



2.1 | FROM FOOD WEBS TO ECOLOGICAL NETWORKS: LINKING NON-LINEAR TROPHIC INTERACTIONS WITH NUTRIENT COMPETITION

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Food webs traditionally specify the structure of who eats whom among species within a habitat or ecosystem. A yet-to-be realized ideal is a food web model that includes the quantity consumed and the ecological relevance of every trophic interaction among all species within a community. Far short of this ideal, current food web models provide partial yet critically important information about species' extinction risks and relative abundances by describing the dynamics of energy flow and consumer species' biomasses (Yodzis, 1998; Borrvall et al., 2000). This exclusive focus on feeding relationships or "trophic interactions" enables models of complex food webs (Brose et al., 2003; Kondoh, 2003a; Williams and Martinez, 2004a) to also incorporate exploitative and 'apparent' competition (Holt et al., 1994; Holt and Lawton, 1994) among heterotrophs. However, this focus ignores similar interactions among autotroph producers or "basal species" consuming abiotic resources (e.g., nutrients, light, etc.) along with other 'non-trophic' interactions such as many forms of facilitation and competition. In particular, the logistic growth of

the food webs' producers or 'basal' species in these models typically approximates nutrient- or detritus-dependent growth of basal species each non-competitively consuming an independent pool of resources.

Explicit models of shared nutrient consumption including competition among producers for multiple resources (Tilman, 1982; Grover, 1997; Huisman and Weissing, 1999) are largely separate from trophic ecology. Still, many experimental and theoretical studies bridge this gap by elucidating how predation interacts with other non-trophic processes, such as nutrient consumption, to regulate species distribution and abundance (Menge and Sutherland, 1987; Leibold, 1996; Proulx and Mazunder, 1998; Gurevitch et al., 2000; Chase et al., 2002, and references therein). Many of these synthetic insights are based on (1) linear trophic interactions, (2) competition for one nutrient resource, (3) very simple communities (i.e., <4 spp), and (5) an equilibrium-based analytical framework. Such insights are suspect due to the discrepancy between 1-5 and frequently observed nonlinear population dynamics (Kendall et al., 1998), much greater trophic diversity and complexity (Williams and Martinez, 2000), and multiple plant nutrients in nature.

Here, we present an approach for exploring the interplay of complex trophic interactions and consumption of multiple abiotic resources among producer species using non-linear and non-equilibrium numerical simulations. This approach transforms simple food-web models into more general models of complex ecological networks and can be scaled up to systems with many more species and abiotic resources. We first describe the model and then illustrate its potential for exploring the interplay between abiotic resource competition and trophic interactions.

THE MODEL

Our model couples a nutrient-producer model (León and Tumpson, 1975; Tilman, 1982; Grover, 1997; Huisman and Weissing, 1999) with a bioenergetic model of herbivore-producer interactions (Yodzis and Innes, 1992). Both approaches have simulated non-equilibrium species dynamics that have provided important insights in this area of research that are difficult to obtain with linear, equilibrium-based models (McCann et al., 1998; Huisman and Weissing, 1999). However, these well established models had yet to be synthesized into one framework.

Our synthesis begins with a nutrient-producer model consisting of five producer species competing for five limiting resources and then expands

producer-herbivore components by adding five herbivores each of which consume one of the producer species. One producer called the “guzzler” has the highest rate of consumption of the most limiting nutrient which causes it to become the competitive dominant in many nutrient-producer studies. The term “guzzler” avoids confounding a component of a very general model with results from its numerical simulation. It also avoids contradictory terminology when the conventionally termed “competitive dominant” fails to numerically dominate the community. Instead, ‘competitive dominance’ as used here describes results of models that apply to different species depending on the context rather than a context-independent inherent species trait. In accordance with these fundamental distinctions, the other producer species with lower resource consumption rates are called “sippers.” Such species are often called ‘competitively subordinate’ in nutrient-producer studies.

