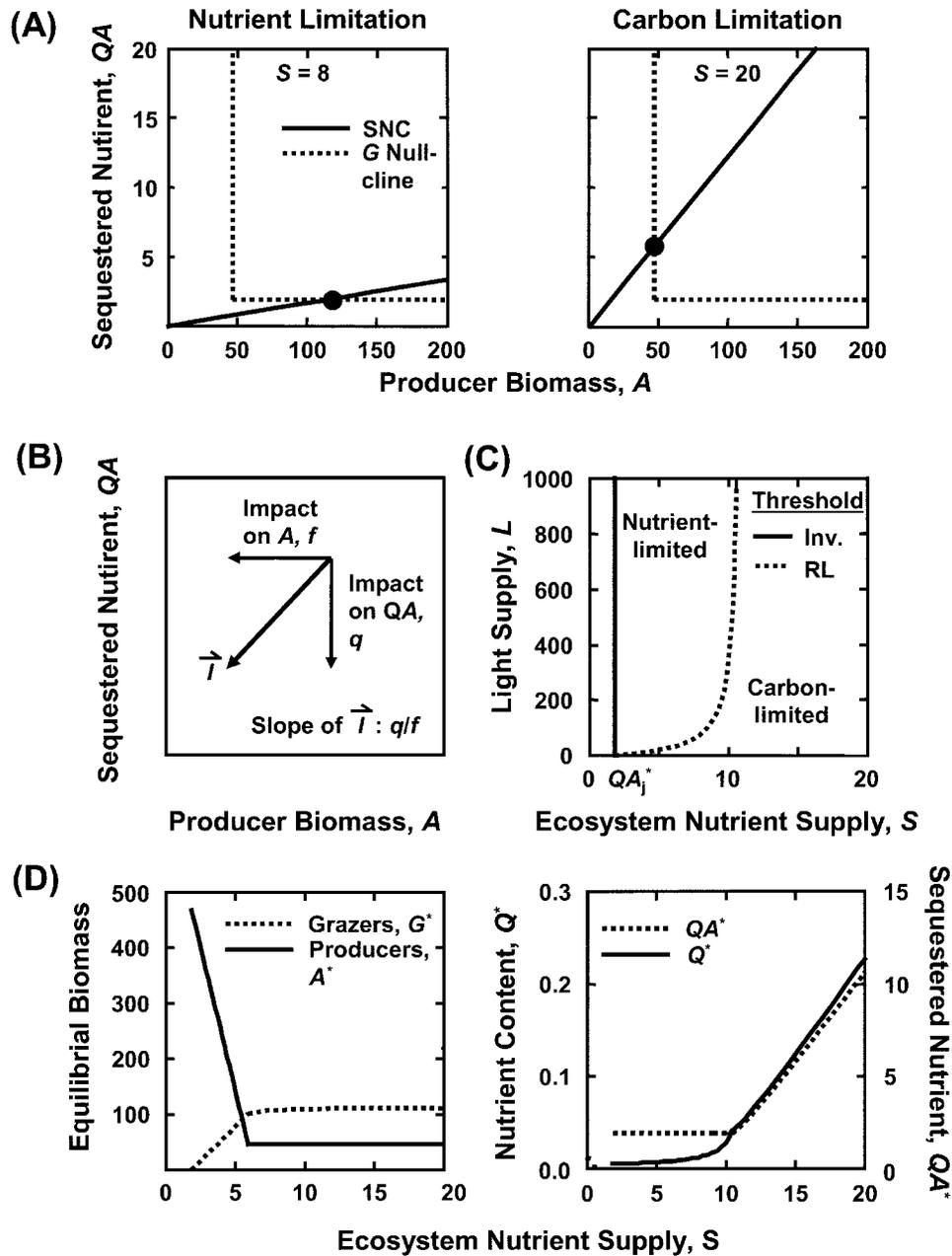


Figure 1: Components of the single-grazer case. *A*, Grazer nullcline is L shaped in producer carbon (A)-sequestered nutrient (QA) phase space. The grazer is carbon limited in the vertical section and nutrient limited in the horizontal section. At equilibrium, the system nutritional constraint (SNC) intersects with the nutrient-limited or carbon-limited section of the grazer nullcline. The SNC's slope reflects the plant's nutrient content. *B*, Grazer's impact vector (\vec{T}) contains two components: the per capita impact of grazers on QA , q , and their per capita impact on A , f . *C*, Nutrient-limited grazer can invade a plant-only ecosystem if nutrient supply exceeds the grazer's minimal nutrient requirement, QA^* , the invasion (*Inv.*) threshold. The grazer becomes carbon limited as S increases past the resource limitation (*RL*) threshold. *D*, Once a nutrient-limited grazer can persist, equilibrial plant biomass (A^*) decreases while grazer biomass (G^*) and plant nutrient content (Q^*) increase with increasing S , assuming constant L . Sequestered nutrient is locked at the grazer's QA^* until the grazer becomes carbon limited. Once carbon limited, grazer's A^* fixes plant biomass, while G^* , QA^* , and Q^* increase with S . Parameters are as in table 1, with $L = 750$.

$$G_j^* = \frac{S}{2q} + \frac{u\beta}{2f} - \frac{C_{CL}}{2ef^2q}, \quad (6a)$$

$$Q^* = \frac{ef^2S - qu\beta + C_{CL}}{2df}, \quad (6b)$$

where

$$C_{CL} = \{ef^2[4q(dk_Q - efs)u\beta + e(fs + qu\beta)^2]\}^{1/2}. \quad (6c)$$

At this stable equilibrium, plant biomass rests at the minimal sequestered carbon requirement of the grazer, A^* (see also app. A in the online edition of the *American Naturalist* for stability analysis). Plant nutrient content, sequestered nutrient, and grazer biomass are positive functions of S when the grazer is carbon limited (fig. 1D). Additionally, G^* increases and Q^* and QA^* decrease with increasing degree of β (eqq. [6]).

