Disentangling Resource and Apparent Competition: Realistic Models for Plant-herbivore Communities

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We analyse a model food web in which two plant species compete for a nutrient and are attacked by a herbivore species, with both resource and apparent competition occurring between plants. Simple rules based on equilibrium nutrient concentration (R^*) and herbivore density (H^*) have been proposed to govern competitive outcomes (e.g. Holt *et al.*, 1994, *Am. Nat.* **144**, 741–771), but these earlier analyses assumed linearity of the nutrient-dependent plant growth function and the herbivore functional response. We now relax these assumptions. When plant growth is nonlinear, there is a rich set of potential trade-offs among plant competitive ability, plant maximal growth rate, plant defenses against herbivores, and preferences of herbivore attack on plants. Given stability, asymptotic outcomes can include exclusion of one plant species, priority effects wherein exclusion depends on initial conditions, and herbivore-mediated coexistence. Nonlinear herbivore functional responses potentially frustrate the application of simple rules for competitive outcomes. Nevertheless, there are circumstances in which simple rules appear to perform well. In these cases, graphical theory relates properties of food chains (nutrient, herbivore, and one plant species only) to asymptotic outcomes in food webs (with both plant species). Competitive outcomes in the graphical theory are summarized by R^* and H^* quantities. Our approach works best when plant species differ greatly in nutrient-dependent growth rates, and herbivores preferentially attack plants with high ratios of nutritional benefit to cost (measured by handling and processing times). A parameterized model of *Daphnia* and several algal species suggests that our approach could perform well in practice.

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1. Introduction

The influence of natural enemies on interactions among competitors is a recurring theme in ecology. Perhaps the most common view is that predation (or herbivory) overrides the influence of competition, in the sense that coexistence may be possible in the presence of natural enemies, but not otherwise. Certainly, there are many theoretical (e.g. Cramer & May, 1972; Jost *et al.*, 1973a; Armstrong, 1979) and empirical (e.g. Paine, 1966; Jost *et al.*, 1973b; Lubchenco, 1978; Inouye *et al.*, 1980) studies

illustrating this possibility. However, natural enemies might also reinforce competitive interactions, so that dominance by a single competitor in the presence of natural enemies might be stronger than in their absence (Holt, 1987; Holt & Lawton, 1994). Or, they might reverse patterns of competitive dominance, so that one competitor dominates in their presence and another in their absence (Crawley & Pacala, 1991). Natural enemies might even introduce competition where it would not otherwise occur: if one prey supports a population of predators that attack another prey, and vice versa, then the two prey have a negative indirect interaction, showing what Holt (1977) called "apparent competition".

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For many organisms, competitive interactions in the absence of natural enemies are indirect, mediated by the availability of resources. This is especially true among primary producers, whose growth-limiting resources are mostly simple chemical substances. In the absence of herbivores or spatial heterogeneity, theory predicts that competition among plants for a single nutrient resource follows a simple rule based on the amount of available nutrient present at equilibrium when plant j grows alone with no competitors, an amount denoted R^*. The rule is: the plant with the lowest R^* will competitively exclude the others (Powell, 1958; Stewart & Levin, 1973; Armstrong & McGehee, 1980; Tilman, 1982). This rule is largely model-independent, and emerges from a wide variety of underlying physiological mechanisms of resource consumption and utilization (Tilman, 1990). Thus, R^* is a synthetic parameter, distilling the action of many biological mechanisms into a single number. The predictive value of the R^*-rule has been experimentally supported in many systems (Tilman, 1977; Hansen & Hubbell, 1980; Tilman & Wedin, 1991a,b; Grover, 1997).

Holt *et al.* (1994) proposed that a similar synthetic parameter could be used to predict the outcome of apparent competition: the equilibrium density of natural enemies supported by a given prey population when its competitors are absent. We will denote this density by H^*, because we treat herbivores and their plant prey in this paper. When both resource and apparent competition occur, we proposed that competitive outcomes might be predicted from the values of R^* and H^* for each competitor growing alone in a food chain with the herbivore. To examine this proposition, we analysed a simple food web (Fig. 1) containing a nutrient R consumed by two producer populations, X_1 and X_2, which are both eaten by a herbivore, H.

Our results suggested one could apply R^*- and H^*-rules to predict competitive outcomes in systems with two trophic levels and a limiting nutrient, much as the R^*-rule characterizes systems with one trophic level and a limiting nutrient. However, our most detailed analyses relied on a number of simplifying assumptions. These included density-independent losses for prey and predator; all density-dependence arises implicitly from consumption of shared resources. We also assumed linear functional responses, and that per capita growth rates of prey and predator depended linearly on consumption. For prey that are plants consuming a nutrient, and predators that are herbivores consuming plants, these assumptions led us to a Lotka–Volterra model of a food chain with stable equilibria.
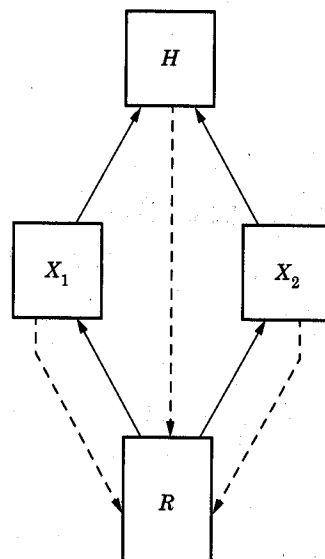

FIG. 1. Food web containing two plants (X_1, X_2) growing under limitation by a nutrient resource (R), and grazed by a herbivore (H). Solid arrows show consumption flows; dashed arrows show flows of nutrient recycling from all populations to the available nutrient pool.

In this paper, we begin to evaluate the robustness of our approach, by relaxing the assumptions of linearity in ecological rate processes. We return to the food web of Fig. 1, and consider nonlinear forms of the plant growth rate, and herbivores with nonlinear functional responses. We do retain the assumptions of density-independent losses, and stability of food chain equilibria. Nonlinear coupling of nutrients, plants, and herbivores has been examined before, in models where herbivores were specialists restricted to feeding on only one plant type (Wolkowicz, 1989, 1990; Grover, 1994, 1995). Competitive outcomes and community assembly rules were related to equilibrium nutrient concentrations, i.e. R^*s, of subcommunities with various combinations of plant and herbivore species. As yet, the complications that could arise with generalist herbivores are less well explored. Earlier investigations of generalist herbivores with nonlinear rate processes examined conditions for an equilibrium of all three species in the food web and showed that its feasibility and stability depend on nutrient supply (Jost *et al.*, 1973a; Armstrong, 1979).

We extend these earlier investigations in several ways. We present graphical approaches intended to show how nutrient concentration and herbivore density relate to invasibility conditions and equilibria in the food web, and we relate outcomes to the quantities R^* and H^* that we emphasized in our own earlier work. We explore in detail how competitive outcomes relate to biological trade-offs involving

plant defenses and their costs, herbivore feeding preferences, the nutritional benefits derived from particular plant species, and the costs herbivores might experience in obtaining such benefits. We also present a parameterized model of a planktonic algal-herbivore system, to test some of the insights obtained from simpler analytical models. The exercise of parameterization is not meant to construct a model specifically corresponding to any particular "real" system. Rather, we use data from natural populations to demarcate zones of parameter space, within which we can assess the utility of the graphical models for interpreting the outcome of more complex models with realistic magnitudes for nonlinearities in functional responses.

2. Basic Models

Our approach focusses on a "resource-dependent food web" (*sensu* Grover, 1997), where the model equations trace the flow of a nutrient resource through a series of trophic interactions. We assume that the system is closed to immigration by plants or herbivores, and we ignore complications of population structure and developmental time lags. The symbol R denotes nutrient availability (i.e. concentration), X_1 and X_2 denote densities of the two plant species, and H denotes herbivore density.

Plant species j grows at a per capita rate $\mu_j(R)$, which is an increasing, saturating function. Mathematically, $d\mu_j/dR > 0$, $d^2\mu_j/dR^2 < 0$, and $\mu_j(0) = 0$. Plants suffer two forms of density-independent losses. Species-specific losses at a per capita rate ϵ_j result in recycling of the nutrient content of dead plant matter. We also allow for losses at a per capita rate D, which applies indiscriminately to nutrient, plants and herbivores. The nutrient content of the latter losses is not recycled, but is instead exported from the habitat. Such a process resembles dilution in a chemostat (Grover, 1997), and is a simple way to represent turnover of all system components. We call D the "habitat turnover rate". Applying the same export rate to all system components might be reasonable in plankton, where hydrodynamic turnover of well-mixed aquatic habitats can remove components indiscriminately (Powell & Richerson, 1985). This assumption of indiscriminate removal is probably untrue in many habitats, however, where system components are exported at different rates. We comment on this below.

Plants also suffer losses to herbivory, described by the herbivore's functional response—its per capita rate of consumption for each plant species,

$\iota_j(X_1, X_2)$. We assume that the functional response increases with the density of the species consumed, and potentially decreases with the density of the other species. Mathematically, $\partial \iota_j/\partial X_j > 0$, $\partial \iota_j/\partial X_k < 0$ for $j \neq k$, and $\iota_1(0, X_2) = \iota_2(X_1, 0) = 0$. We also define functional responses when only one plant species is present: $\iota_1(X_1) = \iota_1(X_1, 0)$ and $\iota_2(X_2) = \iota_2(0, X_2)$.

We assume that plants are substitutable resources for herbivores, such that either plant species in principle could support a herbivore in a simple food chain, based on that plant alone. There are constant efficiencies (e_j) of conversion of ingested plant matter to herbivore production. The per capita rate of herbivore growth is thus $\Sigma_j e_j \iota_j$. For the aquatic systems we model below, it is convenient to measure plant (algal) density with carbon mass (e.g. μmol C l^{-1}), and herbivores (zooplankton) in units of individuals per unit volume. Doing so, $e_j \equiv \alpha_j/b$, where b is the carbon mass of one herbivore, and α_j is the assimilability of algal carbon. Like plants, herbivores suffer two types of density-independent losses. Those at a per capita rate δ result in nutrient recycling, while those at a per capita rate D lead to nutrient export.

These assumptions allow a wide variety of possible shapes for the herbivores' net-growth isocline in the X_1X_2-plane (see Holt, 1983). Below, we examine type I and II functional responses (Holling, 1959), for which the herbivore isocline for zero growth is a negatively-sloping straight line in the X_1X_2-plane connecting the points $X_1 = X^*_{1(1H)}$ and $X_2 = X^*_{2(2H)}$, which are the equilibrium densities of each plant in its own food chain, consisting of itself and the herbivore. We use the superscript "*" to indicate the equilibrium value of a state variable, and a subscript of the form "($\cdot$)" to indicate the species composition of the community to which that equilibrium refers: e.g. the subscript "(jH)" refers to a community of just plant j and the herbivore. In this paper, plants are "linearly substitutable" resources for herbivores (*sensu* Tilman, 1982).

We also assume a particular form of "preference" by herbivores for different plants, using the conventions of zooplankton ecology. The "clearance" or "attack" rate (F_j) is the rate at which plant matter is removed from habitat units by an individual herbivore (e.g. volume per animal per time), in effect, the contribution of that herbivore to a plant population's per capita loss rate. Formally,

$$F_j = \frac{\iota_j(X_1, X_2)}{X_j}. \tag{1}$$

For plant species $j = 1, \ldots, n$, dimensionless preference coefficients w_j are assigned as

$$w_j = \frac{F_j}{F}, \qquad (2)$$

where $F = \max_j\{F_j\}$, so that $0 < w_j \leqslant 1$ (Vanderploeg & Scavia, 1979). Herbivore preferences are thus scaled by reference to the "most edible" plant (with the highest per capita losses to herbivory). We assume the w_j are fixed for all values of X_1 and X_2 (as is true for the type I and II functional responses examined below). Thus the term "preference" as used here need not imply complex choice behavior by herbivores, but merely something akin to biased sampling by an inefficient filter.