Our model of herbivore-producer biomass dynamics is based on a widely used (McCann and Yodzis, 1994; McCann and Hastings, 1997; McCann et al., 1998) bioenergetic model of trophic interactions (Yodzis and Innes, 1992) that has been recently extended to n species (Brose et al., 2003; Williams and Martinez, 2004a). The rate of change in the biomass (B) of species i with time t is modeled as:

$$B_i'(t) = G_i(N) - x_i B_i(t) + \sum_{j=1}^n (x_i y_{ij} F_{ij}(B) B_j(t) - x_j y_{ji} F_{ji}(B) B_j(t) / e_{ji}) \quad (1)$$

where $G_i(N)$ describes the growth of producer species; x_i is the mass-specific metabolic rate of species i ; y_{ij} is a measure of the maximum ingestion rate concerning resource j per unit metabolic rate of species i ; and e_{ji} is the biomass conversion efficiency of species j consuming i (see Yodzis and Innes, 1992, for parameter details). We used a type II functional response for the flow of biomass from resource j to consumer i :

$$F_{ij}(B) = \frac{B_j(t)}{B_j(t) + B_{0ji}} \quad (2)$$

where B_{0ji} is the “half saturation density” or density of the resource at which the consumer attains half its maximal rate of consumption (Holling, 1959a, b).

To avoid the ambiguous use of “resource” (see eq. 1), we hereafter call producer resources N_i “nutrients.” These are still broadly defined and may include any abiotic resource that is subject to constant turnover such as light or nitrogen. We examine the dynamics resulting from shared abiotic resources or nutrients by modifying the producer growth

of Yodzis and Innes' (1992) original model using a well-studied nutrient consumption model:

$$G_i(N) = r_i \text{MIN} \left(\frac{N_1}{K_{1i} + N_1}, \dots, \frac{N_5}{K_{5i} + N_5} \right) B_i(t) \quad (3)$$

that depends on the concentrations of five limiting nutrients N_l . This model has been widely used in plant ecological theory (León and Tumpson, 1975; Tilman, 1982; Grover, 1997; Huisman and Weissing, 1999) and experiments (Tilman, 1977; Huisman et al., 1999). In (3), r_i is the maximum growth rate of species i that is non-zero only for producer species, K_{li} is the half saturation constant for nutrient l , and MIN is the minimum operator. Therefore, $G_i(N)$ follows a Monod equation and is determined by the nutrient that is most limiting. The variation in the density of nutrient l is given by

$$N_l'(t) = D(S_l - N_l) - \sum_{i=1}^n (c_{li} G_i(N)) \quad (4)$$

where c_{li} is the content of nutrient l in species i . Nutrients are exchanged at a turnover rate D with a supply concentration of S_l , and removal depends on the current nutrient concentration in the system, N_l . Species have biomass loss rates due to metabolism but not turnover since species are not assumed to be passively drifting out of the system. We used Yodzis and Innes' (1992) empirical estimates for the bioenergetic parameters: $y_{ij} = 6$ for invertebrates, $y_{ij} = 3.9$ for ectotherm vertebrates, $y_{ij} = 0$ for producers, $e_{ji} = 0.45$ for herbivores and $B_{0ji} = 0.5$. We assumed resource-consumer body size ratios, L , of 0.1 and, in the spirit of McCann and Yodzis (1994), calculated consumer metabolic rates as

$$x_i = ax_p [L^{0.25}]^{T-1} \quad (5)$$

where x_p is the metabolic rate of primary producers (0.2), T is the consumer's trophic level and a is a constant that equals 0.54 for invertebrates and 3.48 for ectotherm vertebrates (Yodzis and Innes, 1992). This yields metabolic rates of 0.06 for invertebrate and for 0.39 ectotherm vertebrate herbivores. The parameters of the growth function are $D = 0.5$, $r_i = 1$ and $S_l = 1$. The first nutrient is the one most needed by all producer species as it has the highest content in their biomasses ($c_{1i} = 1$ and $c_{ki} = 0.5$ with $k > 1$). The half saturation densities of producer species' growth are given by:

$$K_{ii} = \begin{pmatrix} K' & 0.12 & 0.12 & 0.12 & 0.12 \\ 0.06 & 0.20 & 0.16 & 0.10 & 0.02 \\ 0.10 & 0.06 & 0.20 & 0.16 & 0.06 \\ 0.16 & 0.10 & 0.06 & 0.20 & 0.09 \\ 0.20 & 0.16 & 0.10 & 0.06 & 0.09 \end{pmatrix}$$

where rows represent five nutrients and columns five producer species.

