Research

Food quality, nutrient limitation of secondary production, and the strength of trophic cascades

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Recent meta-analyses confirm that the strength of trophic cascades (indirect positive effects of predators on plant biomass through control of herbivores) varies among ecosystem types. In particular, most terrestrial systems show smaller cascades than most aquatic ones. Ecologists still remain challenged to explain this variation. Here, we examine a food quality hypothesis which states that higher quality plants should promote stronger trophic cascades. Food quality involves two components: digestion resistance of plants and magnitude of stoichiometric imbalance between plants and herbivores (where stoichiometry involves ratios of nutrient:carbon ratio of tissues). Both factors vary among ecosystems and could mediate conversion efficiency of plants into new herbivores (and hence control of plants by herbivores). We explored the food quality hypothesis using two models, one assuming that plant stoichiometry is a fixed trait, the other one allowing this trait to vary dynamically (but with a minimal nutrient:carbon ratio of structural mass). Both models produce the same suite of results. First, as expected, systems with more easily digested plants promote stronger cascades. Second, contrary to expectations, higher (fixed or minimal) nutrient:carbon ratio of plants do not promote stronger cascades, largely because of the net result of ecosystem feedbacks. Still, the model with dynamic stoichiometry permits positive correlations of realized plant nutrient:carbon ratio and cascade strength (as predicted), mediated through digestion resistance. Third, lower nutrient:carbon ratio of herbivores promotes stronger cascades. However, this result likely cannot explain variation in cascade strength because nutrient:carbon stoichiometry of herbivores does not vary greatly between terrestrial and aquatic ecosystems. Finally, we found that predation promotes nutrient limitation of herbivores. This finding highlights that food web processes, such as predation, can influence stoichiometry-mediated interactions of plants and herbivores.

The trophic cascade is a classic yet controversial concept in ecology. In a trophic cascade, predation on herbivores indirectly increases plant biomass by reducing herbivory. Although this concept is simple, the empirical evidence supporting it generates controversy as experimental studies suggest that cascade strength varies substantially among ecosystem types (Strong 1992, Polis 1999, Halaj and Wise 2001, Shurin et al. 2002, Borer et al. 2005). The latest meta-analyses confirmed that trophic cascades are weaker in terrestrial systems than aquatic ones, but they also revealed that cascades vary greatly in magnitude even among different types of aquatic systems (Shurin et al. 2002, Stibor et al. 2004).

The empirical controversy has inspired comparative and theoretical work exploring mechanisms that could generate variation in cascade strength. Currently viable mechanisms include (Shurin et al. 2006): differences in body size among plants and herbivores (Body size hypothesis; Shurin and Seabloom 2005), where a large ratio of herbivore:plant size should yield stronger cascades. Also, systems where producers have higher mass-specific productivity rates (e.g. plankton) should yield larger cascades than those with lower productivity rates (e.g. forests; plant productivity hypothesis, Shurin and Seabloom 2005). Finally, systems with more efficient herbivores (e.g. higher attack rates, lower

losses) should produce larger cascades than those with less efficient herbivores (Herbivore efficiency hypothesis; Strong 1992, Polis 1999, Borer et al. 2005).

A fourth related but distinct possibility involves resource quality of plants. This Food quality hypothesis states that poorer food quality should yield smaller trophic cascades. The idea stems from the observation that terrestrial plants often provide poorer quality food for herbivores than do aquatic producers. This poor quality might stem from differences in digestibility. After all, many terrestrial plants contain more indigestible carbon (owing to structural and defensive compounds) than aquatic producers do. This factor becomes germane if herbivores have more difficulty controlling fairly indigestible plants (Borer et al. 2005). Therefore, all else being equal, smaller cascades might be expected in terrestrial systems (less digestible food) than in aquatic ones (more digestible food). Poor food quality can also result from stoichiometric imbalances. Large stoichiometric imbalances between herbivores (high nutrient:carbon ratio) and plants (low nutrient:carbon ratio) can induce nutrient limited production of herbivores and decrease conversion efficiency of digested food (as summarized by Sterner and Elser 2002). Thus, larger stoichiometric imbalances might also yield poor quality food, all else being equal. This possibility is relevant because aquatic plants typically show higher nutrient:carbon ratio of tissues than do terrestrial producers, while nutrient:carbon ratio of herbivores varies much less between terrestrial and aquatic systems (Cebrian 1999, Elser et al. 2000a, Sterner and Elser 2002). Therefore, low food quality driven by larger elemental imbalances between plants and herbivores might also mute cascades.

Given these facets of plant quality, we explored the effect of variation in digestibility and stoichiometric imbalance between plants and herbivores for trophic cascades using two different models. While both assume that digestibility is a fixed trait of plants, the first represents nutrient:carbon ratio of producers as a fixed trait. This assumption is extreme, but it permits us to separate effects of digestibility from plant stoichiometry. The second model allows nutrient:carbon ratio of plants to vary dynamically with environmental nutrient supply, digestibility, stoichiometry of the herbivore, and minimal nutrient:carbon ratio of the plant. We used both models to ask how digestibility of plants and stoichiometric composition of both plants and herbivores influence cascades via conversion efficiency and/or nutrient allocation mechanisms. The model with static producer stoichiometry revealed the major findings of the study, while the model with dynamic nutrient:carbon ratio of producers confirmed them in the face of more complex and realistic feedbacks.

Models

Model 1. Static stoichiometry of plants, and trophic indices

The model

We first considered a model in which nutrient:carbon ratio (by mass) of both plants (q_P) and herbivores (q_H) are fixed traits (following Grover 1997). The carbon biomasses of plants (P), herbivores (H), carnivores (C), and free nutrients (R) follow a set of balance equations (Appendix 1, Table 1):

$$dP/dt = P(rR - aH) \tag{1a}$$

$$dH/dt = H(\min(eaP - \sigma, eaPq_P/q_H) - m - a_C C) \tag{1b}$$

$$dC/dt = C(e_C a_C H - m_C - \sigma_C) \tag{1c}$$

$$R = S - q_P P - q_H H - q_C C \tag{1d}$$

where the growth rate of the producer (Eq. 1a) depends on uptake rate of nutrients, r, and losses due to grazing by herbivores at rate a. Following Sterner (1997) and Hall (2004), growth rate of herbivores (Eq. 1b) depends on food uptake (aP); maximal efficiency at which consumed plants are converted to new herbivore biomass (e), a term that reflects digestibility of plant biomass; and either respiration rate (σ) or the ratio of plant nutrient:carbon ratio (q_P) to that of herbivores (q_H), depending on whether production of the herbivore is limited by carbon or nutrient, respectively. Incorporation of respiration rate in this manner differs from some related models (Muller et al. 2001); however, this assumption does not make a qualitative difference for predictions here (Hall 2004). Production of herbivores is carbon limited when:

$$eaP - \sigma < eaPq_P/q_H, \tag{2}$$

and is otherwise nutrient limited. In the latter case, lower ratios of q_P/q_H exacerbate herbivore nutrient limitation and decrease conversion efficiency of herbivores. The loss rate of herbivores also depends on density-independent factors (m) and predation by top carnivores (C) feeding at rate a_C. We assume that the nutrient:carbon ratio of carnivores (q_C) is sufficiently similar to that of herbivores (q_H) to guarantee carbon limitation of carnivore production. Growth rate of the carnivore (Eq. 1c) then reflects the net balance between gains from feeding on herbivores (at stoichiometry-independent conversion efficiency e_C) and death and respiration (at density-independent rates m_C and σ_C, respectively). Finally, available free nutrients (R, Eq. 1d) follow a mass-balance constraint (Grover 1997). All nutrients in the system (S) not sequestered in plants ($q_P P$), herbivores ($q_H H$), and carnivores ($q_C C$) become available for uptake by plants (R). Enriched systems contain elevated levels of total nutrients (S).

Table 1. List of symbols used in the food chain models and parameter values/ranges.