Pulling all of these assumptions together, plant and herbivore dynamics follow the coupled differential equations:

$$\frac{dX_j}{X_j\, dt} = \mu_j(R) - Hl_j(X_1, X_2)/X_j - \epsilon_j - D,$$
$$j = 1, 2 \quad (3a)$$

$$\frac{dH}{H\, dt} = \sum_{j=1,2} e_j l_j(X_1, X_2) - \delta - D. \qquad (3b)$$

To complete our model, we must also specify nutrient resource dynamics. In common with many ecosystem models of food web and nutrient dynamics (e.g. DeAngelis, 1992), we assume a constant rate of nutrient input (dimensions: concentration time^{-1}). It is algebraically convenient to represent this input rate as the product of a nutrient supply parameter (S, dimensions: concentration) and the habitat turnover rate (D, dimensions: time^{-1}).

We assume that nutrient consumption by plants is proportional to growth rate, at a rate $\mu_j q_j$. The proportionality coefficient q_j is the "quota" of nutrient per unit of plant (e.g. mol nutrient per mol C). As noted above, plants suffer density-independent losses that result in nutrient recycling, at a rate $\epsilon_j q_j X_j$. If b denotes the average carbon mass of one herbivore, its nutrient content is b/γ, where γ is the carbon:nutrient ratio of herbivores. Thus, density-independent losses of herbivores result in nutrient recycling, at a rate $b\delta H/\gamma$. We assume there is recycling of nutrient not assimilated by herbivores during feeding, at a rate $(q_j - \alpha_j/\gamma)Hl_j$. The factor in parentheses is the difference between plant nutrient content and the herbivore's nutrient demand, which we assume to be positive.

Our assumptions about nutrient transformations include constant stoichiometry (carbon:nutrient composition) and yield (relation between individuals and

nutrient content) for both plants and herbivores. We also assume instantaneous recycling of nutrients lost from plants and herbivores. This assumption may be justified by the fact that the decomposers responsible for nutrient recycling are often microorganisms with shorter generation times and more rapid metabolism than other biotic components. However, delays in nutrient recycling could occur in some systems. Beretta et al. (1990) analysed such delays, in a model for a single plant population without herbivores, which combines our eqn (3a) with an appropriate modification of eqn (4). They found that conditions for equilibria and stability resembled (and for many cases were equivalent to) such conditions in models without delays. Whether delays in nutrient cycling would have such benign effects in models of food chains and webs requires further exploration. With respect to the planktonic systems to which we apply our parameterized model, a detailed model of nutrient recycling through detrital pools (Nisbet et al., 1991) makes very similar predictions to simple food chain models assuming instantaneous recycling (e.g. Grover, 1995). Neglect of delays in nutrient recycling greatly simplifies model structure and analysis, and this convenience motivates us to adopt it. It also allows comparison of our results with other models sharing this assumption (e.g. Wolkowicz, 1989, 1990; Grover, 1994, 1995, 1997; Holt et al., 1994).

Pulling together our assumptions about nutrient transformations, we complete our basic model with the differential equation describing change in available nutrient:

$$\frac{dR}{dt} = D(S - R) - \sum_{j=1,2} q_j(\mu_j - \epsilon_j)X_j + \frac{b\delta}{\gamma} H$$
$$+ \sum_{j=1,2}\left(q_j - \frac{\alpha_j}{\gamma}\right)Hl_j. \quad (4)$$

The total nutrient stock in the habitat is the sum of available nutrient (R), nutrient contained in plants ($q_j X_j$), and nutrient contained in herbivores (bH/γ). The coupled system of eqns (3) and (4) displays a mass balance, in the sense that asymptotically as $t \to \infty$, the total nutrient stock in the habitat goes to a constant value:

$$R + \sum_{j=1,2} q_j X_j + \frac{b}{\gamma} H = S. \qquad (5)$$

In this asymptotic state, nutrient input balances nutrient removal. The l.h.s. of eqn (5) is the total nutrient stock: differentiating this and substituting eqns (3) and (4) leads to a linear differential equation

for total nutrient stock, for which eqn (5) is a stable equilibrium solution. Trajectories in the phase space (R, X_1, X_2, H) thus approach a hyperplane defining a constraint on nutrient availability for the system. We refer to this constraint as a "mass-balance constraint" (abbreviated MBC). Because our analyses treat asymptotic outcomes, we assume that this constraint is satisfied. For the special case of a closed system $(D = 0)$, the sum of nutrient in all components [i.e. the l.h.s of eqn [3]] is immediately and forever fixed at its initial value, which we identify with the parameter S in an open system.

We emphasize that the MBC is not itself an assumption of our model. Rather, it is a deduced property of asymptotic dynamics, which follows from our complete budgeting of all nutrient transformations, and the nature of the external nutrient exchanges assumed. Mass-balance constraints can be derived for a variety of similar models, assuming that the environment is constant (Grover, 1995, 1997). In such an environment, the MBC given above holds even if there are limit cycles or chaotic dynamics of nutrient, plants, and herbivores—such dynamics merely redistribute nutrient among these forms, without changing total stock size (see Kot *et al.*, 1992).

Our derivation of the MBC relies on our assumption of indiscriminate removal of all system components, at the habitat turnover rate (D). In most systems, different removal rates probably apply to different system components. If we modify our system in this way, then the analysis of Wolkowicz & Lu (1992) for systems without herbivores is easily generalized to show that the total nutrient stock is bounded as $t \to \infty$. Moreover, if the system reaches a stable equilibrium, state variables will still obey a mass conservation law analogous to our MBC. Thus, we conjecture that relaxing our assumption of equal D for all components will lead to quantitative, but not qualitative differences for the results presented here, which concern equilibrium situations. Leibold (1996) constructed a graphical approach that generalizes the MBC in such circumstances.

A SIMPLE FOOD CHAIN

We build up to the properties of our full food web (Fig. 1) from well-known properties of its subsystems. With no herbivores and only a single plant type present, the nutrient concentration and plant density converge to a globally stable equilibrium, given by

$$R_{(j)}^* = \mu_j^{-1}(D + \epsilon_j) \qquad (6a)$$

$$X_{j(j)}^* = (S - R_{(j)}^*)/q_j, \qquad (6b)$$

which is feasible if $S > R_{(j)}^*$, and if large values of R permit $\mu_j > D + \epsilon_j$ (Hsu *et al.*, 1977) [Fig. 2(a)]. No equilibrium is possible with both plant types present in the absence of the herbivore; instead, the plant with the lower value of $R_{(j)}^*$ competitively excludes the other
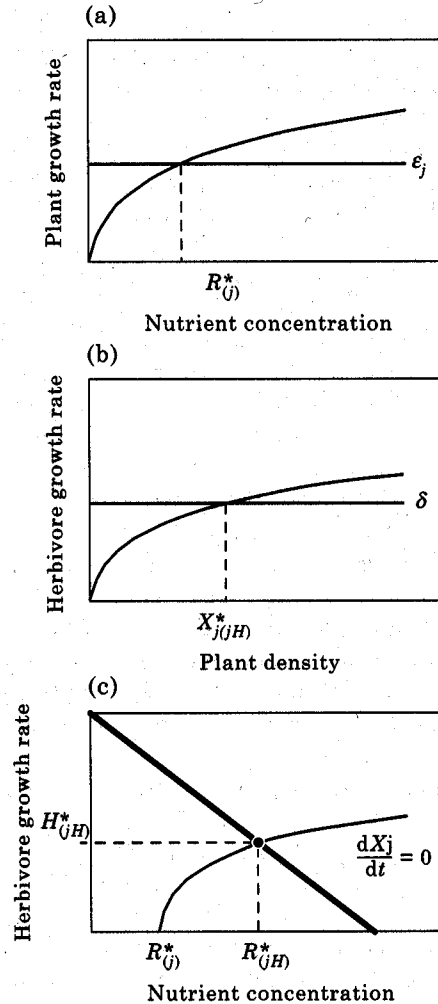

FIG. 2. Graphical analysis of a food chain subsystem of our food web, containing plant j only. Panel (a) shows the per capita growth rate of herbivores as an increasing function of plant density. Herbivore net growth is zero where this function intersects a horizontal line representing the herbivore loss rate (δ), and the corresponding plant density is $X_{j(jH)}^*$. Panel (b) shows the per capita growth rate of herbivores as an increasing function of nutrient concentration. Plant net growth is zero in the absence of herbivores where this function intersects a horizontal line representing the plant loss rate (ϵ_j), and the corresponding nutrient concentration is $R_{(j)}^*$. Panel (c) shows the projected plant isocline for zero growth (curve labelled $dX_j/dt = 0$) and mass balance constraint (heavy line), given that $X = X_{j(jH)}^*$. Their intersection gives the equilibrium herbivore density $H_{(jH)}^*$ and nutrient concentration $R_{(jH)}^*$ for the food chain.

(Hsu *et al.*, 1977; Armstrong & McGehee, 1980; Tilman, 1982).

With just a single plant species present, we now add herbivores, and analyse the new equilibrium, at which plant density is

$$X_{j(j|H)}^{*} = \iota^{-1}\left(\frac{D+\delta}{e_j}\right) \qquad (7)$$

[Fig. 2(b)]. This equilibrium is feasible, and the herbivore can invade when absent, if $X_{j(j)}^{*} > X_{j(j|H)}^{*}$, or equivalently, $S > R_{(j)}^{*} + q_j X_{j}^{*}$; this also requires that large values of X_j permit $e_j \iota_j > D + \delta$ (Jost *et al.*, 1973a; Saunders & Bazin, 1975; Grover, 1994).

We graphically represent the asymptotic properties of the food chain with plant j and the herbivore by projecting from the three-dimensional phase space (R, X_j, H) onto the RH-plane (for details see Holt *et al.*, 1994; Grover, 1997). In three dimensions, the zero-growth isosurface for plant j intersects a plane defined by the equilibrium plant density, at $X_j = X_{j(j|H)}^{*}$. To produce a two-dimensional graph we call the "plant isocline for zero growth", this curvilinear intersection is projected onto the RH-coordinate plane. The MBC is a plane in the three-dimensional phase space, and thus has a linear intersection with the plane at $X_j = X_{j(j|H)}^{*}$. We project this line onto the RH-plane to achieve a two-dimensional representation of the MBC. The graph of the plant isocline zero growth and the MBC [Fig. 2(c)] depicts the asymptotic behavior of R and H, provided that X_j is fixed at its equilibrium value for the food chain. The equilibrium values $R_{(j|H)}^{*}$ and $H_{(j|H)}^{*}$ are found at the intersection of the plant isocline and MBC.

The equation of the plant isocline for zero growth,

$$H = (\mu_j(R) - D - \epsilon_j)\left(\frac{X_{j(j|H)}^{*}}{\iota_j(X_{j(j|H)}^{*})}\right), \qquad (8)$$

has positive slope. This arises because as herbivore density increases, the plant population needs progressively higher nutrient availability to compensate for herbivory. The plant isocline for zero growth is determined by the two bracketed terms in eqn (8). The first depends only on plant characteristics, and implies that the isocline intersects the R-axis at $R_{(j)}^{*}$. We assume that $\mu_j(R)$ saturates at a maximal growth rate r_j, so the plant isocline for zero growth has an upper asymptote proportional to $r_j - D - \epsilon_j$. The second term of this isocline depends on the herbivore's functional response and plant density at equilibrium, reflecting several plant and herbivore characteristics.