Since all producer species have similar r_i and x_p , the lowest half saturation density ($K' < 0.12$) defines producer species 1 or "guzzler" as the most voracious consumer of N_1 per unit biomass when N_1 is limited (Huisman and Weissing, 2001). The four other "sipper" producer species consume N_1 at smaller rates on a per biomass basis. We varied the strength of the nutrient uptake hierarchy by making guzzlers relatively stronger ($K' = 0.05$) or weaker ($K' = 0.11$) while ensuring that both 'strong' and 'weak' guzzlers consume N_1 more effectively than do sippers. Note that guzzling and sipping only refers to the nutrient most needed by the producers (N_1) and not to the four other nutrients ($N_{2,3,4,5}$) present in smaller concentrations in the producers' biomass. Simulations begin with randomly assigned biomass abundances ($B_i(0) = 0.05$ to 1) and end after 2,000 time steps.

This model framework allows us to explore the following questions:

1. How do specialist herbivores alter the patterns of coexistence and relative abundances among producers that exhibit a nutrient consumption hierarchy? How does this effect vary with herbivore physiology (e.g., invertebrate vs. ectotherm vertebrate)?
2. How does the strength of the nutrient consumption hierarchy among producers influence the relative abundance and persistence of herbivores?

RESULTS

In the simpler nutrient-producer model, the modeled nutrient consumption hierarchy directly results in a competitive hierarchy where the guzzler (P1) quickly out-competes the sippers (see P2-5, Figure 1). The strong guzzler reaches abundances ($B_1 > 1.21$) close to its maximum (1.23) after 50 time steps and all sippers are extinct ($B_i < 10^{-30}$) after 1,200 time steps (Figure 1A). The weak guzzler, however, does not dominate the sippers until after 165 time steps (Figure 1B) and attains abundances ($B_1 > 1.21$) close to the strong guzzler's maximum at $t > 1150$. The weak guzzler also allows for the sippers to persist with very low biomasses

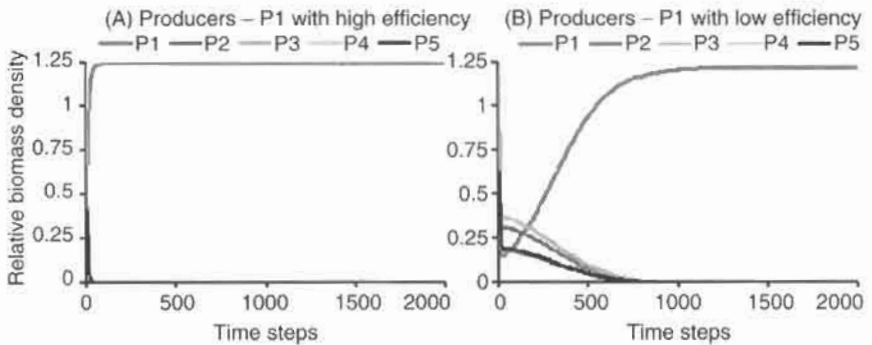


FIGURE 1 | Biomass evolution in producer communities. The guzzler (P1) is strong (A) or weak (B). (See also color insert.)

($B_i < 10^{-5}$) until the end of the simulations ($t = 2000$). Similar results were obtained in replicated runs with varying random initial abundances (data not shown).

The addition of five specialist invertebrate herbivores allows all producers to co-exist independent of the strength of the nutrient consumption hierarchy (Figure 2). In this scenario, the weak guzzler's mean abundance (0.21) is similar to the strong guzzler's (0.24), and both are