Symbol	Units	Meaning/interpretation	Value/range
Variables			
C	$\mu g\ C\ l^{-1}$	biomass (in carbon) of carnivores	–
H	$\mu g\ C\ l^{-1}$	biomass (in carbon) of herbivores	–
P	$\mu g\ C\ l^{-1}$	biomass (in carbon) of plants (producers)	–
Q	$\mu g\ C\ g\ P^{-1}$	dynamic (flexible) nutrient:carbon ratio of plants	–
QP	$\mu g\ P\ l^{-1}$	nutrient sequestered in plants	–
t	day	time	–
Parameters			
a	$day^{-1}\ (\mu g\ C\ l^{-1})^{-1}$	attack rate, herbivores	0.004
a_C	$day^{-1}\ (\mu g\ C\ l^{-1})^{-1}$	attack rate, carnivores	0.005
e	–	digestibility of plants/maximal conversion efficiency	0.4–0.8
e_c	–	conversion efficiency, carnivores	0.5
k_Q	$\mu g\ C\ \mu g\ P^{-1}$	minimal nutrient:carbon ratio of plants	0.001, 0.01
m	day^{-1}	mortality rate of herbivore	0.05
m_C	day^{-1}	mortality rate of carnivores	0.1
q_C	$\mu g\ P\ \mu g\ C^{-1}$	nutrient:carbon ratio of carnivores	0.02
q_H	$\mu g\ P\ \mu g\ C^{-1}$	nutrient:carbon ratio of herbivores	0.025–0.08
q_P	$\mu g\ P\ \mu g\ C^{-1}$	static nutrient:carbon ratio of plants	0.001–0.025
r	$day^{-1}(\mu g\ P\ l^{-1})^{-1},\ day^{-1a}$	maximal growth rate of plants	1
S	$\mu g\ P\ l^{-1}$	nutrient supply concentration to system	0–50
σ	day^{-1}	respiration rate of herbivores	0.1
σ_C	day^{-1}	respiration rate of carnivores	0.05

[a]first for static stoichiometry model, second for dynamic stoichiometry model

Trophic indices and equilibrial behavior

Following an existing measure used commonly in empirical studies (Shurin et al. 2002), we define trophic indices that measure equilibrial biomasses of plants (PTI) and herbivores (HTI) in three level systems divided by that in two level systems, or:

$$PTI^* = P_3^*/P_2^* \qquad (3a)$$

$$HTI = H_3^*/H_2^* \qquad (3b)$$

where asterisks "*" indicate equilibrial values, and subscripts "2" and "3" correspond to bi-level and tri-level chains, respectively. Higher values of PTI and lower values of HTI signify stronger cascades (Shurin et al. 2002). We then determined the dependencies of PTI and HTI on maximal digestibility, e, stoichiometric composition of plants (q_P) and herbivores (q_H), and nutrient enrichment (S) by calculating the partial derivatives of these ratios with respect to the parameters of interest (see Appendix 1 for detailed results).

Regardless of whether carbon or nutrients limit production of herbivores, the model predicts the classic odd-even pattern of biomass accrual along gradients of enrichment (S) where species/trophic levels are added once the system becomes sufficiently productive to support them (Fig. 1A; Oksanen et al. 1981, Grover 1997). Once a trophic level invades, it controls the trophic level immediately below. Hence, biomass of the invading level and that two levels below it increase with enrichment while those directly below it do not respond. For instance, in bi-level systems, herbivore biomass and free nutrients (not shown) increase while plant biomass remains constant (fixed at the herbivore's minimal carbon requirement when carbon limited, or at the biomass yielded by its minimal nutrient requirement when nutrient limited; Fig. 1A; Appendix 1; Hall 2004). In tri-level systems, the biomasses of consumers and plants increase, herbivore biomass remains fixed at the carnivore's minimal carbon requirement (Fig. 1A), and free nutrients do not change (Appendix 1).

Although the food chain model with static stoichiometry confirms this classic pattern, it also introduces a new twist: predation on herbivores may induce or accentuate nutrient limitation of herbivore production. When plants contain a relatively low amount of nutrient per unit carbon (low q_P), nutrients limit grazer production in bi-level and tri-level chains at all levels of nutrient enrichment (Fig. 1B, Appendix 1). In contrast, when plants contain relatively high amounts of nutrients (high q_P), carbon limits production of herbivores at the enrichment level where the carnivore invades. However, with further nutrient supply, the herbivore suffering predation will switch to nutrient limited production even though carbon would otherwise limit its production without predation (compare upper and lower left panels in Fig. 1.B; see Appendix 1 for details). This switch can be understood in two ways. First, it occurs because nutrient enrichment increases carnivore density and thus per capita predation on herbivores ($a_3 C_3^*$). Herbivores must balance increased predation with increased growth, and that balance
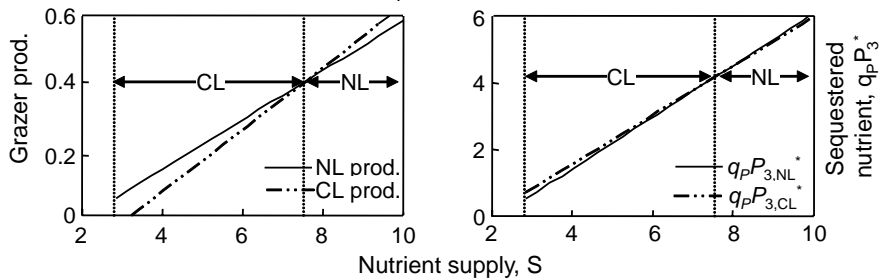
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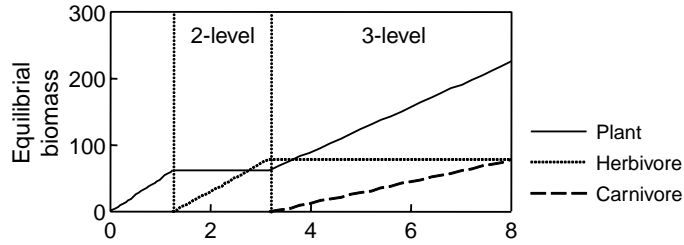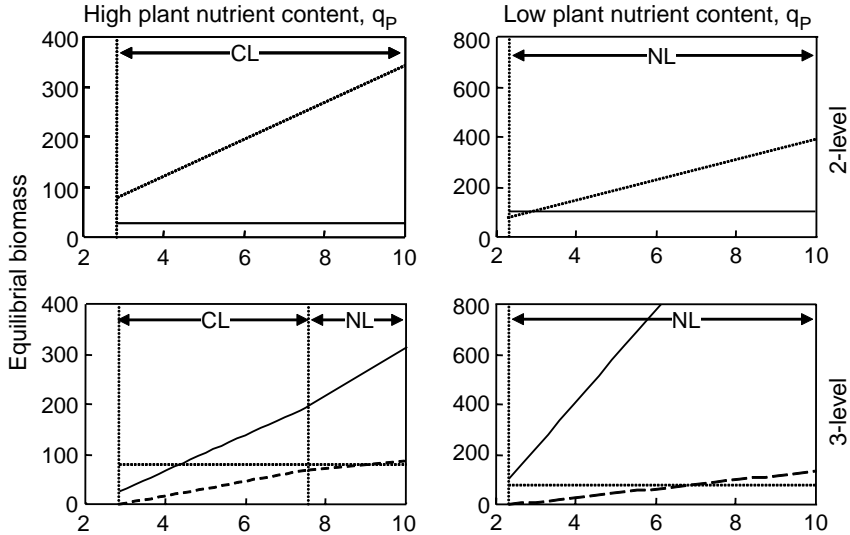
Fig. 1. Equilibrial behavior of the food chain model with static stoichiometry of producers. (A) Higher trophic levels successfully invade and persist with nutrient enrichment (i.e. increasing S). The top trophic level controls biomass of that directly below it, and the top level and two below it increase with enrichment. Free nutrients (not shown) are zero in the one-level system, increase with S in the two-level system, and remain constant in the three-level system. (B) Nutrient:carbon stoichiometry of plants (q_P) and predation by carnivores determine whether nutrients or carbon limit production of herbivores. In bi-level chains, identity of the limiting resource for production of herbivores depends solely on q_P and is independent of S. Low q_P causes nutrient limitation (NL), while high q_P induces carbon limitation (CL). In tri-level chains, low q_P also causes nutrient limitation at all S, whereas at high q_P, nutrient enrichment causes a shift from carbon limitation to nutrient limitation of herbivores. (C) This enrichment-mediated shift in resource limitation occurs at the nutrient supply S where the conversion of ingested plant nutrients to herbivore growth ("NL prod.", $eaPq_P/q_H$) becomes lower than the conversion of ingested plant carbon to herbivore growth ("CL prod.", $eaP - \sigma$). Additionally, this shift occurs when the minimal resource requirement of the grazer coexisting with the carnivore ($q_P P^*_{3,NL}$) exceeds that produced by the system in which carbon limits production of herbivores ($q_P P^*_{3,CL}$).

requires increased intake and assimilation of carbon (P_3^*) and nutrients sequestered by plants ($q_P P_3^*$). As plant biomass (P_3^*) increases with nutrient enrichment, so does the assimilation and conversion of carbon (as $eaP_3^* - \sigma$) and nutrient (as $eaP_3^* q_P / q_H$; Fig. 1C). The latter increases, however, more slowly with increasing plant biomass, since $q_P / q_H < 1$. Consequently, more nutrient enrichment increases plant biomass and eventually reverses inequality (Eq. 2) – and grazer production becomes nutrient limited at sufficiently high levels of nutrient enrichment, S. An alternative explanation is detailed in Appendix 1: the switch to nutrient-limited production of herbivores occurs once the system supporting carbon-limited herbivores cannot meet the minimal nutrient requirements of herbivores suffering predation, $q_P P_{3,NL}^*$; this situation occurs or when $q_P P_{3,NL}^* > q_P P_{3,CL}^*$; Fig. 1C. Nutrient-limited production of herbivores ultimately affects carnivores because of a decreased flow of plant biomass into carnivore biomass. Consequently, nutrient limited production of herbivores in tri-trophic chains implies that plant biomass increases more steeply and carnivore biomass less steeply with further increases in S (Fig. 1B).