Two-Grazer Case. In a system with two grazers, potential coexistence (or alternative stable states) can emerge because the elbow-shaped grazer nullclines can intersect (fig. 2). This intersection requires a trade-off in the minimal resource requirements (A_j^* and QA_j^*), and hence competitive abilities, of the grazers. In the example developed here, this trade-off occurs when grazer 1 (G_1) is a superior nutrient competitor ($QA_1^* < QA_2^*$) but grazer 2 (G_2) is a superior carbon competitor ($A_2^* < A_1^*$; fig. 2). When the SNC crosses the intersection point of grazer nullclines, a feasible two-grazer equilibrium emerges. However, this equilibrium's stability depends on the grazers' relative impacts on A and QA . Thus, four outcomes arise in this one-plant, two-grazer system. The superior nutrient competitor always displaces the superior carbon competitor at low nutrient supply. In this situation, the SNC intersects with the nutrient-limited (horizontal) portions of both grazers' nullclines (fig. 2A). Thus, G_1 displaces G_2 because it requires less sequestered nutrient. At high nutrient supply, the SNC intersects with the carbon-limited (vertical) portions of both grazer nullclines (fig. 2B). Here, G_2 wins because it can depress plant carbon below G_1 's minimal carbon requirement.

At intermediate nutrient supply, the SNC can intersect with the carbon-limited section of G_1 's nullcline and the nutrient-limited section of G_2 's nullcline (fig. 2C, 2D). Thus, a two-grazer equilibrium is feasible:

$$A^* = A_1^*, \quad (7a)$$

$$G_1^* = \frac{1}{f_1q_2 - f_2q_1} \left[f_2(QA_2^* - S) + u\beta q_2 \left(1 - \frac{A_1^*}{QA_2^*} k_Q \right) \right], \quad (7b)$$

$$G_2^* = \frac{1}{f_1q_2 - f_2q_1} \left[f_1(S - QA_1^*) - u\beta q_1 \left(1 - \frac{A_1^*}{QA_2^*} k_Q \right) \right], \quad (7c)$$

$$Q^* = \frac{QA_1^*}{A_1^*}, \quad (7d)$$

where A_j^* and QA_j^* are the minimum sequestered carbon and nutrient requirements of grazer j , respectively. At this equilibrium, each grazer is limited by the resource at which it is the inferior competitor. Equilibrium plant carbon, A^* (eq. [7a]), rests at G_1 's minimal carbon requirement. Similarly, QA^* is set at G_2 's minimal sequestered nutrient requirement (QA_2^* , given eq. [7a], [7d]). As in classical resource competition theory (Tilman 1982; Grover 1997), this equilibrium is stable if each grazer has a larger relative impact on the resource limiting its own growth than its competitor (i.e., $f_1/q_1 > f_2/q_2$), and it is a saddle otherwise (fig. 2C, 2D; see app. A).

When a two-grazer equilibrium is feasible and stable, the complete behavior of this stoichiometrically explicit grazer competition system can be delineated by five key functions of resource supply (see app. A for details). First, nutrient supply must exceed the minimal sequestered nutrient requirement of G_1 (invasion criterion a in fig. 3). Before G_2 can invade the species one plant-only ecosystem, G_1 becomes carbon limited (at resource limitation threshold b in fig. 3A). Once G_1 is carbon limited, G_2 can invade the single-grazer equilibrium (at invasion threshold c in fig. 3A). When resource supply meets this invasion threshold, the two-grazer equilibrium (eqq. [7]) becomes feasible. However, as nutrient supply increases further yet, G_2 displaces G_1 (at invasion threshold e in fig. 3A). At this point, G_2 remains nutrient limited. Therefore, as nutrient supply increases more, G_2 eventually becomes carbon limited (at resource limitation threshold d in fig. 3A). When the two-grazer equilibrium is unstable, these key thresholds still exist, but some are encountered in a different order along a gradient of nutrient supply (fig. 3B).

Resource supply, then, greatly influences species coexistence and turnover. For instance, the grazers can coexist over a larger nutrient supply gradient at higher light than at lower light (fig. 3A). In a system with a feasible two-grazer equilibrium, species composition shifts are guaranteed (from superior nutrient competitor to superior carbon competitor) over a sufficiently large gradient of nutrient supply. However, at a given nutrient supply, shifts in grazer composition are not guaranteed over a gradient of light supply. As shown elsewhere (app. A), the invasion/feasibility thresholds of the two-grazer equilibrium ap-