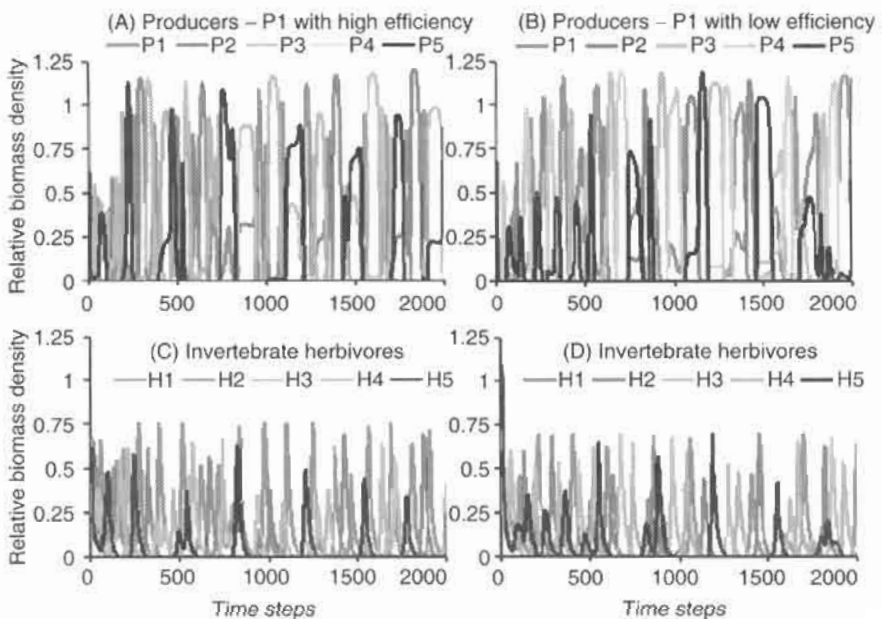


FIGURE 2 | Biomass evolution in producer-invertebrate herbivore communities. The guzzler (P1) is strong (A, C) or weak (B, D). (See also color insert.)

comparable to the sippers' mean abundances (P2-5, mean = 0.16–0.22). The abundance of the strong guzzler's herbivore (see Figure 2C, H1: mean $B_i = 0.15$) exceeds the other herbivores' abundances by a factor of three (see Figure 2C, H2-5: mean $B_i = 0.05$). In contrast, the weak guzzler's herbivore reaches lower abundances (see Figure 2D, H1: mean $B_i = 0.08$) and does not markedly exceed that of the other herbivores (see Figure 2D, H2-5: mean $B_i = 0.06$ –0.07).

Consistent with the results for invertebrate herbivores, adding five specialist ectotherm vertebrate herbivores also allows all producer species to persist (Figure 3). The presence of a strong guzzler allows producers to coexist at roughly similar mean biomass densities (see Figure 3A), whereas weak guzzlers cause a sipper's biomass to dominate (see Figure 3B). In replicated runs, the dominant sipper's identity depends on initial abundances (data not shown). All herbivore species persist at low densities when the guzzler is strong, and the consumer of the strong guzzler dominates the herbivore biomass (see Figure 3C). When the guzzler is weak, sippers have lower abundance minima and their herbivores go extinct (see Figure 3D). The sipper whose herbivore goes extinct first consequently dominates the other producer species. The guzzler's herbivore, however, always persists.

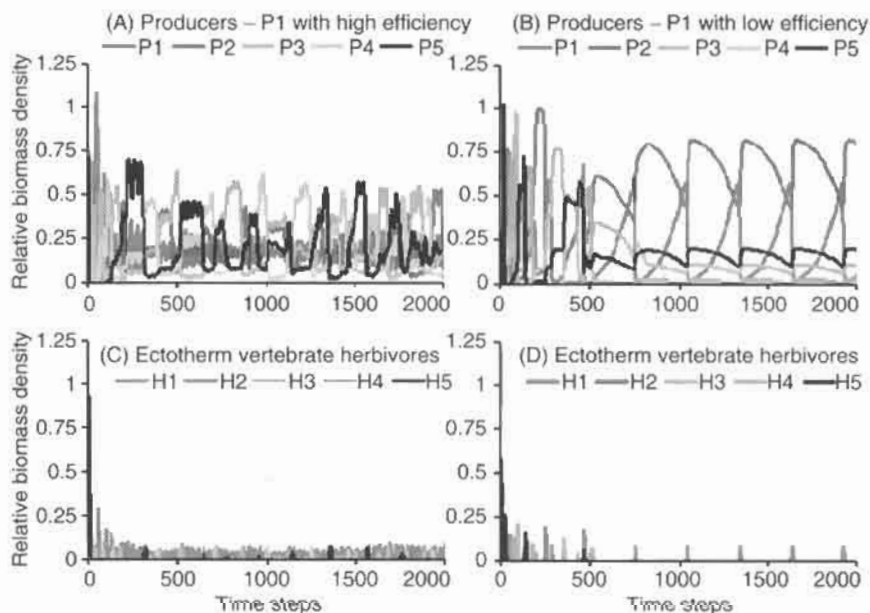


FIGURE 3 | Biomass evolution in producer-ectotherm vertebrate herbivore communities. The guzzler (P1) is strong (A, C) or weak (B, D). (See also color insert.)