Based on the above reasoning we distinguish three cases for our trophic indices as determined by plant nutrient:carbon ratio (q_P) and nutrient supply (S):

(A). Case (1): carbon limits herbivore production in both tri-trophic and bi-trophic chains (high q_P, low S): CL_3/CL_2,

(B). Case (2): nutrients limit herbivore production in tri-trophic chains but carbon limits herbivore production in bi-trophic chains (high q_P, high S): NL_3/CL_2, and

(C). Case (3): nutrients limit herbivore production in both chains regardless of nutrient enrichment (low q_P): NL_3/NL_2.

Predictions for determinants of plant quality: e, q_P, and q_H

We readily see that increased digestibility of plants (i.e. higher e) yields stronger cascades (Table 2). This digestion-mediated increase in conversion efficiency decreases biomass of plants in both two- and three-level systems because higher digestibility enhances control of plants by herbivores (Fig. 2A). However, this decrease is stronger in bi-trophic systems than in tri-trophic systems (Appendix 1). Therefore, higher digestibility actually increases the plant trophic index (PTI; Fig. 2B). Meanwhile, herbivores eating more digestible plants achieve higher biomass without predators. Yet, they do not respond to change in digestibility in tri-trophic chains because the predator fixes

Table 2. Summary of the behavior of trophic indices generated by models with static and with dynamic stoichiometric composition of the producer. In model 1, four parameters (nutrient supply, S; digestibility, e; plant stoichiometry, q_P; and herbivore stoichiometry, q_H) then can influence the plant (P) and herbivore (H) trophic indices via effects on nutrient allocation and realized conversion efficiency, as described in the text and Appendices. In model 2, nutrient supply (S), maximal digestibility (e), minimal nutrient content of the producer (k_Q), and nutrient content of the herbivore (q_H) all influence nutrient content of producers (Q^*) in two-level chains (subscript 2), regardless of whether grazing is limited by nutrients (NL) or carbon (CL). In three level systems (subscript 3), only k_Q influences Q^*. These four parameters (S, e, k_Q, q_H) then can influence the trophic indices. A plus sign, minus sign, and zero indicate a positive effect, negative effect, or no effect (respectively) on Q^* or trophic indices with a small increase in the parameters (as calculated using partial derivatives).

Variable or index	Quantity	S	e	q_P or k_Q	q_H
Model 1. Static stoichiometry of plants					
Plant trophic Index (PTI)[†]	$P_{3,CL}^*/P_{3,CL}^*$	+	+	−	−
	$P_{3,NL}^*/P_{3,CL}^*$	+	+	−	−,+[‡]
	$P_{3,NL}^*/P_{2,NL}^*$	+	+	0	−
Herbivore trophic Index (HTI)[†]	$H_{3,CL}^*/H_{3,CL}^*$	−	−	+	+
	$H_{3,NL}^*/H_{3,CL}^*$	−	−	+	+
	$H_{3,NL}^*/H_{2,NL}^*$	−	−	0	+
Model 2. Dynamic stoichiometry of plants					
Nutrient quota	$Q_{2,NL}^*$	+	+	+	−
	$Q_{2,CL}^*$	+	+	+	−
	Q_3^*	0	0	+	0
Plant trophic Index (PTI)[†]	$P_{3,CL}^*/P_{3,CL}^*$	+	+	−	−
	$P_{3,NL}^*/P_{3,CL}^*$	+	+	−	−,+[‡]
	$P_{3,NL}^*/P_{2,NL}^*$	+	+	0	−
Herbivore trophic Index (HTI)[†]	$H_{3,CL}^*/H_{3,CL}^*$	−	−	+	+
	$H_{3,NL}^*/H_{3,CL}^*$	−	−	0	+
	$H_{3,NL}^*/H_{2,NL}^*$	−	−	0	+

[†] the three versions of each trophic index correspond to case 1, 2, and 3
[‡] sign shifts from minus to plus with increases in enrichment

(A) Response of biomass to e

Producers / Herbivores / Three-level / Two-level

(B) Response of trophic indices to e

PTI, P_3^*/P_2^* (+)

HTI, H_3^*/H_2^* (−)

Nutrient supply, S

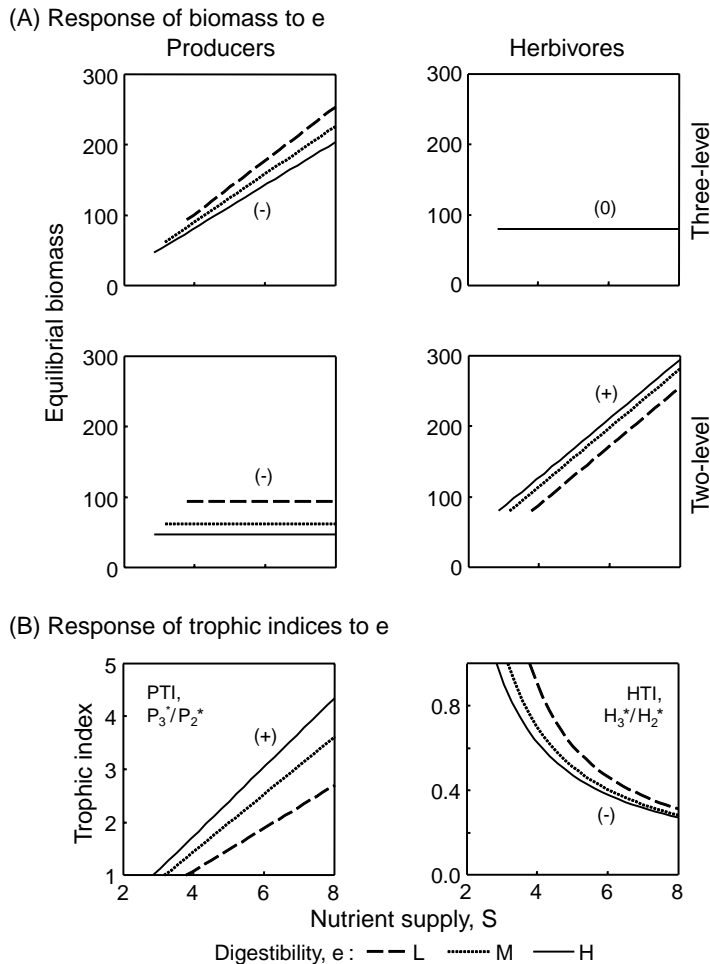Digestibility, e : − − L ········· M —— H

Fig. 2. Response of the model with static stoichiometry of plants to variation in digestibility (maximal conversion efficiency, e). (A) Plant biomass in two level (P_2^*) and three level (P_3^*) systems drops with higher conversion efficiency (where L, M, and H correspond to low, medium, and high levels of e: 0.4, 0.6, and 0.8, respectively). Meanwhile, herbivores do not respond to e in three-level systems (H_3^*), because their biomass is determined solely by traits of the carnivore, but they increase with e in two-level systems (H_2^*). (B) The net result of these responses is that the plant trophic index (PTI; the ratio of P_3^*/P_2^*) increases with higher e because the drop in plant biomass with e is larger in two level systems than three level systems. Meanwhile, the trophic index for herbivores (HTI; the ratio of H_3^*/H_2^*) drops with e. Signs of response with increasing e: (−) means decrease, (+) indicates increase, and (0) denotes no change.

herbivore biomass at the predator's minimal carbon requirement (Fig. 2A). This carbon requirement of the predator does not depend on plant digestibility. Therefore, higher digestibility lowers the trophic index for herbivores (HTI; Fig. 2B). In summary:

$$\uparrow e \Rightarrow \uparrow PTI, \downarrow HTI \qquad (4)$$

These predictions apply whether carbon or nutrients limit production of herbivores (Table 2; Appendix 1).