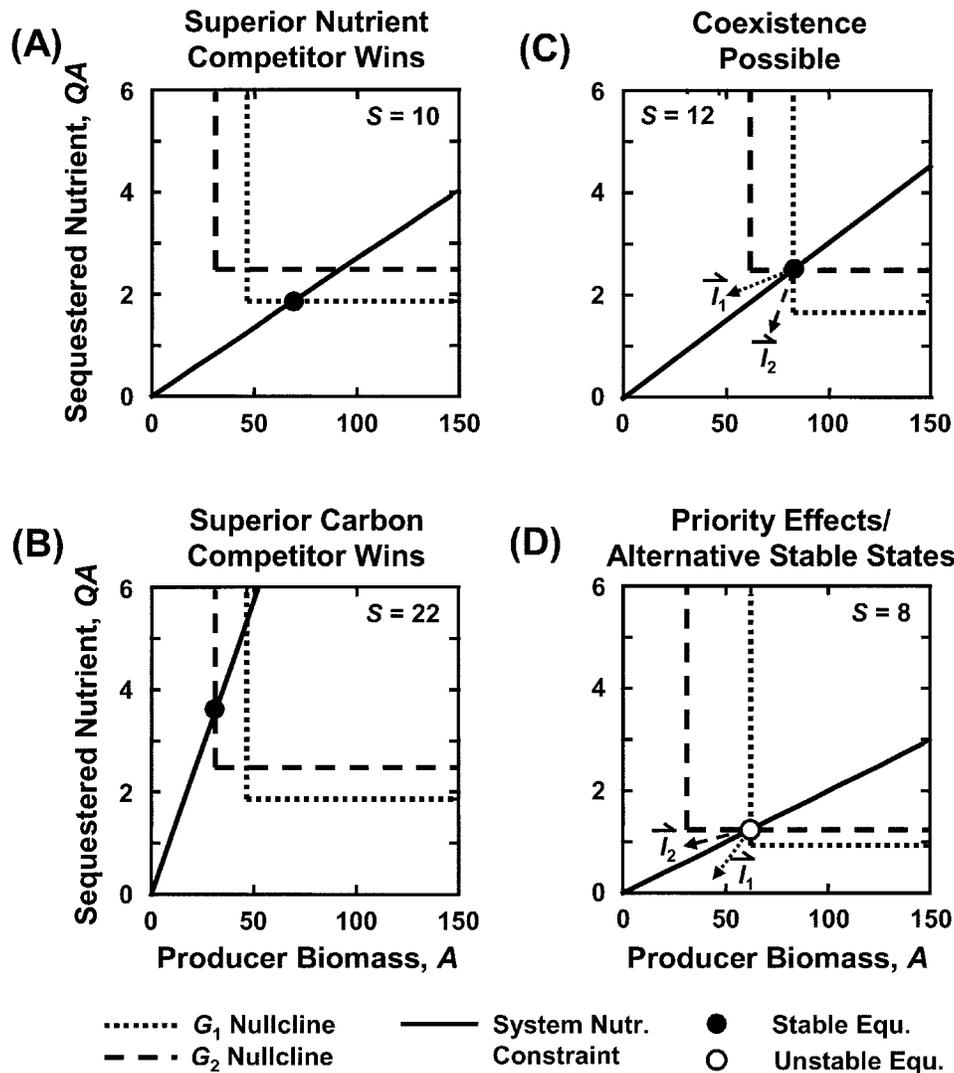


Figure 2: Four outcomes of grazer competition depend on intersection of grazer nullclines with the system nutritional constraint (SNC) and the grazers' impact vectors. Assuming a trade-off in minimal nutrient (QA_1^*) versus minimal carbon requirements (A_1^*) of the grazer, at low nutrient supply (A), the SNC intersects with the nutrient-limited (horizontal) segments of both grazers' nullclines. The superior nutrient competitor (G_1) displaces the superior carbon competitor (G_2) because it has a lower QA_1^* . B, At high nutrient supply, G_2 displaces G_1 because the SNC intersects with the carbon-limited (vertical) sections of both grazers' nullcline. C, At intermediate nutrient supply, stable grazer coexistence is feasible because the SNC intersects with both grazer's nullclines at a single equilibrium. Note that G_1 is carbon limited and G_2 is nutrient limited at this equilibrium. The equilibrium is stable because each grazer consumes more of the resource limiting it than does its competitor (on the basis of the slopes of the impact vectors, I_j). D, With different grazer traits ($q_1 = 0.02$, $q_2 = 0.04$, $f_2 = 0.004$, $e_2 = 0.6$, $d_1 = 0.10$, $d_2 = 0.15$), alternative stable states (priority effects) occur when SNC and grazer nullclines meet at an unstable two-grazer equilibrium. Each grazer here has a larger impact on the resource limiting its competitor. Except where indicated, other parameters follow table 1, with $L = 750$. Impact vectors are exaggerated for visual clarity.

proach asymptotes at particular nutrient supplies. Consequently, if nutrient supply exceeds the upper asymptote, the superior carbon competitor cannot be displaced, regardless of light supply. (This result might be relaxed if light extinction was explicitly modeled, perhaps following Huisman and Weissing [1995]). Assuming the resource gradient starts before this upper asymptote, species com-

position shifts can occur even at constant light : nutrient ratio (i.e., along a line with constant slope L/S in fig. 3A). Thus, shifts in species composition do not require changes in light : nutrient ratio.

Notably, grazers with high nutrient content can have lower minimal nutrient requirements than grazers with lower nutrient content. Thus, the high-nutrient grazer can