The equation of the MBC is

$$H = \frac{\gamma}{b}(S - q_j X_{j(j|H)}^{*}) - \frac{\gamma}{b}R. \qquad (9)$$

Equilibrium plant density, $X_{j(j|H)}^{*}$, is independent of nutrient supply S, as is the plant isocline for zero growth, but the MBC is proportional to nutrient supply. These properties result from our assumptions of density-independent herbivore losses, together with a prey-dependent functional response.

Enriched nutrient supply increases $R_{(j|H)}^{*}$ and $H_{(j|H)}^{*}$. This can destabilize the food chain equilibrium if the herbivores' functional response saturates, producing a stable limit cycle (Appendix A, see also Jost *et al.*, 1973a; Saunders & Bazin, 1975). We consider only systems for which both constituent food chains have stable equilibria. Our approach might sometimes apply to long-term averages of time-varying systems, but more complex outcomes are also possible (see the Discussion). In this model framework, plant density in a food chain is controlled by herbivory and does not depend on nutrient supply. In food webs with two plant species, however, total plant density can increase with nutrient supply, due to species replacement along a supply gradient (Leibold, 1996).

3. Properties of the Full Food Web

In our earlier analyses of linear ι_j and μ_j (Holt *et al.*, 1994), we superimposed graphs of zero-growth isoclines and MBCs for the food chains of two competing plant species. These superimposed graphs revealed invasibility properties, and were used to characterize competitive outcomes in the full food web, associated with particular patterns in the species-specific quantities $R_{(j|H)}^{*}$ and $H_{(j|H)}^{*}$. For instance, both mutual invasibility (i.e. coexistence) and non-invasibility (priority effects) required that one plant species have the lower $R_{(j|H)}^{*}$ and the other have the higher $H_{(j|H)}^{*}$. Based on these results, we proposed predicting invasibility and asymptotic outcomes in food webs, using food chain properties.

Ideally, we would construct similar two-dimensional graphs for the full food web under less restrictive assumptions about μ_j and ι_j, by setting $dH/dt = 0$, obtaining equilibrium values of X_1 and X_2, and projecting the phase space onto the RH-plane. Unfortunately, when the herbivore's functional response is nonlinear, the plant isocline for zero growth in a food chain does not correspond to its zero growth isocline in the full food web.

However, requiring $dH/dt = 0$ does constrain the values of X_1 and X_2 to the herbivore isocline for zero growth in the $X_1 X_2$-plane. This constraint bounds the

feasible positions of the plant isoclines and MBCs in the *RH*-plane and permits some graphical exploration of both invasibility conditions, and the relations of food web outcomes to food chain properties. Before considering this more complex situation of nonlinear functional responses, it is instructive to examine herbivores with a linear functional response, for which the plant isoclines for zero growth are equivalent in food chains and food webs. Extending the results of Holt *et al.* (1994), one can interpret competitive outcomes in terms of herbivore preferences and the costs of plant defenses.

LINEAR FUNCTIONAL RESPONSES, COSTLY DEFENSES, AND ADAPTIVE PREFERENCES

Despite its simplicity, the linear functional response may apply to herbivores grazing relatively scarce, but highly attractive plants (Crawley, 1997). Our treatment of linear functional responses rests on two observations: first, defenses against herbivory might exert costs upon plants, measured by reduced nutrient-dependent growth rates and competitive ability; second, herbivores might preferentially attack plants which provide higher fitness. To begin the analysis, let

$$\iota_j(X_1, X_2) = Fw_j X_j, \qquad (10)$$

where F is the maximum clearance occurring when herbivores ingest an idealized "best" food, to which herbivore preferences for other foods are scaled (eqn 3). We assume plant species 1 is preferred to species 2 (i.e. $w_1 > w_2$).

With a linear functional response, the plant isocline for zero growth in the *RH*-plane becomes

$$H = (\mu_j(R) - D - \epsilon_j)/Fw_j, \qquad (11)$$

which is independent of X_1 and X_2. Thus, plant isoclines for zero growth are equivalent in food chains and food webs. Moreover, food chain equilibria are always stable when the herbivore has a linear functional response, and invasion analyses adequately indicate the stability of any interior equilibrium for the food web (Appendix A). A plant with low preference (w_j) has a zero-growth isocline with steep slope, and the parameter w_j can be interpreted as an inverse measure of defense against herbivory. The relative shapes of zero growth isoclines for two plants depend on their characteristics involving defenses against herbivores and their costs, as detailed in the examples below.

Unlike the plant isoclines for zero growth, the MBCs do depend on X_j and thus differ between food chains and food webs. The MBC equations are

$$H = \frac{\gamma}{b}(S - q_1 X_{1(1H)}^*) - \frac{\gamma}{b}R,$$

$$\text{for food chain 1;} \quad (12a)$$

$$H = \frac{\gamma}{b}(S - q_2 X_{2(2H)}^*) - \frac{\gamma}{b}R, \quad \text{for food chain 2;} \quad (12b)$$

$$H = \frac{\gamma}{b}(S - q_1 X_1 - q_2 X_2) - \frac{\gamma}{b}R,$$

$$\text{for the food web.} \quad (12c)$$

The MBC for the full system shares the common slope of the MBCs for the two food chains, and the MBCs vary only in elevation. For equilibrium analyses, the plant densities in the full food web, X_1 and X_2, lie on the zero-growth isocline for herbivores, which has the equation

$$\frac{X_1}{X_{1(1H)}^*} + \frac{X_2}{X_{2(2H)}^*} = 1. \qquad (13)$$

From this, it follows that any MBC pertaining to the full food web lies between the two MBCs of the constituent food chains. If there is a three-species equilibrium, the MBC of the full food web passes through it; the food chain MBCs thus bound the portion of the *RH*-plane in which a three-species equilibrium is feasible. The elevation of this band is proportional to S, and so feasibility of any three species equilibrium is conditional on nutrient supply.

Competitive outcomes and their relations to the synthetic quantities $R_{(j H)}^*$ and $H_{(j H)}^*$ are now explored by plotting plant isoclines and the MBCs from the food chains, on the *RH*-plane (Figs 3–5; see also Holt *et al.*, 1994; Grover, 1997). A feasible three-species equilibrium occurs if the two plant isoclines for zero growth intersect, with the point of intersection lying between the two food chain MBCs. If the intersection lies outside, no three-species equilibrium is feasible. An intersection of these isoclines occurs when the plant with the lower *R*-intercept of its zero-growth isocline ($R^*_{(j)}$) also has the isocline which rises less rapidly with *R*.

There are two situations leading to such an intersection, and we interpret both as representing costly plant defenses against herbivory. First, reduced w_j (and hence lower losses to herbivory) may reduce competitive ability in environments lacking herbivores, so that $R_{(1)}^* < R_{(2)}^*$. If defense against herbivory is effective, a smaller magnitude for w_2 causes the zero-growth isocline of plant 2 to rise rapidly with *R*, so that it intersects the more slowly rising isocline of plant 1 (Fig. 3).
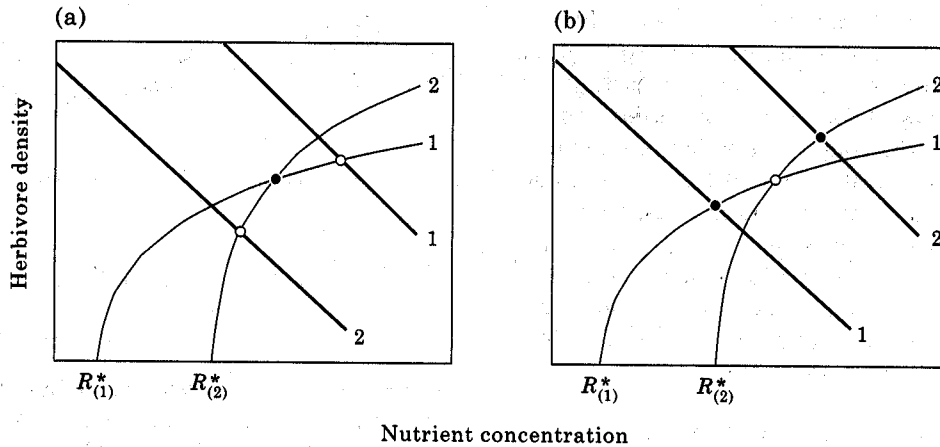
FIG. 3. Graphical analysis of food webs in which herbivores have a linear functional response and plant defenses against herbivory are costly in terms of competitive ability. The forward sloping curves labelled 1 and 2 are food chain isoclines for zero growth of plants 1 and 2, respectively; the negatively sloping heavy lines are their food chain MBCs; solid circles show stable (noninvasible) equilibria, and open circles show unstable (invasible) equilibria. Panel (a) shows adaptive herbivore preferences. Panel (b) shows non-adaptive herbivore preferences.

In the second case, the less-preferred plant is a superior competitor in the absence of herbivores, and has the lower $R_{(j)}^*$. However, the zero-growth isocline of the less preferred plant 2 may nonetheless rise more slowly than that of plant 1, so that an intersection of these isoclines occurs (Fig. 4). The reason is that the plant growth function ($\mu_j(R)$) typically saturates at high nutrient availability, and an intersection of plant isoclines can occur if the less-preferred plant 2 has a lower nutrient-saturated growth rate ($r_j - \epsilon_j$) than plant 1. We interpret this to represent plant defenses that are costly in terms of a plant population's maximal growth rate.

An intersection of plant isoclines for zero growth is necessary for coexistence, but not sufficient. Selective herbivory is insufficient, in itself, to ensure coexistence, because some mechanism must enable invasion of the more edible species in the presence of herbivory. Mutual invasibility implies coexistence at equilibrium, provided the food chain equilibria are stable (Hutson & Law, 1985). The food chain equilibrium with only plant j is invasible by the missing plant type, if the intersection of plant j's MBC and isocline for zero growth falls in a region of the RH-plane below the zero-growth isocline of the missing plant. This then allows the latter a positive net growth rate [e.g. Fig. 3(a)]. When the plant isoclines for zero growth intersect in the region of the RH-plane between the MBCs for the two food chains, the relative positions of these MBCs determine mutual invasibility. If the MBC of the plant species with the lower $R_{(j)}^*$ lies above that of the other, then each food chain equilibrium is respectively invasible by the missing plant species [Fig. 3(a)]. In some cases,

mutual invasibility is associated with a positive correlation of herbivore preference and competitive ability (as in Crawley & Pacala, 1991). However, other correlations of plant traits can also produce herbivore-mediated coexistence in our theory (as elaborated below).

Alternatively, mutual invasibility may fail to hold, in which case neither food chain equilibrium can be invaded by the missing plant. A priority effect occurs, in which a resident plant and herbivore can hold ground against propagules of the other plant. A local stability analysis (Appendix A) shows that mutual invasibility is associated with a stable interior equilibrium, while mutual non-invasibility is associated with an unstable interior equilibrium.

Competitive outcomes strongly depend on the positions of the food chain MBCs. These in turn depend on plant densities at equilibrium in their own food chains ($X_{j(j)H}^*$), and nutrient quotas (q_j). The lower the value of the product $q_j X_{j(j)H}^*$, the higher the elevation of the MBC for that food chain. For now, we assume that quotas are equal for all plants, which implies that the relative elevations of the MBCs are completely determined by equilibrium densities ($X_{j(j)H}^*$). We will relax this assumption below.

The quantity $X_{j(j)H}^*$ is related to potential competitive interactions of herbivore j with other herbivore species, in a manner analogous to $R_{(j)}^*$ for plants competing without herbivores. Experiments with zooplankton herbivores show that species which reduce algal density to the lowest level at equilibrium (lowest $X_{j(j)H}^*$) can competitively displace other species (Rothhaupt, 1990; Grover, 1997). However, if two algal species are available, and each zooplankton

species preferentially attacks the alga for which it has the lower $X_{j(jH)}^*$, stable coexistence is possible (Rothhaupt, 1988). Thus we argue that herbivores potentially raise their fitness by preferentially attacking those plants which they can reduce to low density at equilibrium. We will say that such a herbivore has an "adaptive preference". (In a game theoretic sense, such a preference permits persistence in competition.) Adaptive preferences so defined arise intuitively, from preferential attack on plants with high assimilability, high nutrient content, or low handling times.