Because stoichiometry of herbivores and plants (q_H and q_P, respectively) appears in the same herbivore growth term as digestibility (e), they might be expected to have identical effects on the strength of top-down control and biomass partitioning – at least when nutrients limit production of herbivores. If nutrients limit grazer production, the effect of stoichiometry-mediated conversion efficiency thus should produce larger cascades when elemental imbalances between plants and herbivore are small (i.e. q_P/q_H is close to 1), because larger q_P/q_H ratios enhance realized conversion efficiency. Larger q_P/q_H ratios, in turn, can be achieved by increasing q_P or decreasing q_H. Thus, making an analogy to the results for digestibility (e), one might expect:

$$\uparrow q_P \Rightarrow \uparrow PTI, \downarrow HTI \qquad (5a)$$

$$\uparrow q_H \Rightarrow \downarrow PTI, \uparrow HTI \qquad (5b)$$

The effects of stoichiometry are, however, not that simple, due to ecosystem-level feedbacks – changes in q_P and q_H also influence how nutrients, and thus biomass, are partitioned (allocated) among trophic levels. Because of the mass balance constraint (Eq. 1d), more nutrients sequestered in plants ($q_P P^*$) or herbivores ($q_H H^*$) mean that less can be allocated to other food web compartments. Thus, in addition to their direct effects on plant to herbivore conversion efficiency, stoichiometric traits may affect cascade strength indirectly through feedbacks caused by altered patterns of nutrient allocation among trophic levels.

The allocation effect is best illustrated with an example. For the case 1 (carbon-limited herbivores in both chains), carbon limited herbivores in two-level systems ($H^*_{2,CL}$) are negatively affected by plant nutrient:carbon stoichiometry (q_P) through an allocation effect. Higher plant nutrient:carbon stoichiometry means that more nutrients are sequestered in plant biomass, $q_P P^*_{2,CL}$, thus less nutrients are allocated to the herbivore trophic level. The latter result yields less equilibrial herbivore biomass, $H^*_{2,CL}$. Interestingly, this allocation effect then indicates that, although growth rate (production) of herbivores is not limited by the nutrients contained in plants, their equilibrial biomass ($H^*_{2,CL}$) is ultimately determined by nutrients sequestered in plants (through mass balance constraints). Meanwhile, herbivore biomass in three-level systems ($H^*_{3,CL}$) is set at the minimal carbon requirement of the carnivore; thus, it does not respond to plant stoichiometry. In sum, in the situation where carbon limits production of herbivores in two- and three-level chains (case 1), increasing plant nutrient:carbon stoichiometry (q_P) ultimately increases the trophic index for herbivores ($H^*_{3,CL}/H^*_{2,CL}$). This result contradicts expectations (Eq. 5a), but the result emerges due to a nutrient allocation effect, not due to stoichiometry-mediated conversion efficiency.

In Appendix 1, we consider the responses of both trophic indices to each stoichiometric trait in detail; here we summarize the key results (Table 2, Fig. 3). For case 1 (CL_3/CL_2) and 2 (NL_3/CL_2), plant stoichiometry (q_P) does not influence the denominator of PTI or the numerator of HTI. As a result, the net response of PTI and HTI, driven either by the nutrient allocation effect or stoichiometry-mediated conversion efficiency, operate in opposite directions than described by Eq. 5a (Fig. 3). For case 3 (NL_3/NL_2), PTI does not respond to plant nutrient:carbon stoichiometry; this trait influences conversion efficiency of both numerator and denominator identically, so its effects cancel (Fig. 3). The trophic index for herbivores in case 3 does not respond to q_P because neither numerator nor denominator depend on it.

For cases 1 (CL_3/CL_2) and 2 (NL_3/CL_2), herbivore stoichiometry (q_H) again does not influence the denominator of PTI or the numerator of HTI. Given this result, we found that the two indices respond largely as described by Eq. 5b – but due to nutrient allocation effects, not stoichiometry-mediated conversion efficiency (Table 2, Fig. 3). In the exception (case 2, high nutrient supply), there is a change in sign of PTI when an opposing influence of q_H on stoichiometry-mediated conversion efficiency outweighs the effect of nutrient allocation. Also, in case 3 (NL_3/NL_2), the trophic indices follow Eq. 5b, but again due to a nutrient allocation effect. In this case, q_H influences conversion efficiency identically in both numerator and denominator of the indices. Thus, these effects of q_H on conversion efficiency cancel, leaving only a signal of nutrient allocation on the trophic indices (Fig. 3).

Model 2. Dynamic stoichiometry of plants, and trophic indices

Modified model

Many producers are flexible in their nutrient:carbon stoichiometry while metazoan herbivores are relatively more homeostatic (Sterner and Elser 2002). To consider plants with dynamic (flexible) stoichiometry, we modify the model above to incorporate dynamic nutrient:carbon ratio, Q (while retaining Eq. 1c; Appendix 2):

$$dP/dt = P(r(1 - k_Q/Q) - aH) \qquad (6a)$$

$$dH/dt = H(\min(eaP - \sigma, eaPQ/q_H) - m - a_C C) \qquad (6b)$$

$$Q = (S - q_H H - q_C C)/P. \qquad (6c)$$

In this model, plant production (Eq. 6a) depends on Q following the Droop-variable stores representation (Grover 1997), where k_Q is the minimal nutrient:carbon ratio of the plant (and corresponds to the stoichiometry of plant structure). When nutrients limit herbivores, the production efficiency of herbivores (Eq. 6b) depends on the ratio of nutrient:carbon ratio of plants to that of herbivores, Q/q_H. Finally, we assume that nutrient uptake by plants is instantaneous and that plants do not have upper limits to their ability to store nutrients. As a consequence, no free nutrients exist and all nutrients of the system (S) not contained in herbivores ($q_H H$) or top consumers ($q_C C$) are contained in plants (QP) with stoichiometry Q. While this assumption cannot be strictly true (Hall 2004), this common approach maintains analytical tractability because dynamic nutrient quota follows a mass balance equation (Eq. 6c; Loladze et al. 2000, Muller et al. 2001, Hall 2004).
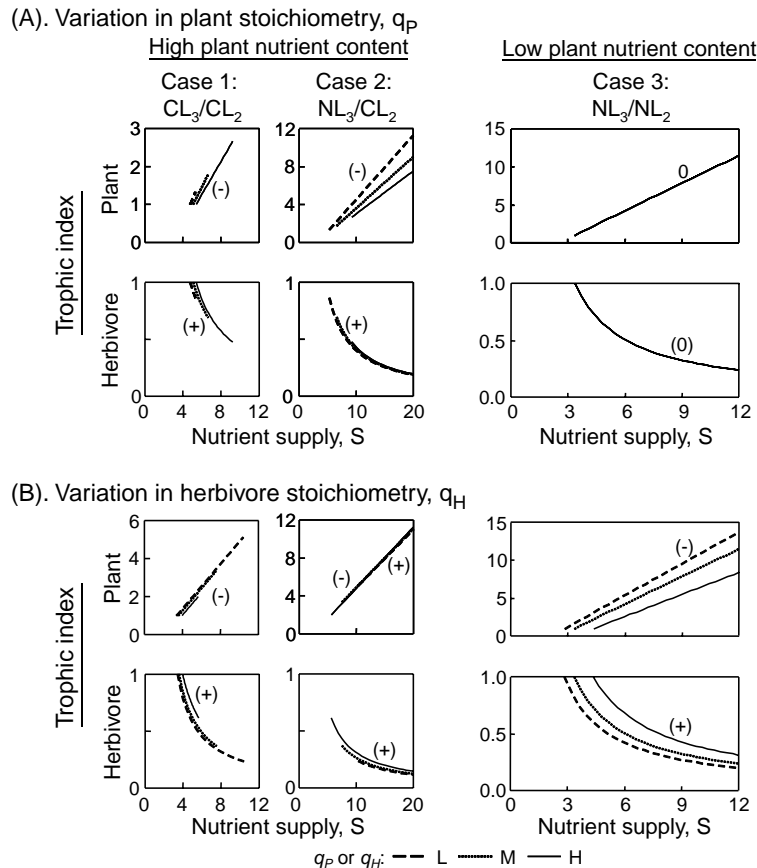
Fig. 3. Responses of trophic indices for plants (PTI) and herbivores (HTI) to variation in nutrient:carbon stoichiometry of (A) plants (q_P) and (B) herbivores (q_H). Three separate cases are considered. At high q_P and low levels of enrichment (S), we see carbon limitation (CL) of herbivores in both tri-level and bi-level chains (case 1). With higher enrichment but still high q_P, we see a shift to nutrient limitation (NL) of herbivore production in tri-level systems (case 2). Finally, at low q_P, we see nutrient limitation of herbivore production in both bi- and tri-level chains, regardless of enrichment. Responses of the trophic indices in each case are described in the text and Table 2. Signs of response with increasing q_P and q_H: ($-$) means decrease, ($+$) indicates increase, and (0) denotes no change.

Effects of parameters on dynamic plant stoichiometry, and shifts in resource limitation

In this model, parameter values affect dynamic (flexible) nutrient:carbon ratio (Q) of plants. Trait Q is most commonly measured by empiricists, forms the basis for the aquatic-terrestrial contrast in nutrient stoichiometry (Elser et al. 2000a), and influences conversion efficiency through the ratio Q/q_H. However, empirical relationships between Q and trophic indices described could be caused by a variety of factors that influence Q. In bi-level systems, this model (Eq. 6) indicates that Q increases with nutrient supply (S), maximal digestibility (e), and minimal nutrient:carbon ratio of plants (k_Q) but decreases with nutrient:carbon ratio of herbivores (q_H; Table 2). Thus, digestibility and herbivore stoichiometry can potentially influence the denominator of the two cascade indices themselves and via their influence on Q. However, in tri-level systems, nutrient

quota responds only to minimal nutrient:carbon ratio of plants (Table 2, Appendix 2).