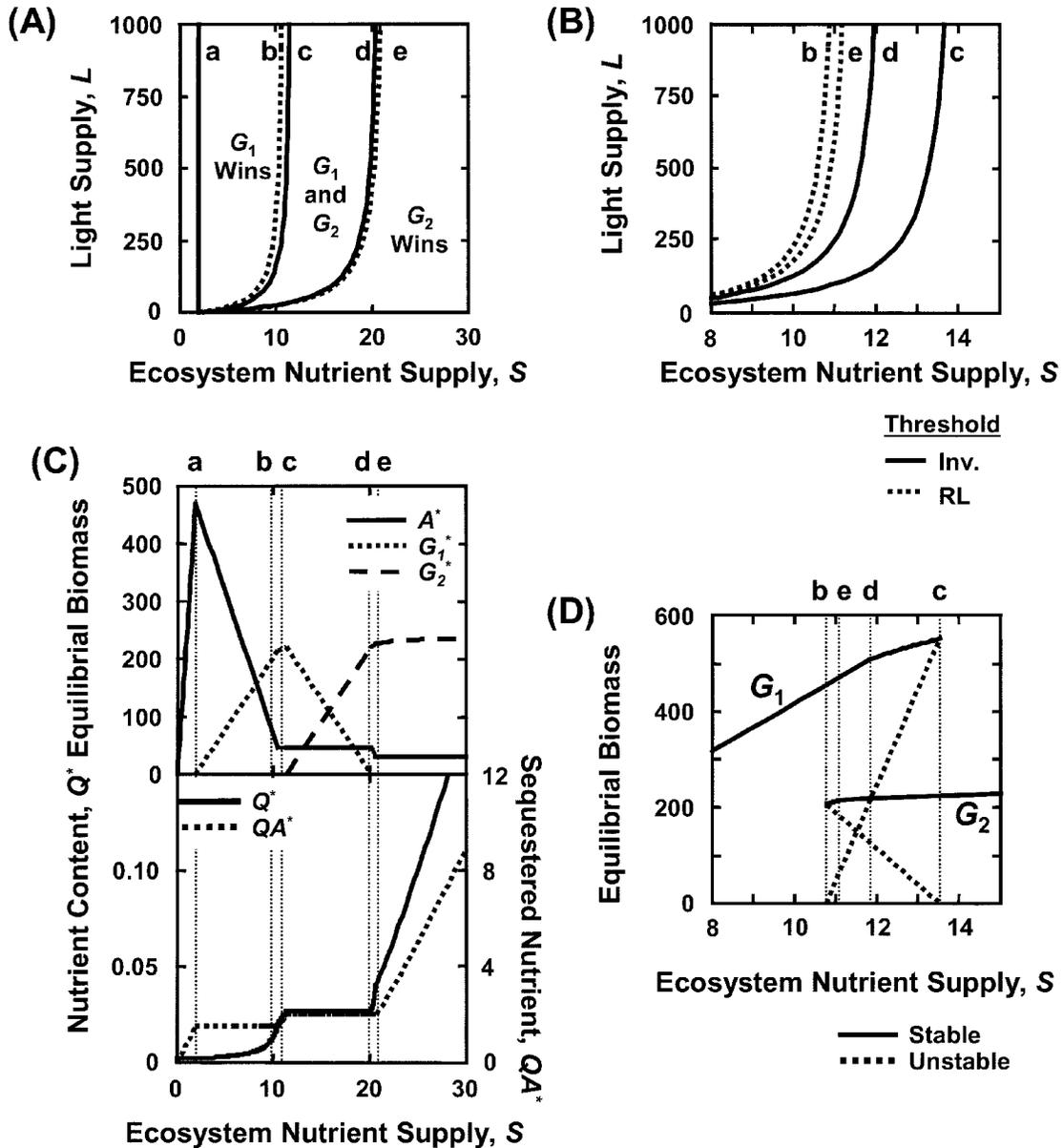


Figure 3: Coexistence, priority effects, and species replacement over resource supply gradients. *A*, Five key thresholds delineate outcomes of grazer competition when the two-grazer equilibrium is stable. Along an increasing nutrient supply gradient, these thresholds move from the boundary invasion/feasibility (*Inv.*) threshold (*a*) of the superior nutrient competitor (G_1), to the resource limitation (*RL*) threshold (*b*) of G_1 , to the interior invasion/feasibility threshold (*c*) of the superior carbon competitor (G_2), to the interior invasion/feasibility threshold (*d*) of G_1 , to finally, the *RL* threshold (*e*) of G_2 . *B*, When the two-grazer equilibrium is a saddle, some of the thresholds are encountered in a different order. Most important, the interior invasion/feasibility thresholds of G_1 and G_2 are reversed. Also, here G_2 becomes carbon limited (past its *RL* threshold) before the interior invasion/feasibility thresholds are encountered. *C*, At constant light ($L = 750$), replacement and coexistence of grazers impact partitioning of biomass and nutrients among trophic levels. *D*, When grazer traits promote alternative stable states, only one grazer can persist at intermediate nutrient supply, but the unstable two-grazer equilibrium (a saddle) introduces priority effects between thresholds *b* and *c*. In *B* and *D*, grazer parameters are $q_1 = 0.02$, $q_2 = 0.04$, $f_2 = 0.004$, $e_2 = 0.6$, $d_1 = 0.10$, $d_2 = 0.15$; other parameters follow table 1.

win competition for low-nutrient food. This result arises because nutrient content of a grazer (q_j) comprises only one component of its minimal nutrient requirement. Hence, if grazer 1 has higher nutrient content than grazer 2 ($q_1 > q_2$), it can still compete superiorly for nutrients ($QA_1^* < QA_2^*$) if $q_1/q_2 < A_2^*/A_1^*$. However, because $q_1/q_2 > 1$, such a superior nutrient competitor must also compete superiorly for carbon (i.e., $A_1^* < A_2^*$ so that $A_2^*/A_1^* > 1$ also). Consequently, the superior nutrient competitor must have lower nutrient content than the superior carbon competitor if coexistence and species replacement of grazers are possible. This constraint gets relaxed below (see “Modification 1”). Incidentally, coexistence requires that the traits q_j and A_j^* do not differ too much among species to ensure that $q_1/q_2 < A_2^*/A_1^*$.

The possibility of grazer coexistence also changes allocation of biomass and nutrients among plants and grazers. When grazers coexist, A^* , Q^* , and QA^* are insensitive to changes in light supply/saturation because they are determined solely by A_j^* and QA_j^* demands of the grazers (see two-grazer equilibrium, eqq. [7]; fig. 3C). Thus, when they stably coexist, nutrients and biomass are mainly shifted between the two grazers (eqq. [7]; fig. 3C): as nutrient supply increases (at a given light supply), nutrients and biomass are increasingly sequestered in the superior carbon competitor. When unstable, the two-grazer equilibrium is a saddle that creates alternative stable states (and priority effects) for the grazers between the grazers’ resource limitation thresholds (fig. 3D). Thus, grazer biomass can be either higher (at G_1^*) or lower (at G_2^*) at intermediate resource supply (fig. 3D).

Once G_2 becomes carbon limited after having displaced the superior nutrient competitor, a species with a lower minimal carbon requirement can invade (fig. 4). If the regional species pool contains species $j = 1, 2, 3, 4, \dots, N-1, N$ with traits arranged as $A_1^* > A_2^* > A_3^* > A_4^* > \dots > A_{N-1}^* > A_N^*$ but $QA_1^* < QA_2^* < QA_3^* < QA_4^* < \dots < QA_{N-1}^* < QA_N^*$, an extended base model predicts species replacement patterns of G_1 alone, potential coexistence of G_1 and G_2 , G_2 alone, potential coexistence of G_2 and G_3 , G_3 alone, ..., G_{N-1} alone, potential coexistence of G_{N-1} and G_N , and, finally, G_N alone (fig. 4). In the resource supply range permitting coexistence of G_1 and G_2 to G_{N-1} and G_N , the model predicts an overall decrease in equilibrium plant biomass from A_1^* to A_{N-1}^* , an increase in sequestered nutrients in plants from QA_2^* to QA_N^* , and an increase in plant nutrient content from less than QA_2^*/A_1^* to greater than QA_N^*/A_{N-1}^* (fig. 4B). If differences in QA_j^* and A_j^* appear small in this replacement series $j = 1 \dots N$, this regional version of the base model predicts that shifts in composition of grazers may reduce variation in the plant’s biomass, nutrient content, and sequestered nutrient over

very broad gradients of resource supply as compared with single-grazer situations (figs. 3, 4).

Modification 1: Grazer Respiration

The grazer balance equation (eq. [1a]) in the base model can contain a hidden assumption: if the loss rate term includes respiration, the grazer respire carbon but also nutrients. An alternative representation separates respiration rate (r_j) from death rate (δ_j) in the grazer equation’s minimum function (Sterner 1997; E. McCauley and R. Nisbet, unpublished manuscript; but see “Discussion”). The grazer balance equation becomes

$$\frac{dG_j}{dt} = \min\left(e_j f_j A - r_j, e_j f_j A \frac{Q}{q_j}\right) G_j - \delta_j G_j. \quad (8)$$

In this modified equation, the grazer becomes carbon limited when

$$q_j \left(1 - \frac{r_j}{e_j f_j A}\right) < Q. \quad (9)$$

Thus, the threshold between nutrient and carbon limitation is a function not only of the elemental imbalance between grazer and plant (Q/q_j), as in the base model, but also feeding rate (f_j), respiration rate (r_j), and maximal conversion efficiency (e_j) of grazer j and A . (One could also add more detail by including different conversion efficiencies for carbon and nutrient.) This grazer remains carbon limited when feeding on plants with lower Q than the grazer in the base model (eqq. [1]).