For a type I functional response

$$X_{j(jH)}^* = \frac{b(D + \delta)}{F w_j \alpha_j}. \qquad (14)$$

Herbivores are automatically predisposed towards adaptive preferences, because a preferred plant species (high w_j) will tend to have a lower equilibrium density. If herbivores prefer plants in relation to their assimilability, then $w_1 > w_2$ when $\alpha_1 > \alpha_2$, so certainly $X_{1(1H)}^* < X_{2(2H)}^*$, and the preference is adaptive.

Given our provisional assumption of equal plant quotas, and our definition of adaptive preferences, relative positions of the plant MBCs are dictated by herbivore preferences. When these are adaptive, the MBC for species 1 lies above that for species 2. Non-adaptive preferences produce a reversed configuration. We now illustrate several cases pertinent to interpreting the parameterized model developed below, and which highlight the roles of costly defenses and herbivore preferences in determining competitive outcomes. Then we relax the assumption of equal plant quotas, and assume alternatively that herbivore preferences and plant characteristics are determined by differences in plant nutrient content.

Some examples

We first consider cases in which costs of a plant species' defenses against herbivores reduce its ability to compete for nutrient in the absence of herbivores. Let species 2 be more heavily defended than species 1, also an inferior competitor ($R_{(2)}^* > R_{(1)}^*$). We assume that the defense costs do not affect growth rate at saturating nutrient availability (i.e. we assume $r_2 - \epsilon_2 \geqslant r_1 - \epsilon_1$). Graphically, these assumptions imply that the zero-growth isocline for species 1 lies above that for species 2 at low nutrient concentrations (Fig. 3). However, the zero-growth isocline for species 2 rises more steeply with nutrient concentration, and eventually intersects the zero-growth isocline of
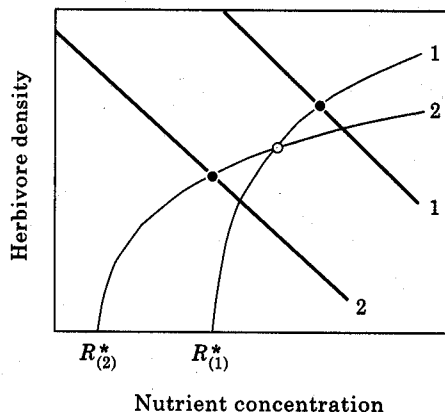

FIG. 4. Graphical analysis of food webs in which herbivores have a linear functional response, plant defenses against herbivory are costly in terms of nutrient-saturated growth, and herbivore preferences are adaptive. The forward sloping curves labelled 1 and 2 are food chain isoclines for zero growth of plants 1 and 2, respectively; the negatively sloping heavy lines are their food chain MBCs; solid circles show stable (noninvasible) equilibria, and open circles show unstable (invasible) equilibria.

species 1. This intersection corresponds to a potential interior equilibrium.

For the interior equilibrium to be feasible, the intersection of the zero-growth isoclines must lie between the two MBC-lines (as drawn in Fig. 3). The width of this feasible band does not depend on nutrient supply, but its elevation does. For a feasible interior equilibrium, nutrient supply must not be so low that the feasible band falls below the equilibrium point, nor so high that it falls above.

When the interior equilibrium is feasible, the next question is whether it is stable (producing coexistence), or unstable (producing priority effects). Herbivore preferences are critical. If these are adaptive, the MBC-line for species 1 lies above that for species 2. Plotting these lines together with the plant isoclines for zero growth [Fig. 3(a)] shows that the food chain equilibria with either plant species occur at values of R and H for which the missing plant species has positive net growth, and so can invade. Thus, there is coexistence. Alternatively, if herbivore preferences are not adaptive, then the MBC-line for species 2 lies above that for species 1. Plotting these lines together with the plant isoclines [Fig. 3(b)] shows that the food chain equilibria with either plant species occur at values of R and H for which the missing plant species has negative net growth, and so is excluded. Thus, there is a priority effect.

To summarize, with costly defenses against herbivory, intermediate nutrient supplies produce a feasible equilibrium for all three species. This implies coexistence if herbivore preferences are adaptive, and
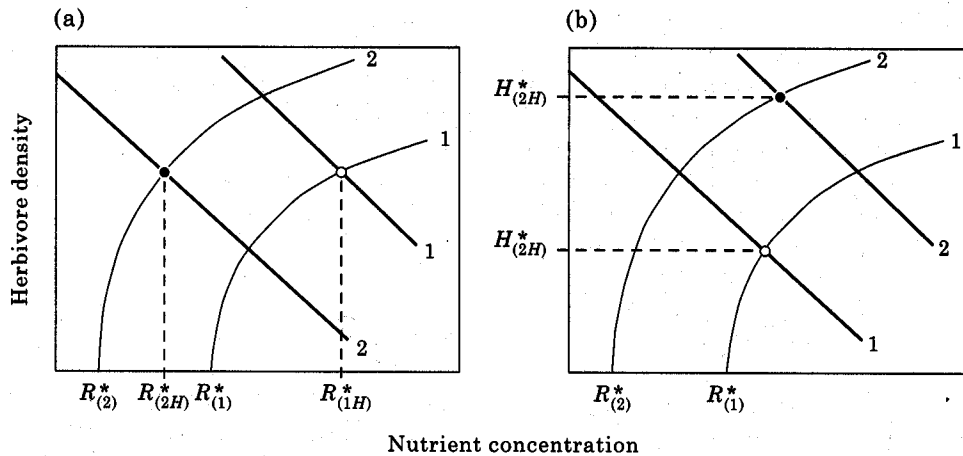
FIG. 5. Graphical analysis of food webs in which herbivores have a linear functional response and plant defenses against herbivory are not costly. The forward sloping curves labelled 1 and 2 are food chain isoclines for zero growth of plants 1 and 2, respectively; the negatively sloping heavy lines are their food chain MBCs; solid circles show stable (noninvasible) equilibria, and open circles show unstable (invasible) equilibria. Panel (a) shows adaptive herbivore preferences. Panel (b) shows non-adaptive herbivore preferences.

priority effects if they are not. Comparing the equilibria of the food chains with single plant species, coexistence is associated with rank orderings $R^*_{(2H)} < R^*_{(1H)}$ and $H^*_{(1H)} > H^*_{(2H)}$ [Fig. 3(a)]. The first ordering implies that species 2 is more tolerant of low nutrient availability when growing with herbivores. Notably, this reverses the situation without herbivores, for which $R^*_{(1)} < R^*_{(2)}$, implying that species 1 is the more tolerant of low nutrient availability. This reversal is diagnostic of coexistence, and indicates a reversal of the plant species' competitive abilities under herbivory. No such reversal occurs when there are priority effects, in which case the food chain equilibria have the orderings $R^*_{(2H)} > R^*_{(1H)}$ and $H^*_{(1H)} < H^*_{(2H)}$ [Fig. 3(b)]. Nutrient supplies lower than those producing a feasible interior equilibrium lead to exclusion of species 2, and nutrient supplies higher than those producing a feasible interior equilibrium lead to exclusion of species 1. These outcomes are associated either with lower $R^*_{(jH)}$ for the winner, or higher $H^*_{(jH)}$, depending on herbivore preferences (Grover, 1997).

We next consider cases in which costs of defenses against herbivory affect the nutrient-saturated growth rate. We assume that the better-defended species 2 is a superior competitor in the absence of herbivory (i.e. $R^*_{(2)} < R^*_{(1)}$), which has a lower net growth rate at saturating nutrient availability (i.e. $r_2 - \epsilon_2 \leqslant r_1 - \epsilon_1$). If this disadvantage is sufficiently large, then the zero-growth isocline for species 1 lies below that for species 2 at low nutrient concentrations, but rises more steeply with R, so that it eventually intersects the zero-growth isocline of species 2 (Fig. 4).

When nutrient supply is neither too low nor too high, the intersection of these isoclines lies between

the MBC-lines for the two food chains (as drawn in Fig. 4). Herbivore preferences now determine whether there is coexistence or priority effects. For example, with adaptive preferences the MBC-line for species 1 lies above that for species 2. Plotting these lines together with the plant isoclines for zero growth predicts priority effects (Fig. 4). By assuming that herbivore preferences are not adaptive, a graph predicting coexistence for this arrangement of the plant isoclines for zero growth could also be constructed.

In the illustrated case of priority effects, the equilibria of the food chains for either plant species alone follow the rank orderings $R^*_{(2H)} < R^*_{(1H)}$ and $H^*_{(1H)} > H^*_{(2H)}$ (Fig. 4). Moreover, $R^*_{(2)} < R^*_{(1)}$. Thus, species 2 is more tolerant of low nutrient availability with or without herbivores. Priority effects are associated with a consistent ordering of R^* quantities with and without herbivores [see also Fig. 3(b)]. Nutrient supplies lower than those producing priority effects lead to exclusion of species 1 (associated with the ordering $R^*_{(2H)} < R^*_{(1H)}$). Nutrient supplies higher than those producing priority effects lead to exclusion of species 2 (associated with the ordering $H^*_{(1H)} > H^*_{(2H)}$).

We next consider cases in which defenses against herbivory are not costly, so that a plant which is heavily defended suffers no disadvantage in its nutrient-dependent growth rate. Specifically, assume that without herbivores species 2 is a superior competitor for the nutrient ($R^*_{(2)} < R^*_{(1)}$), and that in rich habitats with saturating nutrient availability, species 2 also grows more rapidly ($r_2 - \epsilon_2 \geqslant r_1 - \epsilon_1$). Graphically, the zero-growth isocline for species 2 always lies above that for species 1 (Fig. 5).

Immediately, this implies that both coexistence and priority effects are impossible—species 2 has advantages all across the boards and always outcompetes species 1.

The invasion analysis supporting this conclusion can be portrayed graphically once the positions of each plant species' MBC-lines are determined. These depend on herbivore preferences. If these are adaptive, the dominance of species 2 is associated with a ranking $R^*_{(2H)} < R^*_{(1H)}$ (note that the ranking of $H^*_{(2H)}$ and $H^*_{(1H)}$ is indeterminate) [Fig. 5(a)]. The victory of species 2 is attributable to its reduction of nutrient availability below the level which species 1 requires to compensate for its losses, including herbivory. Alternatively, if herbivore preferences are not adaptive, the dominance of species 2 is associated with a ranking $H^*_{(2H)} > H^*_{(1H)}$ (note that the ranking of $R^*_{(2H)}$ and $R^*_{(1H)}$ is indeterminate) [Fig. 5(b)]. The victory of species 2 is attributable to its support of a herbivore population above the level which species 1 can tolerate on the available nutrients.

It is not surprising that when defenses against herbivory are not costly, the less-preferred plant species always displaces a species preferred by the herbivore. Our analysis emphasizes that the outcome stems from the inability of the preferred species to persist under the regime of nutrient availability and herbivore density enforced by the less-preferred species. This regime is characterized by the synthetic quantities $R^*_{(2H)}$ and $H^*_{(2H)}$.

Finally, we consider cases in which herbivore fitness depends on obtaining the same nutrient that limits plant growth. Such cases seem likely in nitrogen-limited terrestrial ecosystems (McNeill & Southwood, 1978; Mattson, 1980; Hartley & Jones, 1997), and phosphorus-limited freshwater ecosystems (Sterner & Hessen, 1994). It is adaptive for herbivores to prefer plants with high nutrient content (q_j), and we now relax our assumption that nutrient content is equal for all plants.