Similar to the model with fixed stoichiometry of plants, we studied a variation with dynamic nutrient stoichiometry. This model allowed us to explore how plant and herbivore trophic indices respond to changes in nutrient supply (S), digestion (e), and herbivore stoichiometry (q_H), as well as to changes in minimal plant stoichiometry (k_Q, the approximate analogue to q_P in the fixed stoichiometry model). As in the static-stoichiometry case, either nutrients or carbon can limit production of herbivores along gradients of enrichment and with varying food chain length. In contrast to the food chain model with static plant stoichiometry, production of grazers switches from nutrient- to carbon limitation with enrichment in two-level systems (Fig. 4; Hall 2004). This switch occurs as plants become more nutrient-rich (i.e. nutrient:carbon ratio, Q, increases)
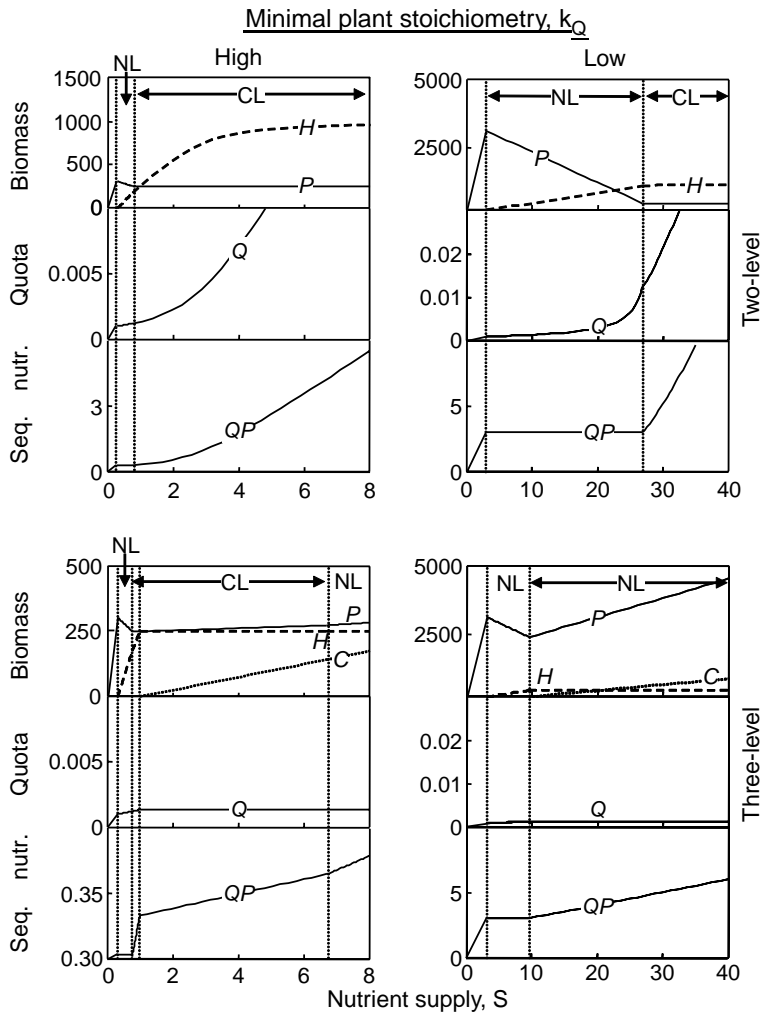
Fig. 4. Shifts between carbon limited (CL) and nutrient limited (NL) production of herbivores in two- and three-level chains when plant stoichiometry varies dynamically. Biomass in plants (P), herbivores (H), and carnivores (C) accrues with dynamic (flexible) nutrient:carbon ratio (quota, Q) and sequestered nutrient (QP) of plants in two cases: plants have higher or lower minimal quota (k_Q).

along the gradient of nutrient supply. Before this switch point, nutrients sequestered by plants (QP_2^*) just meet the minimal nutrient needs of the herbivore but plant biomass exceeds the minimal carbon demands. The increase in Q therefore results in enhanced realized conversion efficiency and decreased plant biomass (Fig. 4, Appendix 2; Hall 2004). After the switch point, plants exceed this minimal nutrient requirement, and plant biomass remains fixed at the herbivore's minimal carbon requirement.

Once carnivores enter the system, two scenarios emerge that resemble those in the model with static stoichiometry. When minimal nutrient content of producers (k_Q) is high, carbon may limit herbivores when consumers enter the system. Once they invade,

carnivores eventually induce nutrient limitation of herbivore production, given high enough nutrient supply, even though the flexible nutrient:carbon ratio (Q) of producers remains unresponsive to enrichment (Appendix 2). The explanation parallels that in the static stoichiometry scenario (high q_P; Fig. 1B) where predation on herbivores increases the minimal nutrient and carbon requirements of herbivores and where plant nutrients (QP_3^*) increase with increasing S more slowly than does plant carbon (P_3^*), eventually flipping production of herbivores to nutrient limitation. In contrast, when plants have low minimal quota, herbivores remain nutrient limited before and after consumers invade (Appendix 2). Again, this result parallels that from the static stoichiometry model (low q_P;

Fig. 1.B). Therefore, we have three cases which parallel those produced by the model with static stoichiometry of plants.

Effects of parameters on trophic indices

Flexible nutrient:carbon ratio of plants adds complexity to analyses linking stoichiometry to strength of trophic cascades (Appendix 2). However, we arrive at the same basic set of conclusions as in the case with static stoichiometry of plants (Table 2). First, increases in both nutrient supply (S) and maximal conversion efficiency/digestibility (e) enhance cascades (i.e. increase plant trophic index, PTI, and decrease herbivore trophic index, HTI), regardless of which resource limits production of herbivores. Interestingly, this result can involve dynamic (flexible) stoichiometry, Q: since increases in digestibility also elevate this flexible nutrient:carbon ratio of plants, a positive correlation between flexible nutrient:carbon ratio and strength of trophic cascades can emerge if digestibility largely drives flexible nutrient:carbon ratio (Table 2). Second, increases in the minimal nutrient quota (k_Q) produce either a decrease (case 1, 2) or no change (case 3) in PTI, and either an increase (case 1) or no change in HTI (case 2, 3). Finally, elevated herbivore nutrient content (q_H) decreases PTI (except in case 2 at high levels of enrichment) and increases HTI. Like in the static stoichiometry case, results for q_H which meet these expectations involve effects of q_H on nutrient allocation rather than conversion efficiency.

Discussion

We have pursued additional explanation for variation in trophic cascades among ecosystem types based on differences in food quality. Our analysis required us to dissect quality of plants as food for herbivores into two separate components: digestibility and degree of stoichiometric imbalance between producers and herbivores. One might expect both processes to operate similarly since both can potentially influence conversion efficiency (Sterner and Elser 2002). Therefore, highly indigestible plants or those with low nutrient content (relative to herbivores) should be weakly affected by control from herbivores, leading to muted trophic cascades (Polis and Strong 1996). However, our food chain models with either static or dynamic producer stoichiometry both revealed conflicting results concerning these two components of food quality. Variation in digestibility consistently yields the expected pattern: systems with plants that are more easily digested show stronger trophic cascades, all else being equal. This result makes intuitive sense and offers little controversy. In contrast, systems with a higher fixed or minimal

nutrient:carbon ratio of plants show either weaker or similarly strong trophic cascades. This discrepancy arises because plant stoichiometry can influence how efficiently plants are converted to herbivores (when herbivores are nutrient limited) but also shapes how nutrients are allocated among trophic levels. Finally, decreases in herbivore nutrient:carbon ratio usually produce larger cascades than predicted. Yet, this phenomenon arises through allocation pathways rather than stoichiometry-mediated changes in conversion efficiency.

These results have three important implications for empiricists who consider links between stoichiometry and variation in the strength of trophic cascades in nature. First, the possibility that herbivore stoichiometry affects trophic cascades likely cannot explain systematic differences in cascade strength among ecosystems (Shurin et al. 2002, 2006, Borer et al. 2005) since herbivore stoichiometry is fairly similar in terrestrial and aquatic systems (Elser et al. 2000a, Sterner and Elser 2002). Second, although elemental composition of plants varies widely between terrestrial and aquatic systems (Elser et al. 2000a, Sterner and Elser 2002), our models indicate that variation in cascade strength should not be caused by variation in nutrient:carbon ratio of plants (static stoichiometry model) or minimal nutrient:carbon ratio of plants (dynamic stoichiometry model). Third, the dynamic model permits a positive correlation between cascade strength and realized nutrient:carbon ratio of plants – if this nutrient quota is flexible and mainly influenced by digestion resistance, not minimal nutrient content (DeMott and Tessier 2002). Plants that are more digestible should, all else being equal, have higher realized nutrient content (at equilibrium) and promote stronger trophic cascades. Thus, positive correlations between cascade strength and plant stoichiometry among systems may ultimately be driven indirectly by variation in digestion resistance rather than directly by differences in minimal nutrient:carbon ratio of plants (DeMott and Tessier 2002).