DISCUSSION AND CONCLUSIONS

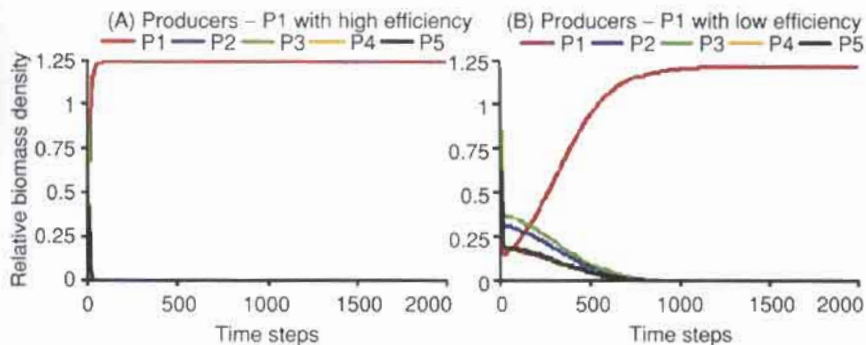
We have coupled a plant-nutrient competition model with a dynamic food web model. In contrast to prior studies, we simulated non-equilibrium plant-herbivore food webs with non-linear trophic interactions and producers whose growth depended on several limiting nutrients. Our results demonstrate that the herbivore physiology and strength, as well as the presence of a nutrient consumption hierarchy among producers strongly affect producer and herbivore population dynamics, relative abundances, and coexistence. Specialized herbivory allowed producer species to co-exist despite asymmetric nutrient consumption that otherwise generates competitive exclusion. This is consistent with empirical observations of predation promoting coexistence of competing prey (Gurevitch et al., 2000; Chase et al., 2002). Producers co-exist because a specialized herbivore effectively controls the abundance of the most effective nutrient consumer among the producers—the guzzler. Since there is no trade-off between nutrient uptake efficiency and vulnerability to herbivory, this effect does not rely on the assumption that the guzzler is preferentially consumed. Rather, this strong ‘keystone-like’ effect emerged from dynamics that quickly transformed the guzzler’s higher nutrient uptake into increased abundance of its herbivore relative to other herbivores. These results suggest that changes in the producers’ consumptive abilities can have “bottom-up” effects on the relative abundance distributions of higher trophic levels, which in turn regulate the strength of top-down effects. Lower nutrient supply or stronger herbivory, however, cause producer species to go extinct (data not shown), which is consistent with empirical findings (Proulx and Mazunder, 1998; Chase et al., 2002).

Our results illustrate how consumer physiology associated with the difference between ectotherm vertebrates and invertebrates might strongly affect plant-herbivore dynamics. The metabolic rates determine the herbivores’ biomass loss per time step. All else being equal, the higher mass-specific metabolic rates of ectotherm vertebrates are therefore responsible for lower biomass minima. This reduces the abundance of the sippers’ ectotherm vertebrate herbivores enough for the latter to go extinct, thus releasing sippers from top-down control. Our non-equilibrium approach shows that sippers regularly drop to lower abundance minima than the guzzler does, which makes extinction of the sippers’ ectotherm vertebrate herbivores more likely. Initial abundances determine which sipper’s herbivore goes extinct first. Extinction releases that sipper from top-down control and allows it to out-compete all other producers. In contrast, invertebrate herbivores achieve higher relative