For simplicity, we assume that preference is proportional to plant nutrient content ($w_j = kq_j$), as is the herbivore's growth efficiency ($e_j = k'q_j$). Keeping our convention that species 1 is preferred, it has a higher nutrient content than species 2. Assuming the herbivore has a linear functional response, and substituting the above identities into eqns (7) and (10), in its own food chain plant j reaches the equilibrium density

$$X^*_{j(H)} = \frac{D + \delta}{Fkk'q_j^2}. \qquad (15)$$

This quantity decreases with q_j, so that herbivore preference for plants of higher nutrient content is

"adaptive" in the sense used in previous cases. The herbivore attacks more strongly those plant species which it reduces to low density at equilibrium.

For the food chain with plant j, the equation of the MBC-line is

$$H = \frac{\gamma}{b}\left(S - \frac{D + \delta}{Fkk'q_j}\right) - \frac{\gamma}{b}R, \qquad (16)$$

which shows that elevation of the MBC increases with q_j.

Plant species with low nutrient content tend to have lower $R^*_{(j)}$ than those with higher nutrient content; that is, they are good nutrient competitors in the absence of herbivory (Tilman, 1990; Tilman & Wedin, 1991a). Therefore, we assume that the zero-growth isocline of a species with a low nutrient content intersects the R-axis nearer the origin than the zero-growth isocline of a species with high nutrient content. Given the favorable effects of high nutrient content on photosynthesis and plant productivity (Mooney & Gulmon, 1979, 1982), it is reasonable to expect the nutrient-saturated growth rate of a plant species to increase with nutrient content. We again assume proportionality: $r_j = k''q_j$. Then, for very large R, the plant isocline approaches an asymptote at

$$H = (k'' - D - \epsilon_j)\frac{1}{Fkq_j}. \qquad (17)$$

Plant species 2 has lower nutrient content than species 1, and is less preferred by herbivores. Its isocline for zero-growth lies above that for species 1 at low nutrient availability, and $R^*_{(2)} < R^*_{(1)}$. However, according to eqn (17), the zero-growth isocline for species 2 reaches a higher asymptote than that for species 1, unless the plant species with higher nutrient content has a very large disadvantage in density-independent losses (i.e. high ϵ_j). Barring this, the plant isoclines intersect, giving an interior equilibrium. As noted above, species 1 with its high nutrient content also has a higher MBC than species 2. This leads us to the construction of Fig. 4. Therefore, when plant nutrient contents determine both herbivore preferences and plant growth characteristics, we predict priority effects at intermediate nutrient supplies.

Several aspects of the scenario we just sketched appear to hold for some plant communities attacked by mammalian herbivores (Bryant et al., 1991). Tundra and steppe vegetation may be alternative states developing due to priority effects induced by such herbivores (Zimov et al., 1995). The relationships between nutrient content, plant growth characteristics, and herbivore preferences are undoubtedly more complex than the simple proportionality we
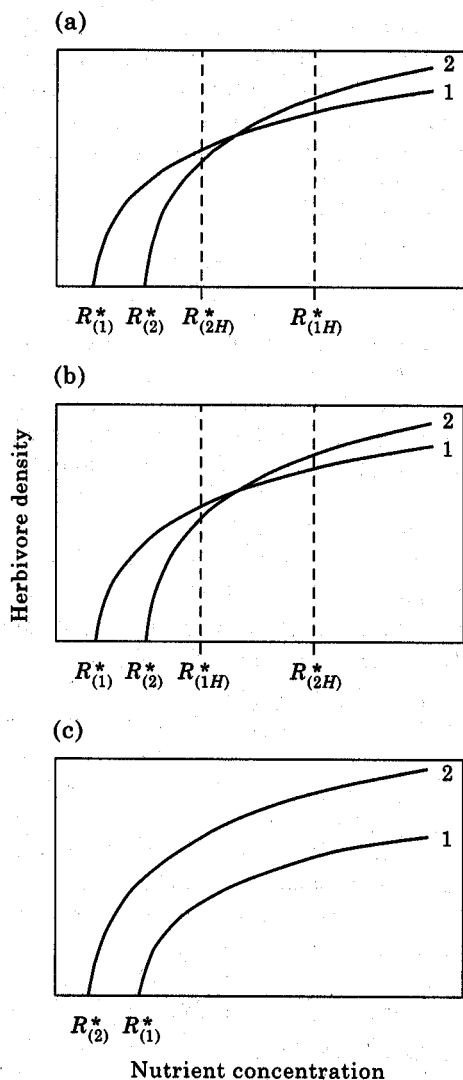
(a)

(b)

(c)

FIG. 6. Scaled growth rates (labelled curves) of competing plants in food webs with herbivores that have a type II functional response. Panel (a) shows a mutually invasible case leading to herbivore-mediated coexistence of plants; plant defenses are costly in terms of competitive ability. Panel (b) shows a mutually noninvasible case leading to priority effects; plant defenses are costly in terms of competitive ability. Panel (c) shows plant defenses that are not costly, for which the less-preferred plant 2 prevents invasion by plant 1 under all conditions.

assumed (e.g. Chapin, 1980; Hartley *et al.*, 1995; Hartley and Jones, 1997). More complicated relationships might lead to a broader range of possibilities, including perhaps herbivore-mediated coexistence instead of priority effects.

NONLINEAR FUNCTIONAL RESPONSES

Analysis

When the herbivore's functional response is nonlinear, a plant species' isoclines in its own food

chain and in the full food web do not coincide, complicating graphical theory. Although coexistence or priority effects require an intersection of the plant isoclines for the full food web, this does not necessarily correspond to an intersection of the food chain isoclines, limiting their utility as analytical tools. Moreover, the relationships between the synthetic quantities $R_{(jH)}^*$ and $H_{(jH)}^*$ and competitive outcomes can be very complex. We illustrate some of the possibilities arising with a type II, or saturating, functional response which allows for limitation of ingestion rate by "handling" time, including possibly gut processing and mastication (Crawley, 1997). Specifically, we use a modified disk equation for two food types (Murdoch & Oaten, 1975):

$$I_j(X_1, X_2) = \frac{F w_j X_j}{1 + \sum_{j=1,2} F w_j \tau_j X_j}, \quad (18)$$

where τ_j represent handling time for plant species j. The parameters F and w_j are as before, and plant 1 is assumed to be preferred ($w_1 > w_2$). Our analysis shows that, although their action becomes more complicated, the principles of costly defenses and adaptive preferences can still organize these food webs. We also identify some of the cases where food chain properties successfully predict food web outcomes, or fail to do so.

Our analysis assumes that food chains with one plant species have stable equilibria. This depends on the balance between the stabilizing influence of intraspecific competition among plants for the nutrient, and the potentially destabilizing influence of saturation in the herbivore's functional response (Appendix A). If the former is sufficiently strong, food chain equilibria are stable. High nutrient supply destabilizes equilibria, by shifting the balance between these stabilizing and destabilizing forces.

Substituting eqn (18) into our basic model [eqns (3) and (4)], the resulting plant isoclines for zero growth intersect if

$$(\mu_1(R) - D - \epsilon_1)/w_1 = (\mu_2(R) - D - \epsilon_2)/w_2, \quad (19)$$

for some R. We refer to each side of eqn (19) as "scaled growth rates", because the nutrient-dependent growth curves ($\mu_j(R)$) of the plants have been "rescaled" by subtracting density-independent losses and dividing by the selectivity coefficient.

Invasibility of food chain equilibria, the conditions allowing a three-species equilibrium, and the costs of plant defenses are related to the scaled growth rates, which we plot as functions of R. If their graphs for the two plants intersect [Fig. 6(a) and (b)], a

three-species equilibrium and either coexistence or priority effects occur; otherwise, there is competitive exclusion [Fig. 6(c)]. Intersecting scaled growth rates can occur when plant defenses are costly in terms of ability to compete in the absence of herbivores (so that $R^*_{(1)} < R^*_{(2)}$, provided w_2 is small enough to make plant 2's scaled growth rate rise more rapidly than that of species 1. Intersecting scaled growth rate curves can also occur with $R^*_{(2)} < R^*_{(1)}$, if plant defenses
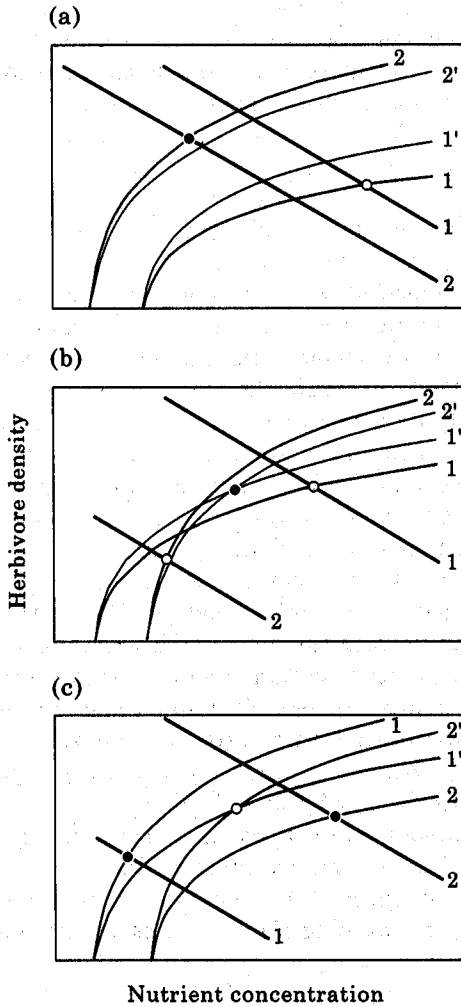

(a)

(b)

(c)

Nutrient concentration

FIG. 7. Relations between plant isoclines in food webs and food chains when herbivores have a type II functional response. The forward-sloping curves labelled 1 and 2 are food chain isoclines for zero growth of plants 1 and 2, respectively; the negatively sloping heavy lines are their food chain MBCs. The forward-sloping light curves labelled 1' and 2' are isoclines for zero growth of the plants in the full food web; solid circles show stable (noninvasible) equilibria, and open circles show unstable (invasible) equilibria. Panel (a) shows plant defenses that are not costly, and herbivore preferences that are adaptive. Panel (b) shows plant defenses that are costly in terms of competitive ability, and herbivore preferences that are adaptive. Panel (c) shows plant defenses that are costly in terms of competitive ability, and herbivore preferences that are not adaptive.

are costly in terms of maximal growth rate, although we do not consider this case further here.

For linear functional responses, plant isoclines for zero growth are obtained from scaled growth rates by multiplying the factor $1/F$ [see eqn (11)]. For type II functional responses, the zero growth isocline for plant j in its own food chain is the scaled growth rate multiplied by the factor

$$\xi^*_{(j)} \equiv (1 + Fw_j\tau_j X^*_{j(jH)})/F, \qquad (20)$$

which represents the proportional extent to which herbivore ingestion is saturated at equilibrium. For the full food web, a family of curves represents the possible positions of plant j's isocline for zero growth. This family is the scaled growth rate multiplied by the factor

$$\xi \equiv (1 + Fw_1\tau_1 X_1 + Fw_2\tau_2 X_2)/F, \qquad (21)$$

where X_1 and X_2 satisfy eqn (13). The factor ξ thus represents the extent of saturation of herbivore ingestion, for values of plant densities producing zero herbivore growth in the full food web. The more ξ differs from ξ^*_1 and ξ^*_2, the more plant isoclines for the food web differ from those for the food chains.