This modification mainly yields only quantitative nuance to competition among grazers. The new grazer equation yields different minimal sequestered carbon and nutrient demands:

$$A_j^* = \frac{\delta_j + r_j}{e_j f_j}, \quad QA_j^* = \frac{\delta_j q_j}{e_j f_j}, \quad (10)$$

respectively. If respiration was ignored in the base model, the new minimal carbon requirement of grazer j (A_j^*) exceeds that of the base model, but minimal nutrient requirement does not change. Regardless, one can readily show that outcomes of competition in this modified model qualitatively resemble those in the base model. However, this version does permit species coexistence even when G_1 has higher nutrient content than G_2 if $q_1/q_2 < [A_2^* - r_2/(e_2 f_2)]/[A_1^* - r_1/(e_1 f_1)]$. Thus, a trade-off of $QA_j^* - A_j^*$ traits does not require positive correlation between q_j and QA_j^* .

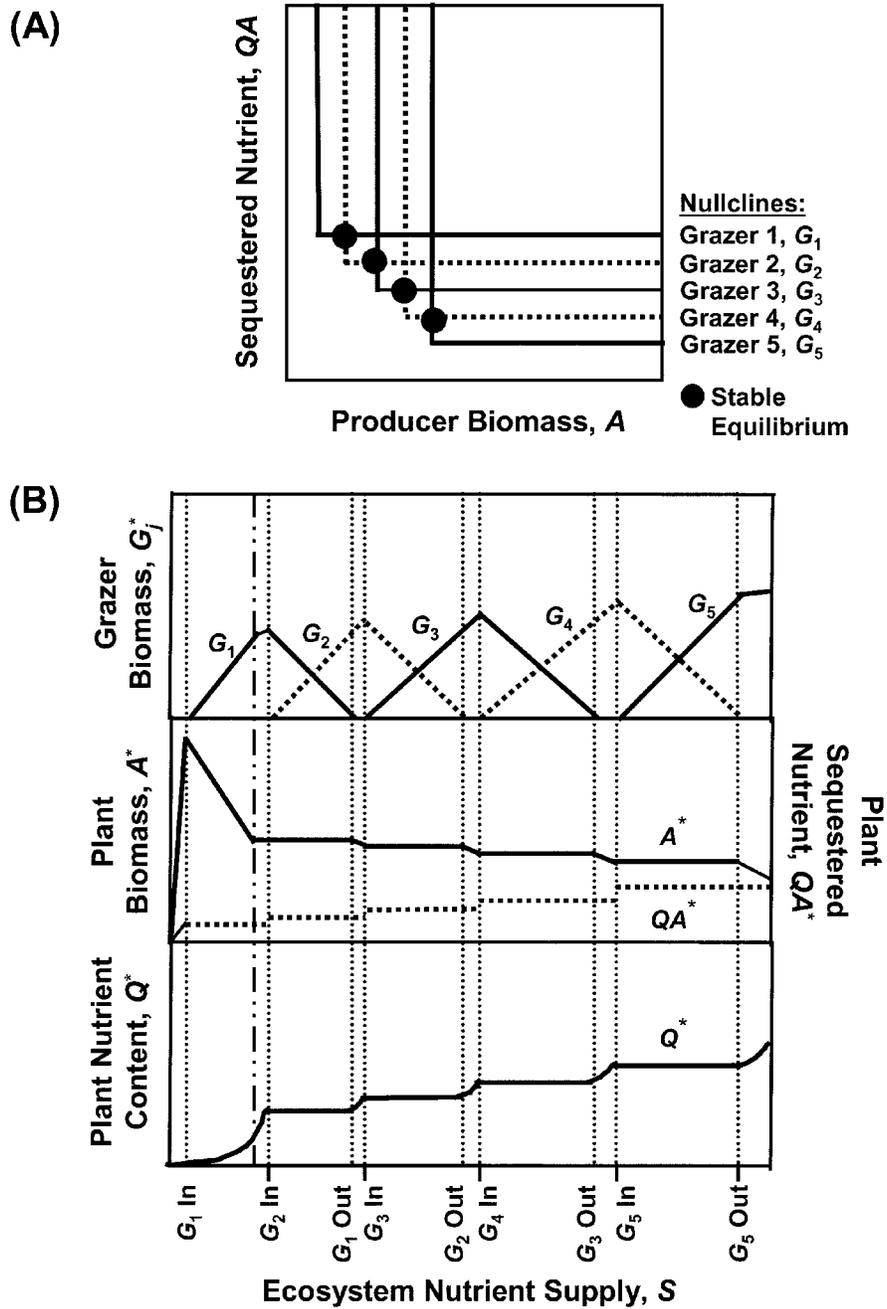


Figure 4: Qualitative outcomes of grazer competition in ecosystems with a large regional species pool exhibiting trade-offs in minimal sequestered nutrient (QA_j^*) and carbon (A_j^*) requirements. A, Possible stable equilibria for grazers as determined by intersections of nullclines in A - QA space. B, Composition of grazer assemblages shifts from relatively good nutrient competitors to relatively good carbon competitors over a nutrient gradient (keeping light supply constant). Winners of competition must become carbon limited before another grazer can invade. This illustration assumed that grazer coexistence was stable at each pairing.