Before fully accepting these results derived from linear, stable food chains, we should first confirm their generality with similar study of more non-linear variants of these models. These other models allow for oscillations and other exotic, non-linear behaviors (e.g. homoclinic bifurcations that promote extinction of grazers; Andersen 1997, Abrams 1999, Loladze et al. 2000, Scheffer et al. 2000, Muller et al. 2001, Diehl 2007). Such features can certainly complicate analyses. Yet, the increased behavioral repertoire is germane because predators can destabilize plant–herbivore interactions to varying degrees across systems (Halpern et al. 2005).

In the meantime, both models revealed that predation should exacerbate nutrient limitation of herbivores.

Predators do this either by preventing herbivores from ever becoming limited by carbon, or by switching production of herbivores from carbon to nutrient limitation once the system becomes sufficiently enriched. Both scenarios involve predation-driven increases in the minimal demand of herbivores for nutrient sequestered in plants. (An analogous phenomenon occurs in Muller et al.'s [2001] and Hall's [2004] analyses when varying death rates of the herbivore). While both food availability (plant biomass) and predation mortality increase with enrichment, the rate at which herbivores convert food to growth increases faster for the carbon than for the nutrient fraction of ingested plant biomass. Therefore, herbivores may become nutrient limited with enrichment – even though the nutrient:carbon ratio of plant biomass does not change with nutrient supply. (This is true for both models, because dynamic stoichiometry of plants does not change with enrichment in tri-trophic systems with nutrient-limited production of herbivores). Related models suggest that other food web processes, such as stoichiometry-mediated coexistence of herbivores (Hall 2004, Hall et al. 2006) and variation in species composition of plants (Hall et al. 2005, 2006, 2007), also influence whether nutrients or carbon limit production of herbivores. Combined, these results emphasize that species interactions may extensively shape nutrient:carbon stoichiometry of plants and/or the extent of nutrient limitation of herbivore production.

Of course, models with homogenous trophic levels inevitably simplify – perhaps oversimplify – natural food webs. Heterogeneity within trophic levels is often cited as a factor that diminishes the strength of trophic cascades (Leibold 1989, Power 1992, Abrams 1993, Wootton et al. 1996, Leibold et al. 1997, Agrawal 1998). For instance, strength of cascades may hinge on the presence of inedible plants or abundance of key herbivores, such as *Daphnia* in freshwater lakes (Carpenter and Kitchell 1993, Elser et al. 2000b). However, this heterogeneity hypothesis did not receive supported by a recent meta-analysis (Borer et al. 2005). Nonetheless, heterogeneity, stoichiometry, and trophic cascade theory could be studied simultaneously in future theoretical work. Theory and data suggest links between stoichiometric food quality, species composition of herbivores, and species and stoichiometric composition of producers (Diehl 2003, Hall 2004, Hall et al. 2004, 2006, 2007, Loladze et al. 2004, Moe et al. 2005).

Our findings have two implications for understanding inter-ecosystem variation in cascade strength and for future development of stoichiometric food web theory. First, factors other than nutrient:carbon ratio of plants (fixed or minimal stoichiometry) may be responsible for the pattern of stronger top-down control in water than on land. A number of other hypotheses based on size and growth rates have been proposed, and these might show more promise for explaining the pattern of systematic variation (Shurin et al. 2002, 2006, Borer et al. 2005, Shurin and Seabloom 2005). Our models never showed stronger cascades as a consequence of increasing static or minimal nutrient:carbon ratio of plants, the basis for the stoichiometric portion of the food quality hypothesis. However, they do show stronger cascades with increases in digestibility of plants (the other component of food quality considered here), and the model with flexible stoichiometry of plants suggests that these increases can indirectly produce a correlation between higher nutrient:carbon stoichiometry and stronger cascades. Second, the models revealed that predators can indirectly influence the extent of nutrient limitation of herbivore production across gradients of productivity. This latter finding supports a growing body of evidence that food web processes can influence the stoichiometry of interactions among species.

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Appendix 1. Equilibria, trophic indices and stability of tri-trophic model with static stoichiometry of plants.

In this Appendix, we present equilibria and trophic indices and characterize stability of the tri-trophic models with static stoichiometry of plants. We also consider how equilibria and trophic indices respond to variation in four key parameters: nutrient enrichment (S), plant digestibility/maximal conversion efficiency (e), nutrient content of producers (q_P), and nutrient content of herbivores (q_H), as summarized in Table 2 and A1.

Equilibria

The model with static stoichiometry produces three sets of non-trivial equilibria. The plant-only equilibrium occurs when $P_1^* = S/q_P$ (which only requires that $S > 0$). The bi-trophic, plant (P)-herbivore (H) equilibrium when carbon limits production of herbivores is:

$$P_{2,CL}^* = (m + \sigma)/(ae) \tag{A1a}$$

$$H_{2,CL}^* = \frac{r(S - q_P P_{2,CL}^*)}{a + q_H r} = \left(\frac{r}{a}\right) R_{2,CL}^* \tag{A1b}$$

$$R_{2,CL}^* = aH_{2,CL}^*/r \tag{A1c}$$

which requires for feasibility that $S > q_P P_{2,CL}^*$. This requirement states that the amount of nutrients supplied to the ecosystem must exceed the amount of nutrient sequestered in the minimal carbon requirement of the herbivore ($q_P P_{2,CL}^*$), which increases as plants become more nutrient rich (higher q_P). At

this equilibrium, plants respond only to e, not the other parameters of interest (S, q_P, q_H). Freely available nutrients ($R^*_{2,CL}$) increase with enrichment, and herbivore biomass ($H^*_{2,CL}$) equals the ratio of production (from uptake of free nutrients) to grazing losses of the plant (see Table A1 for other effects). Both $R^*_{2,CL}$ and $H^*_{2,CL}$ decrease as stoichiometry of plants (q_P) or herbivores (q_H) becomes higher.

With enough enrichment, this system can support carnivores (C). Specifically, this occurs when nutrient supply exceeds:

$$S > R^*_{3,CL} + q_H H^*_{3,CL} + q_P P^*_{2,CL} \qquad (A2)$$

which demands that external nutrient supply (S) exceed freely available nutrients ($R^*_{3,CL}$), nutrient contained in herbivores ($q_H H^*_{3,CL}$) at the tri-trophic equilibrium, and nutrients contained in plants fulfilling the herbivore's minimal carbon requirement ($q_P P^*_{2,CL}$). When feasible, this tri-trophic equilibrium becomes:

$$H^*_{3,CL} = (m_C + \sigma_C)/(a_C e_C) \qquad (A3a)$$

$$R^*_{3,CL} = a H^*_{3,CL}/r \qquad (A3b)$$

$$C^*_{3,CL} = \frac{ae(S - R^*_{3,CL} - q_H H^*_{3,CL} - q_P P^*_{2,CL})}{aeq_C + a_C q_P} \qquad (A3c)$$

$$P^*_{3,CL} = \left(\frac{a_C}{ae}\right) C^*_{3,CL} + P^*_{2,CL} \qquad (A3d)$$

In this three-level food chain, herbivore biomass is determined solely by traits of the carnivore (i.e. those with a "C" subscript), not the parameters of interest (S, e, q_P, q_H; Table A1). However, producer biomass increases with enrichment but decreases with the other parameters. In particular, plant biomass decreases as nutrient:carbon ratio of herbivores (q_H) increases because herbivores sequester more nutrient (i.e. $\partial q_H H^*_{3,CL}/\partial q_H > 0$) that cannot be used for carnivores and plants. Also, higher nutrient:carbon ratio of producers yields less producers. However, these decreases of plant biomass with q_P and q_H do not reflect an effect of stoichiometry on efficiency of herbivore production (since carbon limited production of herbivores implies that this efficiency is fixed at the maximal efficiency).