With nonlinear functional responses, invasion conditions cannot be assessed graphically by superimposing food chain isoclines. To determine competitive outcomes, one must compute the equilibria of both food chains, and compare the scaled growth rates of the two plants at each food chain equilibrium. If plant j is at equilibrium in its own food chain, the missing plant will invade if it has the higher scaled growth rate at the nutrient concentration $R^*_{(jH)}$. Suppose defenses are costly in terms of competitive ability (so that $R^*_{(1)} < R^*_{(2)}$) and the scaled growth rates intersect at a value $R = R^c$. If $R^*_{(2H)} < R^c < R^*_{(1H)}$, then each food chain is invisible at equilibrium by the missing plant [Fig. 6(a)]. Herbivore-mediated coexistence thus occurs. If $R^*_{(1H)} < R^c < R^*_{(2H)}$, then each food chain is not invisible at equilibrium by the missing plant [Fig. 6(b)], and priority effects occur. If defenses are not costly, then plant 2's scaled growth rate lies above that of plant 1 for all values of R [Fig. 6(c)]. The less-preferred plant 2 competitively excludes plant 1.

We have so far regarded herbivore preferences as "adaptive" if the preferred plant 1 allows the herbivore to persist at a lower plant density, i.e. if $X^*_{1(1H)} < X^*_{2(2H)}$. For a type II functional response, an alternative (and intuitive) definition of an adaptive preference could be based on the benefit of assimilated matter accruing to a herbivore consuming a unit of plant j (α_j), relative to the costs measured by

handling time (τ_j). Herbivore preferences would then be deemed "adaptive" if

$$\frac{\alpha_1}{\tau_1} > \frac{\alpha_2}{\tau_2}. \qquad (22)$$

When this condition is met, herbivore preferences are also "adaptive" with respect to plant densities required for persistence, because $X^*_{1(1H)} < X^*_{2(2H)}$. If we now assume that plants have equal nutrient content, satisfaction of eqn (22) implies that the food chain MBC for plant 1 lies above that for plant 2.

The factors ξ^*_i and ξ that convert scaled growth rates into isoclines depend on herbivore preferences and cost-benefit ratios of plant foods. For example, suppose that preferences are adaptive, but that defenses are not costly, so that the scaled growth rates of plants 1 and 2 do not intersect [Fig. 6(c)]. Nor do the plant isoclines for zero growth [Fig. 7(a)]. Satisfaction of eqn (22), together with eqn (13), implies that $\xi^*_1 < \xi < \xi^*_2$. Positions of plant isoclines for zero growth in the food web are controlled by the factor ξ, while these positions in food chains are controlled by the factors ξ^*_1 and ξ^*_2. Therefore, the zero-growth isocline for plant 2's food chain is displaced upward from its food web position, while that for plant 1's food chain is displaced downward [Fig. 7(a)]. This displacement increases with the difference between ξ^*_1 and ξ^*_2, which depends in turn on the difference between the benefit-cost ratios of the plant species. Even if this difference is extreme, the graph obtained by superimposing the food chain isocline and MBC plots resembles the corresponding plot under the simpler theory for linear functional responses [compare Figs 7(a) and 5(a)]. Like the simpler case, competitive dominance by plant 2 would be revealed by plotting both plants' MBCs and isoclines for zero growth.

Graphs of food chain isoclines and MBCs may also sometimes be useful when defenses are costly in terms of $R^*_{(j)}$, and preferences are adaptive in terms of cost-benefit ratios. The scaled growth rate curves intersect, and rescaling them by the common factor ξ preserves the intersection. In particular, a unique value ξ' applies to the three-species equilibrium represented by their intersection. Because $\xi^*_1 < \xi' < \xi^*_2$, the zero-growth isocline for plant 2's food chain is displaced upward relative to the zero-growth isocline for the three-species equilibrium, while the zero-growth isocline for plant 1's food chain is displaced downward [Fig. 7(b)]. The plant isoclines in their own food chains are thus distorted from their positions for the equilibrium of the full food web. Provided that this distortion is not too great, coexistence again would be revealed by plotting both

plants' food chain isoclines and MBCs [note the resemblance of Fig. 7(b) to Fig. 3(a)].

Next, consider herbivore preferences that are not adaptive. Then, $\xi^*_1 > \xi > \xi^*_2$, and the MBC for plant 2's food chain lies above that for plant 1's food chain, if the plants have equal nutrient content. Suppose also that defenses are costly in terms of competitive ability, with priority effects at intermediate nutrient supplies. The scaled growth rate curves intersect, and rescaling them by the common factor ξ preserves their intersection at $R = R^c$ [Fig. 7(c)]. Because $\xi^*_1 > \xi > \xi^*_2$, the zero-growth isocline for plant 1's food chain is displaced upward, relative to the zero-growth isocline for the three-species equilibrium, while the zero-growth isocline for plant 2's food chain is displaced downward, [Fig. 5(c)]. If these displacements are large, a graph of food chain MBCs and zero-growth isoclines would incorrectly suggest competitive dominance by plant 1.

We do not present the full range of logically possible constellations of adaptive vs. non-adaptive herbivore preferences, and different costs of plant defenses. Further analysis suggests that food chain graphs tend to reveal competitive outcomes in the food web under certain circumstances. Graphical theory is most informative when there are large differences between plant species in their nutrient-dependent growth rates, and smaller differences in their interaction with the herbivore. Nonlinearity of the herbivore's functional responses frustrates graphical theory most severely when plant species have similar nutrient dependent growth rates, and large differences in their interaction with the herbivore, and especially when it renders food chain equilibria unstable [see also Abrams et al. (1998)].

Numerical model of freshwater plankton

The applicability of our approach clearly depends on the quantitative properties of plants and herbivores. Therefore, we parameterized a numerical model for an ensemble of freshwater plankton for which extensive data are available. Although many aspects of this model are unrealistic, we carried out this exercise to explore the operational possibilities of our theory. We used published data on five species of planktonic freshwater algae, and the important herbivore Daphnia. Our parameterized model for the Daphnia-algal interaction is similar to that used in Grover (1995), and includes a nonlinear functional response. Our goal is to evaluate whether food chain properties (zero-growth isoclines, MBCs, $R^*_{(jH)}$ and $H^*_{(jH)}$) reveal outcomes pertaining to full food webs.

We parameterized our model of resource and apparent competition using phosphorus as the
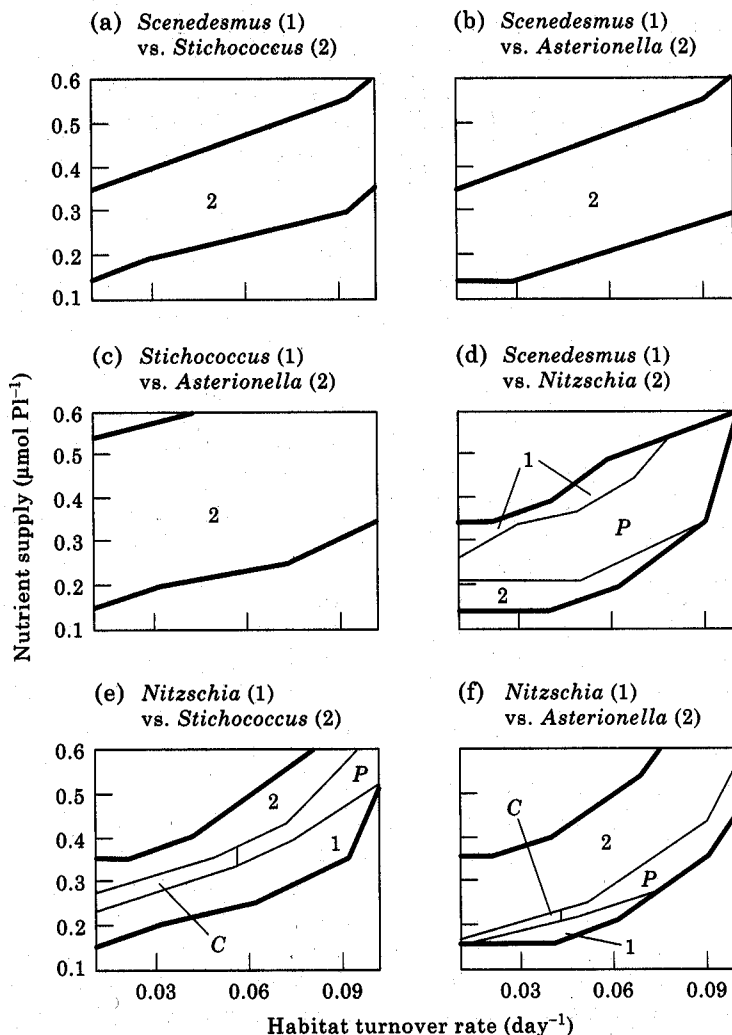
FIG. 8. Outcomes of competition between various pairs of algae under herbivory by *Daphnia*, according to the parameterized model. Each panel shows a rectangle of parameter space formed by a range of habitat turnover rates (*D*) and nutrient supplies (*S*). For each food chain, 100 combinations of *D* and *S* were examined to delineate the region of parameter space in which there was a feasible, stable equilibrium. For each species pair, the intersection of these regions bounds the parameter space in which both food chains have feasible, stable equilibria, and these bounds are drawn as heavy lines. For combinations of *D* and *S* below and to the right of the lower heavy line, at least one food chain is infeasible; for combinations of *D* and *S* above and to the left of the upper heavy line, at least one food chain is unstable. For combinations of *D* and *S* falling within the admissible region for each species pair, invasibility of the food chain equilibria was assessed, to judge competitive outcomes. Additional points in the admissible region were examined near the more complicated boundaries. For several parameter combinations, the invasion results were checked against long-term simulations with various initial conditions, and found to agree. Numbers and letters indicate competitive outcomes: 1—the preferred alga (listed first in the labels) excludes the less-preferred; 2—the less-preferred alga excludes the preferred; C—coexistence; P—priority effects.

limiting nutrient (Appendix B) and analysed predicted interactions among these species. These predictions depend on two environmental parameters, habitat turnover rate (*D*) and total nutrient supply (*S*). The former parameter potentially represents turnover from several processes: hydraulic flushing, sinking and other exchanges among stratified water layers, the action of predators not explicitly represented in our model, etc. Values of *D* from 0.01 to 0.1 d⁻¹ are plausible. We consider *S* to range from 0.1 to 0.6 μmol P l⁻¹, representing habitats that would

conventionally be considered oligotrophic to mesotrophic (Rast *et al.*, 1991). Such habitats often contain *Daphnia* spp. In constructing a parameterized model, we relied on data collected from many sources, differing in conditions such as temperature, pH, etc., which probably affect many parameters' values. We do not intend our numerical model to represent any particular system. Instead, we use it primarily to introduce biologically plausible complications, and to test insights obtained from simpler analytical models, using parameters within biologically sensible bounds.