Modification 2: Predation on Grazers

Predation on grazers can influence this $QA_j^* - A_j^*$ trade-off, however. To illustrate, I couple the plant equation (eq. [1a]) with modified grazer and plant nutrient content equations:

$$\frac{dG_j}{dt} = \min\left(e_j f_j A - r, e_j f_j A \frac{Q}{q_j}\right) G_j - \delta_j G_j - f_{P,j} P \quad (11a)$$

$$Q = \frac{S - \sum_j q_j G_j - q_P P}{A}, \quad (11b)$$

respectively, to include a predator held at constant biomass, P . (The assumption provides analytical convenience here but could represent a managed P population or one whose dynamics are much slower than grazer-plant dynamics; e.g., Scheffer et al. 2000.) This predator feeds on grazer j at rate $f_{P,j}$ and it has nutrient content q_P but does not itself become nutrient limited. Adding a predator changes the minimal carbon and nutrient requirements of the grazer to

$$A_{j,P}^* = A_j^* + A_j^* \left(\frac{f_{P,j}}{\delta_j + r_j} \right) P = A_j^* + A_j^* \lambda_j P \quad (12a)$$

$$QA_{j,P}^* = QA_j^* + QA_j^* \left(\frac{f_{P,j}}{\delta_j} \right) P = QA_j^* + QA_j^* \eta_j P \quad (12b)$$

where

$$\lambda_j \equiv \frac{f_{P,j}}{\delta_j + r_j}, \quad \eta_j \equiv \frac{f_{P,j}}{\delta_j}. \quad (13)$$

As P increases, the new minimal carbon requirement with a predator ($A_{j,P}^*$) increases linearly from the no-predator minimal carbon requirements (A_j^*) with a slope of $\lambda_j A_j^*$. Here, λ_j for a carbon-limited grazer is the ratio of loss rates of grazers as a result of predation and other causes (eq. [13]). Similarly, the new minimal nutrient requirement with a predator ($QA_{j,P}^*$) is a positive, linear function of both minimal nutrient requirements without a predator (QA_j^*) and η_j , the ratio of losses from predation and other causes for the nutrient-limited grazer (eq. [13]).

Because minimal resource requirements now depend on predation, predators can either facilitate or interfere with species coexistence and turnover. In the models without predation, coexistence of G_1 with G_2 minimally required a trade-off in minimal resource requirements ($QA_2^* > QA_1^*$, but $A_2^* < A_1^*$). However, because they become func-

tions of P , this trade-off is not always guaranteed over a gradient of P . In fact, the rankings of these traits can switch if

$$1 < \frac{QA_2^*}{QA_1^*} < \frac{\eta_1}{\eta_2} \quad \text{and} \quad 1 > \frac{A_1^*}{A_2^*} > \frac{\lambda_2}{\lambda_1}, \quad (14)$$

respectively. This result reveals that at sufficient P , the superior nutrient competitor could become the superior carbon competitor and vice versa. Alternatively, predators could alter competitive hierarchies among grazers and thereby facilitate their coexistence.

Modification 3: Dynamic Nutrient Content of the Plant

This modified model of grazer competition can become more realistic by explicitly representing dynamics of nutrient content of plants and free nutrients. The algebraic equation for plant nutrient content in the previous two models assumed that plants absorbed all nutrients in the ecosystem not sequestered in grazer biomass. Although mathematically convenient, this representation unrealistically assumed that the ecosystem contained no free nutrients (i.e., $R = 0$ always). Thus, further modification of the model includes a dynamic equation for Q :

$$\frac{dQ}{dt} = v(R) - u\beta \left(1 - \frac{k_Q}{Q} \right) Q, \quad (15)$$

where

$$v(R) = \begin{cases} v_{\max} R/h, & R \leq h \\ v_{\max}, & R > h \end{cases} \quad (16a)$$

$$R = S - \sum_j q_j G_j - QA. \quad (16b)$$

Here, the change in Q now reflects the balance between gains through uptake of free nutrients, $v(R)$, and losses by dilution by growth. The loss component follows a standard form (Grover 1997), but the nonstandard nutrient uptake term merits explanation. Uptake of free nutrients (R) by the plant follows a piecewise function that approximates the more standard Monod (Type II) representation (following Armstrong 1994). In this form, nutrient uptake depends linearly on maximal nutrient uptake (v_{\max}) and on the nutrient level at which uptake fully saturates (h). Rate of nutrient uptake increases linearly (with slope v_{\max}/h) when this saturation constant exceeds R . Once $R > h$, nutrient uptake saturates and cannot exceed v_{\max} ; R reflects the difference between total ecosystem nutrients and those not sequestered in grazers or plants (eq. [16b]).

This structure implicitly incorporates instantaneous nutrient recycling and a mass-balance constraint (Grover 1997).

The details of this model appear elsewhere (app. B in the online edition of the *American Naturalist*), but grazer competition and species composition shifts largely follow the principles of the simpler cases. The new analysis adds a saturation threshold that delineates saturation of the plant's nutrient uptake rate. In a system with a single species, the grazer can invade a plant-only system if nutrient supply exceeds its minimal nutrient requirement (feasibility threshold a in fig. 5A, 5B). When the grazer becomes nutrient-limited, nutrient uptake rate of plants may or may not become saturated (depending on whether saturation threshold d intersects with resource limitation threshold b ; this scenario occurs only for grazer 2 in fig. 5B). If the nutrient uptake rate does become saturated, another equilibrium with a nutrient-limited grazer applies. As nutrient supply increases further, this nutrient-limited grazer eventually becomes carbon limited (at resource limitation threshold b in fig. 5A, 5B). Once the grazer remains carbon limited at equilibrium, the plant's nutrient uptake rate becomes saturated if not already (at saturation threshold c in fig. 5A, 5B) as nutrient supply increases further. Once crossed, this saturation threshold dictates a different equilibrium for the carbon-limited grazer.

Grazer competition in this model follows a now familiar progression. Assuming it can invade an ecosystem with plants (i.e., S meets threshold a in fig. 5C), G_1 excludes G_2 at low nutrient supply. G_1 switches from nutrient limitation to carbon limitation (at resource limitation threshold b in fig. 5C) before G_2 can invade (at invasion threshold c in fig. 5C) and potentially coexist. Then, G_2 eventually displaces the superior nutrient competitor (at invasion threshold d in fig. 5C). Once it has outcompeted the other species, G_2 then switches from nutrient to carbon limitation (limitation threshold e in fig. 5C). Nutrient uptake of the plant may become saturated if G_2 is nutrient limited or carbon limited (depending on light supply and saturation thresholds f and g , respectively, in fig. 5C). In this model, the slope of the grazers' impact vectors (q_j) on plant nutrient content determines whether the two-grazer equilibrium is stable (if $q_2 > q_1$) or a saddle (if $q_2 < q_1$; app. B). Thus, when the superior nutrient competitor has greater nutrient content than the superior carbon competitor, alternative stable states arise. When the two-grazer equilibrium is unstable, these invasion, saturation, and resource-limitation thresholds are crossed in a different order (analogous to the base model).