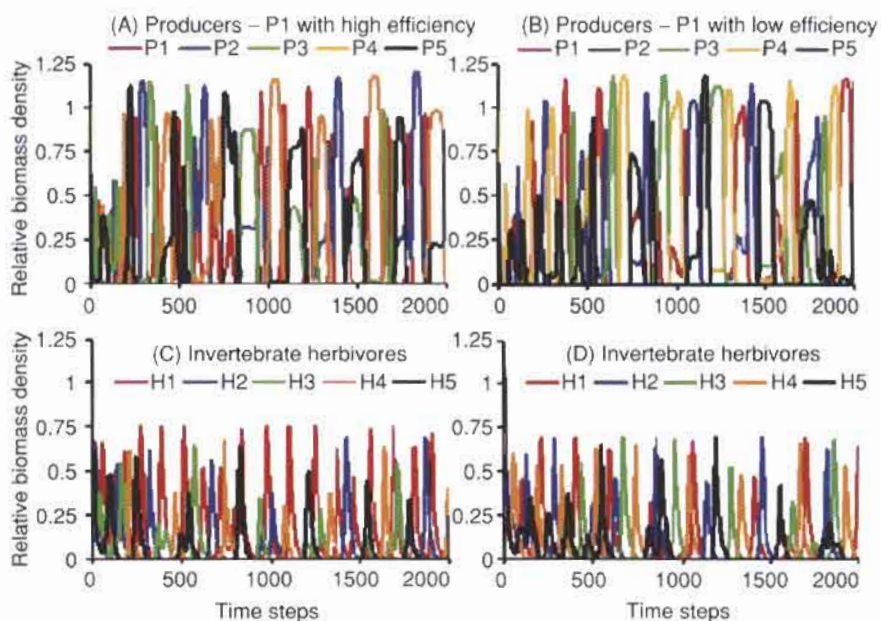
interactions between trophic and non-trophic processes regulate species coexistence and community stability. Further work is needed to understand the organizing processes of complex communities. Moving from models of food webs to more complex ecological networks that include other non-trophic interactions such as nutrient competition, facilitation, and mutualism will enable us to more rigorously analyze the complex interaction dynamics in natural systems such as keystone interactions and their context dependency (Paine, 1969, 1974; Menge et al., 1994). Following successful integration of these interactions, fitting the models to field conditions and field testing them is an exciting yet problematic next step (Martinez and Dunne, 2004; Paine, 2004).

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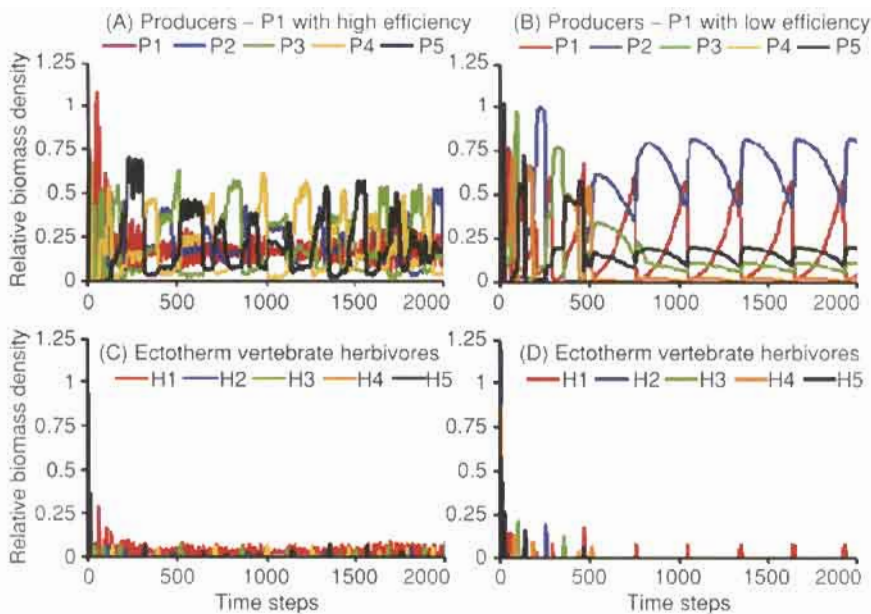
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CHAPTER 2.1 FIGURE 1 | Biomass evolution in producer communities. The guzzler (P1) is strong (A) or weak (B).



CHAPTER 2.1 FIGURE 2 | Biomass evolution in producer-invertebrate herbivore communities. The guzzler (P1) is strong (A, C) or weak (B, D).



CHAPTER 2.1 FIGURE 3 | Biomass evolution in producer-ectotherm vertebrate herbivore communities. The guzzler (P1) is strong (A, C) or weak (B, D).

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