TABLE 1

Summary of results of numerical analyses, and relationships of food web outcomes to food chain properties (see also Fig. 8)

Species pair	Nutrient supply	Habitat turnover rate	Outcome in full food web	Outcome predicted by food chains	Relative values of synthetic parameters	Herbivore preferences	Costs of defenses
Stichococcus (1) vs. *Stephanodiscus* (2)	Any consistent with stability	Any	Preferred species wins	Preferred species wins	$R_{(1)}^* < R_{(2)}^*, H_{(1)n}^* > H_{(2)n}^*$	Adaptive	Costly in terms of competitive ability
Asterionella (1) vs. *Stephanodiscus* (2)	Any consistent with stability	Any	Preferred species wins	Preferred species wins	$R_{(1)}^* < R_{(2)}^*, H_{(1)n}^* > H_{(2)n}^*$	Adaptive	Costly in terms of competitive ability
Scenedesmus (1) vs. *Stichococcus* (2)	Any consistent with stability	Any	Less-preferred species wins	Less-preferred species wins	$R_{(2)}^* < R_{(1)}^*, R_{(2)n}^* < R_{(1)n}^*$	Adaptive	Costly in terms of nutrient saturated growth rate
Scenedesmus (1) vs. *Asterionella* (2)	Any consistent with stability	Any	Less-preferred species wins	Less-preferred species wins	$R_{(2)}^* < R_{(1)}^*, R_{(2)n}^* < R_{(1)n}^*$	Adaptive	Costly in terms of nutrient saturated growth rate
Stichococcus (1) vs. *Asterionella* (2)	Any consistent with stability	Any	Less-preferred species wins	Less-preferred species wins	$R_{(2)}^* < R_{(1)}^*, H_{(2)n}^* > H_{(1)n}^*$	Not adaptive	Costly in terms of nutrient saturated growth rate
Scenedesmus (1) vs. *Nitzschia* (2)	Low	Any	Less-preferred species wins	Less-preferred species wins	$R_{(2)}^* < R_{(1)}^*, R_{(2)n}^* < R_{(1)n}^*$	Adaptive	Costly in terms of nutrient saturated growth rate
	Intermediate	Any	Priority effects	Priority effects	$R_{(2)}^* < R_{(1)}^*, R_{(2)n}^* < R_{(1)n}^*, H_{(1)n}^* > H_{(2)n}^*$	Adaptive	Costly in terms of nutrient saturated growth rate
	High	Any	Preferred species wins	Preferred species wins	$R_{(2)}^* < R_{(1)}^*, H_{(1)n}^* > H_{(2)n}^*$	Adaptive	Costly in terms of nutrient saturated growth rate
Nitzschia (1) vs. *Stichococcus* (2)	Low	Low	Preferred species wins	Preferred species wins	$R_{(1)}^* < R_{(2)}^*, H_{(1)n}^* > H_{(2)n}^*$	Adaptive	Costly in terms of competitive ability
	Intermediate	Low	Coexistence	Coexistence	$R_{(1)}^* < R_{(2)}^*, R_{(2)n}^* < R_{(1)n}^*, H_{(1)n}^* > H_{(2)n}^*$	Adaptive	Costly in terms of competitive ability
	High	Low	Less-preferred species wins	Less-preferred species wins	$R_{(1)}^* < R_{(2)}^*, R_{(2)n}^* < R_{(1)n}^*$	Adaptive	Costly in terms of competitive ability
	Intermediate	Intermediate	Priority effect	Preferred species wins	$R_{(1)}^* < R_{(2)}^*, R_{(1)n}^* < R_{(2)n}^*$	Not adaptive	Costly in terms of competitive ability
	Low	High	Preferred species wins	Preferred species wins	$R_{(1)}^* < R_{(2)}^*, R_{(1)n}^* < R_{(2)n}^*$	Not adaptive	Costly in terms of competitive ability
	Intermediate	High	Priority effects	Priority effects	$R_{(1)}^* < R_{(2)}^*, R_{(1)n}^* < R_{(2)n}^*, H_{(2)n}^* > H_{(1)n}^*$	Not adaptive	Costly in terms of competitive ability
	High	High	Less-preferred species wins	Less-preferred species wins	$R_{(1)}^* < R_{(2)}^*, H_{(2)n}^* > H_{(1)n}^*$	Not adaptive	Costly in terms of competitive ability
Nitzschia (1) vs. *Asterionella* (2)	Low	Low	Coexistence	Preferred species wins	$R_{(1)}^* < R_{(2)}^*, R_{(2)n}^* < R_{(1)n}^*, H_{(1)n}^* > H_{(2)n}^*$	Adaptive	Costly in terms of competitive ability
	Intermediate	low	Coexistence	Coexistence	$R_{(1)}^* < R_{(2)}^*, R_{(2)n}^* < R_{(1)n}^*$	Adaptive	Costly in terms of competitive ability
	High	Low	Less-preferred species wins	Less-preferred species wins	$R_{(1)}^* < R_{(2)}^*, R_{(2)n}^* < R_{(1)n}^*$	Adaptive	Costly in terms of competitive ability
	Intermediate	Intermediate	Priority effect	Preferred species wins	$R_{(1)}^* < R_{(2)}^*, R_{(1)n}^* < R_{(2)n}^*$	Not adaptive	Costly in terms of competitive ability
	Low	High	Preferred species wins	Preferred species wins	$R_{(1)}^* < R_{(2)}^*, R_{(1)n}^* < R_{(2)n}^*$	Not adaptive	Costly in terms of competitive ability
	Intermediate	High	Priority effects	Priority effects	$R_{(1)}^* < R_{(2)}^*, R_{(1)n}^* < R_{(2)n}^*, H_{(2)n}^* > H_{(1)n}^*$	Not adaptive	Costly in terms of competitive ability
	High	High	Less-preferred species wins	Less-preferred species wins	$R_{(1)}^* < R_{(2)}^*, H_{(2)n}^* > H_{(1)n}^*$	Not adaptive	Costly in terms of competitive ability

Species indices are assigned so that species 1 is the preferred species, and species 2 is less-preferred.

In particular, we ask whether the magnitude of nonlinearities in functional responses suffices to prevent the extrapolation of graphical models.

For each algal species, we determined the positions of its food chain isocline for zero growth and MBC-line over the above ranges for D and S. If the positions of these isoclines for algal species in their own food chains are not greatly affected by the nonlinearity of *Daphnia*'s functional response, then their graphs should predict competitive outcomes when the whole food web is assembled. The positions of the food chain isoclines for zero growth are related to the rank-orders of the synthetic parameters $R_{(i)}^*$, $R_{(iH)}^*$, and $H_{(iH)}^*$. For example, consider this pattern: for a given range of nutrient supplies (S) at a fixed habitat turnover rate (D), $R_{(1)}^* < R_{(2)}^*$, at a low nutrient supply, $H_{(1H)}^* > H_{(2H)}^*$ (with any ordering of $R_{(iH)}^*$), and at a high nutrient supply, $R_{(2H)}^* < R_{(1H)}^*$ (with any ordering of $H_{(iH)}^*$). This pattern corresponds to the case of coexistence illustrated in Fig. 3(a). On the other hand, food chain graphs, and the associated patterns of synthetic parameters would fail to diagnose outcomes for the full food webs if the nonlinearity in *Daphnia*'s functional response were sufficiently strong [e.g. Fig. 7(a)]. We used numerical routines to predict the outcomes of the full food web according to the nonlinear model, and compared the outcomes to those predicted by food chain properties.

We examined pairwise combinations of algal species, and restricted D and S to those values for which both of the food chains were feasible (i.e. produced a positive herbivore density), and stable (i.e. we excluded habitats sufficiently enriched to produce limit cycles in a food chain). This is a potentially significant restriction, because food chain models of the sort we use here can exhibit unstable equilibria and large amplitude limit cycles under nutrient-rich conditions (e.g. Kretzschmar *et al.*, 1993; Grover, 1995). The empirical literature documents both stable dynamics of *Daphnia* and algae, and oscillatory dynamics (Murdoch & McCauley, 1985; McCauley & Murdoch, 1987). However, observed oscillations do not appear to be enrichment-driven predator-prey cycles, but arise from other factors such as age-structure (McCauley & Murdoch, 1990). Thus, an equilibrium analysis may be reasonable. For at least some of the species pairs considered here, a variety of competitive outcomes can arise even within the restricted range of parameters associated with stable food chain equilibria.

Regions of parameter space allowing stable equilibria for each species pair are bounded by the heavy lines in Fig. 8, which displays competitive outcomes in the ranges of parameter space examined.

Table 1 summarizes the relationships of these outcomes to food chain properties as summarized by the synthetic parameters $R_{(i)}^*$, $R_{(iH)}^*$, and $H_{(iH)}^*$. For two of the ten possible species pairs (*Scenedesmus* vs. *Stephanodiscus*, and *Nitzschia* vs. *Stephanodiscus*), no values of D and S in the ranges examined predict feasible and stable food chains for both competitors.

Competitive outcomes potentially depend on nutrient supply for all other species pairs, because defenses against herbivory in these systems are always costly. However, because we considered only those nutrient supplies low enough to allow stability, the range of competitive outcomes was often truncated. For example, feasibility and stability for two species pairs (*Stichococcus* vs. *Stephanodiscus*, and *Asterionella* vs. *Stephanodiscus*) are predicted only in a very small region of parameter space, and so results are not plotted. For these two species pairs, dominance by the preferred species was predicted in this small region of parameter space. For three other species pairs (*Scenedesmus* vs. *Stichococcus*, *Scenedesmus* vs. *Asterionella*, and *Stichococcus* vs. *Asterionella*) nutrient supplies low enough for stability led to dominance by the less-preferred species. Other outcomes may occur at higher nutrient supplies.

For all five species pairs, the dominance of a single species in the region of parameter space examined was predicted by numerical study of the food web model, as well as inspection of food chain isoclines and MBC-lines. For the two species pairs in which the preferred species always dominated, two consistent rankings of synthetic parameters also held: $R_{(1)}^* < R_{(2)}^*$, and $H_{(1H)}^* > H_{(2H)}^*$. These imply that the zero-growth isocline for the preferred species lies above that for the less preferred, which implies that the former dominates; this was confirmed by numerical analysis of the food web. For the two species pairs in which the less-preferred species always dominated, the consistent rankings of synthetic parameters were: $R_{(2)}^* < R_{(1)}^*$, and $R_{(2H)}^* < R_{(1H)}^*$. These imply that the zero-growth isocline for the less-preferred species lies above that for the preferred, so that the preferred species dominates, as again shown by numerical analysis of the food web. This latter result corresponds to the case illustrated in Fig. 5(a).

For the three remaining pairs of species, a wider range of competitive outcomes occurred in the region of parameter space allowing feasibility and stability. In each case, increasing nutrient supply shifted the system from dominance by one species, to priority effects or coexistence, to dominance by the other species, before equilibria finally became unstable.

In the case of *Scenedesmus* vs. *Nitzschia*, numerical analysis showed a progression from dominance by the less-preferred species at low S, to priority effects at intermediate S, to dominance by the preferred species at high S [Fig. 8(d), Table 1]. This is also predicted from the food chain isoclines for zero growth and MBC-lines, and summarized by the patterns of synthetic parameters. The case of priority effects illustrated in Fig. 4 corresponds to the predictions of the numerical model.

In the cases of *Nitzschia* vs. *Stichococcus* and *Nitzschia* vs. *Asterionella*, competitive outcomes were more complicated because herbivore preferences change from adaptive at low habitat turnover rates, to non-adaptive at high habitat turnover rates. At any turnover rate, the preferred species dominated at low nutrient supplies, and the less-preferred species dominated at high nutrient supplies. At low turnover rates, intermediate nutrient supplies produced coexistence [Fig. 8(e),(f), Table 1]. The same progression of competitive outcomes is predicted by food chain isoclines for zero growth and MBC-lines, and summarized by patterns of synthetic parameters. The case of coexistence displayed in Fig. 3(a) matches the coexistence observed using the numerical model at low turnover rates.

For these two species pairs at high turnover rates, intermediate nutrient supplies produced priority effects [Fig. 8(e),(f), Table 1]. For sufficiently high turnover rates, the progression of competitive outcomes is correctly predicted by food chain isoclines for zero growth and MBC-lines, and summarized by patterns of synthetic parameters. However, there is an intermediate range of turnover rates high enough to produce priority effects at intermediate nutrient supplies, but for which food chain graphs predict incorrectly that the preferred species should win. Qualitatively, food chain graphs would correctly predict that as the habitat turnover rate increases from low values, there is a transition from coexistence to priority effects [which corresponds to a transition from Fig. 3(a) to Fig. 3(b)]. The food chain graphs fail to locate this transition quantitatively, however, and thus make an inaccurate prediction. The situation is that illustrated in Fig. 7(c), where the food chain isoclines and MBC-lines predict dominance by the preferred species, when in fact priority effects occur. In all our numerical analyses for our parameterized model, this was the only class of outcomes for which the simple approach based on food chain graphs failed.