Discussion

These stoichiometrically explicit models of grazer competition predict changes in species composition and po-

tential coexistence over broad gradients of resource supply, mediated through changes in nutrient content and biomass of plants. Grazer competition in these models resembles resource-ratio models of competition among plants in many key respects (Tilman 1982; Grover 1997). It depends on two niche components of grazers, resource requirements and impacts on resources (Leibold 1995; Grover 1997). Sequestered plant carbon (A) and nutrient (QA) are essential resources for grazers, but unlike in traditional resource ratio models, these resources are packaged within one-prey species. Yet, like resource ratio models, elbow-shaped nullclines determined by these minimal resource requirements can cross given a trade-off in competitive abilities for carbon versus sequestered nutrients. Coexistence can occur when each grazer is limited by the resource for which it competes inferiorly, but each grazer must have a larger relative impact on the resource limiting it. Otherwise, alternative stable states (and associated priority effects) can emerge. A window of coexistence or alternative stable states sits between shifts from dominance by superior nutrient competitors to dominance by superior nutrient competitors along a gradient of increasing nutrient supply. These replacements occur whether light is supplied constant (i.e., at decreasing light : nutrient ratio) or whether light : nutrient ratio is constant (Stern et al. 1997) over a nutrient supply gradient. Thus, unlike resource ratio models, absolute as well as relative supply of resources determine competitive outcomes.

These models also reveal that nutrient content of a grazer does not necessarily correlate with its competitive ability for low-nutrient food. The minimal sequestered nutrient requirement, QA^* , is a function of grazer body composition and several grazer traits: feeding rate, conversion efficiency, death rate, and sometimes respiration rate. All else being equal among species, body composition should correspond directly to differences in QA^* (Grover 1997). However, all else is not equal among species. In zooplankton, feeding rate, respiration rate, digestion efficiency, and predation resistance are known to differ among grazer species and also within species in response to varying environmental conditions. Thus, nutrient content of grazers does not solely determine nutrient demands of grazers. Although other grazer traits have not been ignored, arguably the body composition trait itself has emerged as a focal point of current stoichiometric research (Hessen 1992; Urabe and Watanabe 1992; DeMott et al. 1998; Sterner and Elser 2002). The results here encourage stronger links between body composition and other traits involved in physiology and trophic interactions in future research.

Food web architecture can alter outcomes of stoichiometrically explicit grazer competition. Predation pressure on grazers could exacerbate, eliminate, or even reverse

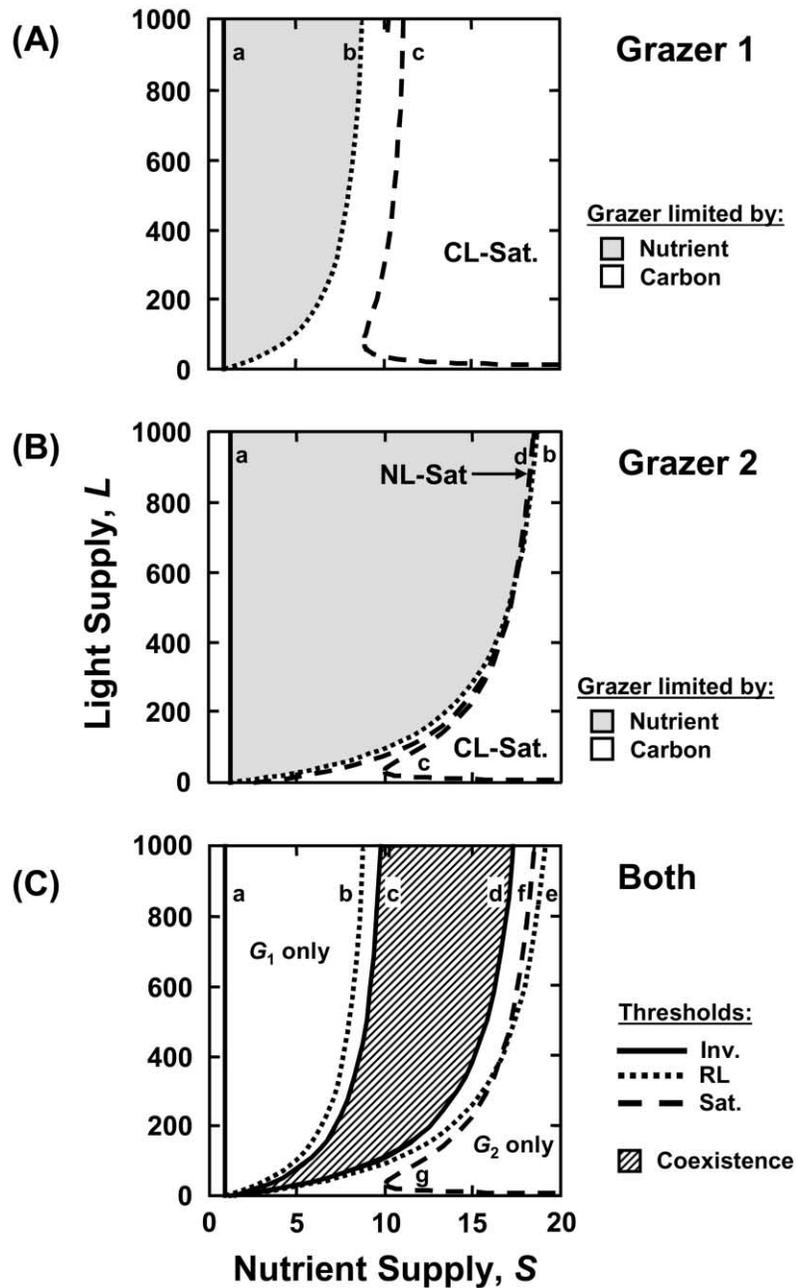


Figure 5: Major thresholds in the model with a dynamic equation for the plant's nutrient content. *A, B*, In the single-grazer case, the grazer invades a plant-only equilibrium past invasion (*Inv.*) threshold *a* and becomes carbon limited past resource limitation (*RL*) threshold *b*. Plant nutrient uptake rate saturates with a carbon-limited grazer (*CL-Sat.*) at saturation (*Sat.*) threshold *c* and with a nutrient-limited grazer (*NL-Sat.*) at saturation threshold *d*. *C*, Qualitative outcomes of grazer competition in this model largely mirror those in the simpler models. Transitions from dominance by the superior nutrient competitor (G_1) to coexistence (*striped region*) to dominance by the superior carbon competitor (G_2), as determined by invasion thresholds *c* and *d*, depend on resource supply. Once G_2 wins competition (past threshold *d*), nutrient uptake rate by the plant saturates at threshold *f* when G_2 is nutrient limited or at threshold *g* when G_2 is carbon limited. Parameter values follow table 1. The unstable two-grazer equilibrium case is not shown here.

trade-offs in minimal nutrient versus minimal carbon requirements among grazers. Of course, previous non-stoichiometric theories revealed that predators can facilitate coexistence of species when competitive ability negatively correlates with predation resistance (Holt et al. 1994; Leibold 1996; Grover 1997). Indeed, predators could facilitate coexistence in stoichiometrically explicit models as well, but, importantly, they may also disrupt stoichiometry-mediated coexistence of grazers. Thus, as stoichiometric approaches to studying food webs develop, predation will likely become a key component (Elser et al. 1998; Hall et al., in press).