These two carbon-limited equilibria characterize traditionally-studied food chains, where stoichiometric imbalance between producers and herbivores does not influence efficiency of production of herbivores. However, once stoichiometry becomes explicit, herbivores can become limited by nutrients. In systems without carnivores, the herbivore becomes nutrient-limited at equilibrium when nutrient content of the producer (q_P) is a quantity less than that of the herbivore (q_H):

$$q_P < q_H m/(m + \sigma) \qquad (A4)$$

which involves death rate (m) and respiration rate (σ) of the herbivore and implies that $q_P < q_H$. When nutrients limit production of herbivores, the bi-trophic, plant–herbivore equilibrium changes to:

$$P^*_{2,NL} = \frac{q_H}{q_P}\left(\frac{m}{ea}\right) = \frac{QP^*_H}{q_P} \qquad (A5a)$$

$$H_{2,NL} = \frac{r(S - QP^*_H)}{a + q_H r} = \left(\frac{r}{a}\right) R^*_{2,NL} \qquad (A5b)$$

$$R^*_{2,NL} = a H^*_{2,NL}/r \qquad (A5c)$$

One can show that, given Eq. A4, this plant equilibrium ($P^*_{2,NL}$) exceeds that with a carbon-limited herbivore. Consequently, both freely available nutrient ($R^*_{2,NL}$) and herbivore biomass ($H^*_{2,NL}$) are lower with nutrient limited than carbon limited production of herbivores. The nutrient-limited plant equilibrium also involves a new synthetic quantity, QP^*_H which is the minimal nutrient requirement of the herbivore (Hall 2004, Hall et al. 2006). At this equilibrium, plant biomass does not respond to enrichment but does increase if production of herbivores becomes more efficient (i.e. higher e or q_P, lower q_H; Table A1). Thus, plant biomass in this bi-trophic system depends on stoichiometry-mediated transfer efficiency. Conversely, herbivore biomass increases with enrichment and two of the three factors increasing realized efficiency (higher e, lower q_H). Grazers also decrease with q_H because of nutrient allocation, since higher nutrient:carbon ratio of the herbivore yields lower free nutrient, and hence lower herbivore biomass.

If nutrient supply is high enough, a carnivore can persist with the nutrient-limited herbivore and the plant. Invasion of this carnivore requires that:

$$S > R^*_{3,NL} + q_H H^*_{3,NL} + QP^*_H \qquad (A6)$$

which is the amount of freely available nutrients ($R^*_{3,NL}$), the amount necessary to support plant production, and nutrient sequestered in herbivores ($q_H H^*_{3,NL}$) plus the minimal sequestered nutrient requirement of the herbivore (QP^*_H). Once the carnivore (C) invades, the tri-trophic equilibrium becomes:

$$H^*_{3,NL} = H^*_{3,CL} \qquad (A7a)$$

$$R^*_{3,NL} = a H^*_{3,NL}/r \qquad (A7b)$$

$$C_{3,NL} = ae\left(\frac{S - R^*_{3,NL} - q_H H^*_{3,NL} - QP^*_H}{aeq_C + a_C q_H}\right) \qquad (A7c)$$

$$P^*_{3,NL} = \frac{q_H}{q_P}\left(\frac{a_C}{ae}\right) C^*_{3,NL} + P^*_{2,NL} \qquad (A7d)$$

In this three-species case, herbivore biomass and freely available nutrient are set by the traits of the producer and plant; these quantities equal those for the tri-trophic equilibrium with carbon limited production of

herbivores (Eq. 3). However, in this nutrient-limited equilibrium, plant biomass increases more quickly and carnivore biomass increases less quickly with enrichment (S) than in the analogous carbon-limited case. Producer biomass also decreases with more efficient production of herbivores when realized efficiency is driven by e and producer stoichiometry, q_P. However, we do see tension between the effects of herbivore stoichiometry, q_H, on conversion efficiency and nutrient allocation. To understand this conflict mathematically and biologically, we can use the product rule from calculus. The product rule tells us that if function $f \equiv q_H/q_P$ (i.e. the efficiency term involving q_H) and function g is set equal to $a_C C^*_{3,NL}/(ae)$, then $\partial(fg)/\partial q_H$ equals $f(\partial g/\partial q_H) + g(\partial f/\partial q_H)$. The efficiency component $(\partial f/\partial q_H)$ naturally increases with q_H, while biomass allocation component decreases with q_H since:

$$\frac{\partial g}{\partial q_H} = \frac{\partial C^*_{3,NL}}{\partial q_H} < 0 \tag{A8}$$

The allocation component exceeds the efficiency component (yielding $\partial P^*_{3,NL}/\partial q_H < 0$) until the system is enriched past:

$$S = R^*_{3,NL} + q_H H^*_{3,NL}\left(\frac{a_C}{mq_C}QP^*_H + 2\right) - mq_C/a_C \tag{A9}$$

This switch point can only happen with positive densities of the three species if:

$$\frac{q_P}{q_H} > \frac{q_H H^*_{3,NL}}{q_C/a_C + q_H H^*_{3,NL}} \tag{A10}$$

which requires fairly high nutrient content of producers relative to herbivores. If this stoichiometric trait requirement is satisfied, past this point of nutrient enrichment, the stoichiometry-mediated efficiency component prevails.

The herbivore in tri-trophic case can switch from carbon to nutrient limitation with increasing enrichment, assuming that plant stoichiometry is less than herbivore stoichiometry (i.e. $q_P < q_H$). This switch occurs when nutrient supply surpasses this level:

$$S = R^*_{3,NL} + q_H H^*_{3,NL} + \frac{q_H \sigma}{q_H - q_P}\left(\frac{q_C}{a_C} + \frac{QP^*_H}{m}\right) - \frac{mq_C}{a_C} \tag{A11}$$

As it turns out, this switch from carbon to nutrient limitation requires that herbivores would be carbon-limited in bi-trophic chains (i.e., $q_P > q_H m/(m+\sigma)$, Eq. A4). Conversely, if nutrients limit production of herbivores without predation (bi-level chain), then nutrients always limit production of herbivores with predation (tri-level chain). This switch point between carbon and nutrient limitation (Eq. A11) occurs when

the nutrient contained in producers in the carbon-limited, tri-trophic chain $(q_P P^*_{3,CL})$ just meets the minimal nutrient demands of the herbivore in the presence of the carnivore $(QP^*_{H,3} \equiv q_P P^*_{3,NL}$; see Fig. 2B for an illustration). In tri-trophic chains, predation on herbivores drives these minimal nutrient demands of herbivores $(QP^*_{H,3})$ beyond the herbivore's minimal demands without carnivores (QP^*_H) with enrichment. In fact, predation can drive $QP^*_{H,3}$ beyond that provided by the tri-trophic system with carbon limited production of herbivores $(q_P P^*_{3,CL})$. Grazers become nutrient-limited past the switch point because at that point, $QP^*_{H,3} > q_P P^*_{3,CL}$.

Trophic indices

General approach

The response of the tropic indices to change in nutrient enrichment (S), plant digestibility (e), and stoichiometry of plants (q_P) and herbivores (q_H) is readily predicted by the quotient rule from calculus. An example using this rule involves the response of the plant trophic index (P^*_3/P^*_2) to plant digestibility, e; the rule states that the change in PTI with e:

$$\frac{\partial(P^*_3/P^*_2)}{\partial e} = \frac{P^*_2(\partial P^*_3/\partial e) - P^*_3(\partial P^*_2/\partial e)}{(P^*_2)^2} \tag{A12}$$

which also implies that response of the plant trophic index to e is positive when $(\partial P^*_3/\partial e)/P^*_3 > (\partial P^*_2/\partial e)/P^*_2$, or the per capita effect of change in e on plants in the tri-trophic chain is larger than that on plants in bi-trophic chains. This result explains why PTI increases with e despite that plant biomass actually decreases with e in both chains – the per capita decrease is larger in bi-trophic chains. To calculate the remaining responses of the two trophic indices to other parameters, one would change the P^*_j values to H^*_j values and e to other parameters as appropriate. Most of the relevant partial derivatives are presented in Table A1, and behavior of the trophic indices can usually be understood from them and Eq. A12 (again, modified appropriately).

Detailed results

PTI and plant stoichiometry (q_P). In contrast to the expectation for plant stoichiometry $(q_P$; Eq. 5a), we find that trophic indices for plants (PTI) decrease or do not change with increasing q_P. More specifically, we see decreases in PTI with higher q_P rather than increases when production of herbivores is carbon limited in bi-level systems (case 1 and 2, relatively high q_P) but no effect of q_P on PTI when herbivores are nutrient limited in bi-level chains (case 3, relatively low q_P; Table 2, Fig. 3). To understand this result, we must study effects of q_P on both the numerator (tri-level biomass) and denominator (bi-level biomass) of

PTI (Table A1). Plant biomass in tri-trophic chains decreases with q_P as it does for maximal digestibility of plants (e; Table A1 and below). This q_P effect with nutrient-limited herbivores (case 2 and 3) involves stoichiometry-mediated conversion efficiency. When carbon limits herbivore production (case 1), plant biomass decreases with q_P, but q_P does not influence conversion efficiency. Thus, the numerator of PTI responds to q_P in all cases as it does for e (even if not due to its effects on conversion efficiency). However, the denominator of PTI (plant biomass in two-level chains) does not respond in an analogous manner. In bi-level chains with carbon-limited herbivores, plant biomass does not respond to q_P because plant biomass is set at the herbivore's minimal carbon requirement (which is not a function of q_P). Thus, for case 1 and 2, without a response of the denominator, PTI decreases rather than increases with q_P for (Fig. 3). In case 3, plants decrease with q_P in nutrient-limited herbivores in tri-level and bi-level chains due to effects on conversion efficiency, a result which resembles that for digestibility e. However, for this third case, stoichiometry (q_P)-driven effects on both numerator and denominator of PTI cancel, leaving no change in PTI (Fig. 3).

HTI and plant stoichiometry (q_P). Changes in plant stoichiometry (q_P) also affects the trophic index for herbivores (HTI) in ways that contrast with results involving digestibility/maximal conversion efficiency (e; Table 2, Fig. 3). To understand this finding, we first point out that, as with e, herbivore biomass (H_3^*) does not respond to q_P in tri-trophic chains because it is set at the minimal carbon requirement of the carnivore (and hence only responds to traits of the carnivore). Thus, the discrepancy lies in the response of the denominator (bi-level biomass) rather than the numerator (tri-level biomass) of HTI (Table A1). In cases with carbon-limited denominators (no. 1 and 2), herbivores decrease (rather than increase) with higher q_P. This effect occurs because herbivore biomass is proportional to nutrients in the system (S) not locked in tissues of the plant ($q_P P_{2,CL}^*$). This latter component increases with q_P (i.e. $\partial q_P P_{2,CL}^*/\partial q_P > 0$), ultimately yielding less herbivore biomass, and therefore smaller HTI (Fig. 3). In the nutrient-limited case (no. 3), herbivores do not respond to q_P. Their biomass is proportional to S minus the nutrient contained in their minimal requirement for nutrient sequestered in plant tissues, QP_H^*. Since this nutrient requirement does not depend on q_P, HTI does not respond to q_P in this case (Fig. 3).

PTI and herbivore stoichiometry (q_H). However, the trophic indices for plants (PTI) can respond as predicted (Eq. 5) to variation in herbivore stoichiometry (q_H). Yet, the mechanisms driving these patterns sometimes involve feedbacks via nutrient allocation among trophic levels rather than the direct effects of q_H on conversion efficiency. For example, we see the allocation effect in three level chains. Regardless of which resource limits production of herbivores, carnivores determine biomass of herbivores (but not q_H); thus, higher q_H increases nutrient sequestered in herbivores ($q_H H_3^*$), ultimately decreasing nutrient available for carnivores. As a result, higher q_H yields less carnivore biomass. Since plant biomass is proportional to carnivore biomass, this allocation effect of q_H decreases plant biomass. In carbon limited three-level chains (case 1), only the allocation effect prevails. However, in nutrient limited, three-level chains, an effect of stoichiometry-mediated conversion efficiency operates in the opposite direction: higher q_H should increase plant biomass because it decreases conversion efficiency. Thus, in three level systems with nutrient limited production of herbivores (case 2 and 3), the response of plant biomass to q_H reflects tension between the allocation effect (decreasing $P_{3,NL}^*$) and the efficiency effect (increasing $P_{3,NL}^*$). The efficiency effect prevails at high nutrient supply; along an enrichment gradient of S, we see first increases, then decreases in $P_{3,NL}^*$ with q_H. Then, in two-level chains, we see no response of plant biomass to q_H in carbon-limited situations (case 1 and 2) because the herbivore's minimal carbon requirement does not involve q_H, and we see increases in plant biomass with q_H when nutrients limit herbivory due to an efficiency effect (case 3). Putting this together, we find that in case 1, PTI decreases with increasing q_H (Fig. 3) through an allocation effect and despite that q_H changes the numerator of PTI differently than does maximal digestibility (e). Thus, the strength of cascades (PTI) responds as predicted to q_H (Eq. 5b) – not because herbivores are more efficient at reducing plant biomass but instead because of an allocation effect. In case 2, we see a shift in response of PTI away from the predicted effect (Eq. 5b) with enough enrichment (Fig. 3). Paradoxically, this shift occurs as the stoichiometry-mediated efficiency effect (involving q_H/q_P) outweighs the allocation effect (involving $q_H H_3^*$). Finally, in case 3, the conversion effects of q_H are identical in numerator and denominator and thus cancel. Therefore, the allocation effect prevails, and PTI responds as predicted (but again, due to mechanisms not anticipated by Eq. 5b; Fig. 3).

HTI and herbivore stoichiometry (q_H). Finally, the trophic index for herbivores (HTI) increases as anticipated with herbivore stoichiometry (q_H). The numerator (tri-level biomass) does not respond to q_H because, as we stated above, only traits of the carnivore determine biomass of herbivores. In both bi-level chains, higher q_H yields less herbivore biomass. This result arises because higher q_H lowers freely available nutrients, R_2^*; H_2^* is directly proportional to

nutrient uptake, and so decreases with R_2^*. In situations with nutrient limited production of herbivores, this response of herbivore biomass to q_H also involves the fact that higher q_H elevates the herbivore's minimal requirement for nutrients sequestered in plant biomass (QP_H^*).

A higher minimal requirement implies lower nutrient available for partitioning into herbivore biomass. Consequently, though the effects of q_H on the denominator of HTI, we find results that match our verbal predictions (Eq. 5b), but this match arises due to allocation phenomena rather than stoichiometry-mediated conversion efficiency.

Stability

Technically speaking, conclusions concerning trophic indices that were derived from the equilibria above strictly apply only to situations in which the relevant equilibria are stable. Stability of these systems can be derived using the familiar Routh-Hurwitz criterion. In system with only plants and a carbon-limited herbivore, the Jacobian matrix becomes:

$$\begin{bmatrix} -rq_p P_{2,CL} & -(a+rq_H)P_{2,CL}^* \\ eaH_{2,CL} & 0 \end{bmatrix} \tag{A13}$$

Stability requires that the trace and the determinant of this matrix are both negative. Based on signs of its elements alone, one can readily see that this system is

stable. The same general result emerges for the analogous two-level case with the nutrient-limited herbivore.

Moving on to the three species chain, we find a new Jacobian matrix (J) for the case with the carbon-limited herbivore:

$$\begin{bmatrix} -rq_p P^* & -(a+rq_H)P^* & -rq_C P^* \\ eaH^* & 0 & -a_C H^* \\ 0 & e_C a_C C^* & 0 \end{bmatrix} \tag{A14}$$

which has the characteristic polynomial $\lambda^3 + A_1\lambda^2 + A_2\lambda^3 + A_3$, where λ are the eigenvalues and A_j are the coefficients. For a three dimensional matrix, the Routh-Hurwitz criteria for stability require from these coefficients that $A_1 > 0$, $A_3 > 0$, and $A_1 A_2 > A_3$. The first criteria is met because $A_1 = -J_{11}$ (where J_{nk} correspond to elements of J). The criterion $A_3 > 0$ is also always met (since $-J_{32}(J_{13}J_{21} - J_{11}J_{23})$ is always positive, based on signs of J). The third criterion ($A_1 A_2 > A_3$) indicates that instability would emerge if:

$$P_{3,CL}^* > \frac{q_C}{q_P}\left(\frac{a_C e_C}{a + q_H r}\right)C_{3,CL}^* \tag{A15}$$

which does not occur as long as the three-level equilibrium is feasible. A similar result follows from the Jacobian matrix of the three-level system where herbivores are nutrient limited. Thus, this three-level system is stable if it is feasible.

Appendix 2. Equilibria, trophic indices, and stability of tri-trophic model with dynamic stoichiometry of plants (available online as Appendix O15875 at www.oikos.ekol.lu.se)

Table A1. Signs of partial derivatives of equilibrial biomass of plants (P_j^*) and herbivores (H_j^*) derived from the model with static stoichiometric of the producer with respect to each parameter, where "+" indicates increase in the equilibrium with an increase in the parameter, "−" indicates a decrease in the equilibrium, and "0" indicates no change.

Resource[a]	Quantity[b]	Nutrient supply, S	Maximum efficiency, e	Plant nutr:C, q_P	Grazer mutr:C, q_H
Carbon	P_2^*	0	−	0	0
	H_2^*	+	+	−	−
	P_3^*	+	−	−	−
	H_3^*	0	0	0	0
Nutrient	P_2^*	0	−	−	+
	H_2^*	+	+	0	−
	P_3^*	+	−	−	−/+[c]
	H_3^*	0	0	0	0

[a] "Carbon" means that carbon limits production of herbivores; "nutrient" indicates nutrient limitation
[b] Subscript refers to number of trophic levels ("2" for bi-level, "3" for tri-level)
[c] Sign of this partial derivative depends upon level of nutrient enrichment, S (Eq. A9)