Results from these models provide plausible explanations for four findings from a recent multigrazer experiment. In seminatural mesocosms, Hall et al. (in press) documented the response of diverse zooplankton grazer assemblages to experimental gradients of light and nutrient supply and predation risk. In this experiment, the water flea *Daphnia pulex* dominated predator-free mesocosms at high nutrient supply but not at low nutrient supply. Sequestered nutrients in plants in these high nutrient supply ecosystems surpassed a critical threshold below which *Daphnia* did not dominate (Hall et al., in press; see also Urabe et al. 2002a, 2002b). Because *Daphnia* are typically superior carbon competitors (Goulden et al. 1982; Gliwicz 1990), these results also suggest that *Daphnia* competes inferiorly for nutrients. Second, predators (notonectids) greatly reduced relative abundance of *Daphnia* at high nutrient supply. These predators likely eliminated *Daphnia*'s competitive advantage in these environments. Third, other zooplankton grazers with higher phosphorus content than *Daphnia* (e.g., *Ceriodaphnia*) dominated grazer assemblages at low nutrient supply, suggesting that they compete superiorly for nutrients. All else being equal among grazers, this result seems problematic (because high phosphorus grazers should compete inferiorly for nutrients). However, the models here permit grazers with high nutrient content to compete superiorly for nutrients. Fourth, the response of *Daphnia* resembled alternative stable states at high nutrient supply without predators. The model suite predicts these states when superior nutrient competitors contain more nutrients than superior carbon competitors.

Stoichiometry-mediated coexistence of grazers can stabilize nutrient content of plants over broad resource gradients. The light : nutrient hypothesis assumes strong linkages between (relative) supply of light and nutrients and nutrient content of plants, which, in turn, should impact grazer growth and population dynamics (Sternner et al. 1997, 1998; Hessen et al. 2002; Urabe et al. 2002a, 2002b). In models examined here, these links do not occur directly in multigrazer systems, however. Instead, when grazers coexist, the nutrient content of plants becomes only indirectly connected to resource supply. Changes in resource

supply directly determine which species coexist, and then this pairing directly determines nutrient content of plants. Therefore, nutrient content of plants should vary less over resource supply gradients in ecosystems with multiple grazers than predicted by food chain models.

Although this study considered three variations of the base model, several modifications could be made in future, more quantitative efforts to understand stoichiometrically explicit grazer competition. One should definitely explore these before trying to link such a model to population dynamics of real organisms. First, more nonlinear forms of the grazer functional response (e.g., Types II and III) should be studied. Such competition models could behave complexly because global bifurcations arise in stoichiometrically explicit nonlinear food chain models (e.g., Andersen 1997; Loladze et al. 2000; Muller et al. 2001). Yet, a model similar to the base model but written with Type II functional responses also predicts stable coexistence of grazers (Loladze et al. 2004). Second, synthesizing units (SU) could be used in the grazer equation to improve its mechanistic clarity (Muller et al. 2001). Like previous models, I employed a minimum function (Leibig's rule) to discretely switch grazer limitation from carbon to nutrients (Andersen 1997; Loladze et al. 2000, 2004). This assumption produced simple analytical solutions and elbow-shaped nullclines. An SU approach would yield smoother, curved nullclines (Muller et al. 2001) and potentially a broader parameter range permitting coexistence (or priority effects). Third, this model suite (and related models) represented respiration coarsely. From a more detailed physiological perspective, respiration involves maintenance, assimilation, and growth (Kooijman 2000). Better models would differentiate between these components to more realistically represent grazer physiology, particularly when the grazer lives on the brink of starvation. Additionally, a more detailed model might include energy (carbon) storage by grazers, requiring another state variable. Fourth, the models here treat light simplistically. The multiplicative Monod term for production based on light and nutrients could be rewritten with an SU (Kooijman 2000), perhaps including light extinction with depth.

Despite considerable room for more mechanistic detail, the model suite analyzed here yielded a powerful overall result: in a closed system, stoichiometric mechanisms can drive species turnover and facilitate stable coexistence of two-grazer species with one plant. Because it closely resembles the resource ratio model for plants, this suite conceptually unifies competition for resources at multiple trophic levels. Other models, such as keystone predation and intraguild predation, also permit local species coexistence under conceptually analogous conditions involving trade-offs in minimal requirements, similarities of traits, intermediate resource supplies, and particular impacts of

species on their resources (Leibold 1996, 1998; Grover 1997; Holt and Polis 1997; Abrams 1998). Coexistence in those models hinges on predation as the stabilizing mechanism (Chesson 2000). Here, competition between grazers for a nutrient and carbon provides the stabilizing mechanism. It seems likely that stoichiometry, when built into other food web models, could increase opportunities for coexistence of species. However, the specifics of food web architecture may alter, and even reduce, such opportunities.

Acknowledgments

Thanks go to J. Bergelson, M. Leibold, V. Smith, T. Wootton, and especially G. Dwyer for comments on an earlier version of the manuscript and P. Amarasekare and R. Nisbet for insights into the theory. Thanks also go to E. Muller and one referee for very helpful comments during review. A referee had a major impact on this article. J. Grover coined the term "system nutritional constraint." Support came from a National Science Foundation (NSF) graduate research fellowship, a University of Chicago Harper Fellowship, a Graduate Assistance in Areas of National Need training grant, and a NSF Doctoral Dissertation Improvement grant (DEB 01-05014, private investigator, M. Leibold). This is contribution 1136 from the Kellogg Biological Station.

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Associate Editor: James P. Grover