Apart from these few cases, analyses based on food chain graphs successfully predicted the competitive outcomes obtained for full food webs. This suggests that the distortion between zero-growth isoclines in food chains and food webs, illustrated in Fig. 7, was relatively small, despite *Daphnia*'s nonlinear functional response. Such low distortion is due to the combination of large interspecific differences in nutrient-dependent growth of algae, with smaller differences in parameters governing their interaction with the herbivore. Note that the half-saturation constants (K_j) of algal growth functions differ more than 100-fold between species, while all other parameters differ five-fold at most (Table B1). Poor performance of food chain graphs only occurred for ranges of D straddling qualitatively different outcomes, due to changes in the adaptiveness of herbivore preferences.

Our results suggest that several strategies potentially characterize algal prey that persist in habitats with high herbivore density. As might be expected, less-preferred algae which are resistant to ingestion by *Daphnia* sometimes dominate. Perhaps less intuitively, their dominance is often associated with a low value of $R_{(jH)}^*$, indicating resource competition as a proximate mechanism of dominance, even in the presence of herbivores. Resistance to herbivory reduces loss rate and can make a species a more effective resource competitor, by reducing the nutrient concentration required to persist at equilibrium. Algae resistant to ingestion do not necessarily dominate habitats with high herbivore density, however. Highly edible algae can persist with large herbivore populations if their maximal growth rates are high. Indeed, such algae could be formidable apparent competitors, associated with high $H_{(jH)}^*$, and supporting *Daphnia* densities high enough to exclude even resistant algae. It is intriguing that dominance by edible algae with high maximal growth rates has in fact been observed in some lakes with large *Daphnia* populations (Sarnelle, 1992, 1993).

Discussion

There is a large theoretical literature on plant-herbivore interactions, much of which essentially examines pairwise predator-prey interactions. Recently, interest has grown in decomposing the "plant box" into populations of differing edibility, so that competition among plants is also considered in the context of herbivory (Armstrong, 1979; Leibold, 1989; Abrams, 1993; Kretzschmar et al., 1993; Holt et al., 1994; Grover, 1995, 1997). Our efforts share much with these previous investigations. However, we have gone further in exploring a range of relationships among plant competitive abilities and herbivore preferences among plant species, in attempting to

understand some of the complexities arising from nonlinearities in herbivore functional responses, and in parameterizing our model realistically for aquatic systems.

In exploring nonlinear plant growth functions, we have uncovered a rich set of biological possibilities. These depend on whether plant defenses are costly, either in terms of competitive ability in the absence of herbivory, or in terms of maximal, resource-saturated growth rate, and also on herbivore preferences for different plant prey. Despite decades of research on plant defenses and herbivore preferences, many of the implications of defenses for population and community dynamics remain unclear (Crawley, 1989; Crawley & Pacala, 1991). We developed our graphical theory to help understand how the outcomes of simultaneous resource and apparent competition are influenced by the nature of plant defenses. Within the limits posed by our simplifying assumptions, the construction of food chain graphs predicts the consequences of assembling two food chains into a food web. The configurations of such graphs are related to the synthetic quantities $R^*_{(H)}$ and $H^*_{(H)}$ that we introduced earlier (Holt et al., 1994). Determining these quantities at several nutrient supplies provides one avenue to operationalize our theory.

In exploring nonlinear herbivore functional responses, our analysis of selected examples suggests that graphical theory and synthetic quantities could be particularly useful when different plant species evoke quantitatively similar functional responses in the herbivore. Then, when comparing food chains and full food webs, distortion in plant isoclines for zero growth will be small. For the type II functional response, our analysis suggests that our approach should apply best to herbivores eating a suite of plants with similar nutritional benefits, relative to costs. With more complex functional responses, such as those representing "switching", herbivore preferences could depend on plant densities, as opposed to the fixed preferences assumed here. Relationships between food chain properties and food web outcomes might then be so complex as to preclude predictability.

Although coexistence of plants mediated by generalist herbivores emerged as a theoretical possibility in our models, we suspect this result needs further critical analysis. Such coexistence is always conditional on nutrient supply, it might be evolutionarily unstable (as plants evolve more effective defenses), and conditions for coexistence might be sensitive to departures from equilibrium assumptions. One general conclusion emerging from our work is that the effects of generalist herbivores are no panacea

for resolving the classical problem of multiple plant species persisting on a few limiting resources.

Throughout this paper we took an equilibrium approach. Simulations of our parameterized Daphnia-algal model (unpublished) suggest that periodic disturbances can dramatically alter competitive outcomes, even when the model has stable equilibria. Patterns of competitive dominance, coexistence, and priority effects can differ from equilibrium predictions in complex ways (Abrams et al., 1998). For example, complicated multiple stable states sometimes appear, involving periodic attractors. We have not explored competitive dynamics in these systems under conditions in which endogenous limit cycles develop, though we suspect they will be equally complex. Nonequilibrium dynamics might be further complicated by factors we have ignored, such as age structure and nutrient storage.

Throughout this paper, we made the simplifying assumption that inter- and intraspecific interactions among plants are entirely indirect, mediated only by nutrients and natural enemies. This assumption does not rule out other niche differences (e.g due to temperature, moisture, etc.) provided that they act primarily by affecting the parameters governing interactions with nutrients and herbivores. This assumption does rule out competition for other resources (e.g. light) or via mechanisms such as allelopathy. To accommodate some of the processes we neglected, one could assume density-dependent plant losses, and substitute a function $\epsilon_j(X_1, X_2)$ in eqns (3) and (4). We are not convinced that adding such phenomenological density-dependent terms to our model would be as valuable as trying to explicitly describe the mechanisms we neglected. Mechanistic models of competition for light (Huisman et al., 1998) and allelopathy (DeFreitas & Frederickson, 1978; Grover, 1997) have been proposed. Combining such models with those presented here would allow exploration of a number of issues we have ignored.

Our assumptions also rule out direct intraspecific interactions among herbivores. To represent these, one could substitute a density-dependent herbivore loss rate or a predator-dependent functional response. If we assume that herbivores have a type I functional response, but modify our eqn (3b) to have a density-dependent loss rate, $\delta(H)$, that is an increasing function, we can show that some of our results are robust. The plant isoclines for zero growth that we constructed in the RH-plane are unchanged, the quantities $R^*_{(H)}$ and $H^*_{(H)}$ are increasing functions of nutrient supply, invasion conditions are related to these graphs and quantities, and competitive outcomes depend on nutrient supply. Some of the

biological trade-offs that we have emphasized may be altered, however. The possible effects of a nonlinear predator-dependent functional response of the form $\iota_j(X_1, X_2, H)$ are much more difficult to anticipate, as models with such functions are not easy to analyse.

A number of complications in the theory of simultaneous resource and apparent competition remain unexplored. Undoubtedly our approach is not robust to all conceivable complications. The critical question is which complications are prevalent and strong enough in nature to frustrate our approach. Simplicity in nature may indeed not exist, but we will not find what we do not seek.

The essence of our theory is this: a plant population growing with herbivores creates certain conditions of nutrient availability (e.g. $R^*_{(jH)}$) and herbivore density (e.g. $H^*_{(jH)}$). Another plant population can invade and persist only if it has a positive net rate of change under these conditions. We emphasize that this notion is operational and testable. The critical quantities are measurable with standard methods, and could be assessed in simple laboratory communities, or in field systems dominated by a few important species. Aquatic systems similar to those we modelled numerically would seem a natural choice for such work, as might some terrestrial systems (Schmitz, 1994, 1997). We look forward to the confrontation of this optimism with real data, although we do not wish to understate the technical difficulties of the required experiments.

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APPENDIX A

Stability Analysis

We first address the stability of food chain equilibria, upon which many of our analyses rely. The food chain system based on plant j alone is a three-dimensional subsystem of eqns (3) and (4), and it may be further reduced to a planar system through the MBC [eqn (5)]. This eliminates the dynamic equation for the nutrient, and the stability of the resulting second order system is assessed by linearization (May, 1974; Nisbet & Gurney, 1982).

Standard analysis leads to two algebraic conditions for stability. The first condition can be written

$$H_{(jH)}^* \left[\frac{\iota_j(X_{j(jH)}^*)}{X_{j(jH)}^*} - \frac{\partial \iota_j}{\partial X_j}\bigg|_* \right] - q_j X_{j(jH)}^* \frac{d\mu_j}{dR}\bigg|_* < 0, \quad (A.1)$$

where equilibrium quantities are indicated as in the main text. The first term (in square brackets) represents any stabilizing or destabilizing tendencies resulting from nonlinearity of the herbivore's functional response. The second term represents intraspecific competition among the plants for the nutrient, and is always stabilizing. If the herbivore's functional response is linear, then the first term is zero, and this stability condition is satisfied, owing to competition for the nutrient. If the herbivore's functional response is saturating (destabilizing), the first condition could still be satisfied if intraspecific competition among the plants for the nutrient were strong. The second stability condition can be written

$$\frac{be_j}{\gamma} H_{(jH)}^* X_{j(jH)}^* \left(\frac{\partial \iota_j}{\partial X_j}\bigg|_*\right)\left(\frac{d\mu_j}{dR}\bigg|_*\right) > 0, \quad (A.2)$$

and it is always satisfied.

Therefore, stability of food chain equilibria rests entirely on the first condition (A.1). For the type II functional response used in the text, this become

$$sH_{(jH)}^* \left(\frac{F^2 w_j^2 \tau_j}{(1 + Fw_j\tau_j X_{j(jH)}^*)^2}\right) - q_j X_{j(jH)}^* \frac{d\mu_j}{dR}\bigg|_* < 0. \quad (A.3)$$

A fully expanded version of this condition is too complicated to yield much insight into how stability relates to the elementary parameters of the model, but two points are clear. First, the saturating functional response is destabilizing, but this tendency can be overcome by sufficiently strong competition for nutrients among plants, in the form of a high nutrient quota and a steep slope for the function $\mu(R)$ at equilibrium. Second, high nutrient supply is destabilizing for two reasons: because $H_{(jH)}^*$ is increased, and because the higher $R_{(jH)}^*$ leads to a lower slope for $\mu(R)$, when this is a typical saturating function.

The food web with both plant species has an interior equilibrium under certain conditions (specified in the main text). In applying a local stability analysis, it is easiest to consider the three-dimensional system of differential equations (3), using the MBC [eqn (5)] to eliminate the dynamic equation for the nutrient. This leads to three algebraic conditions for stability. For a general herbivore functional response $\iota_j(X_1, X_2)$, the first of these can be written

$$H^* \left[\frac{\iota_1(X_1^*, X_2^*)}{X_1^*} + \frac{\iota_2(X_1^*, X_2^*)}{X_2^*} - \frac{\partial \iota_1}{\partial X_1}\bigg|_* - \frac{\partial \iota_2}{\partial X_2}\bigg|_* \right.$$

$$\left. - q_1 X_1^* \frac{d\mu_1}{dR}\bigg|_* - q_2 X_2^* \frac{d\mu_2}{dR}\bigg|_* < 0, \quad (A.4) \right.$$

where "*" denotes a quantity evaluated at the interior equilibrium. The first term (in square brackets) represents any stabilizing or destabilizing tendencies resulting from nonlinearity of the herbivore's functional response. The second and third terms represent intraspecific competition among the plants for the nutrient, and are always stabilizing. If the herbivore's functional response is linear, then the first term is zero, and this stability condition is satisfied, owing to competition for the nutrient. If the herbivore's functional response is saturating (destabilizing), the first condition could still be satisfied if intraspecific competition among the plants for the nutrient were strong.

The second stability condition can be written

$$A_1 B_1 C_2 + A_2 B_2 C_1 + A_1 B_2 D_1 + A_2 B_1 D_2 > 0, \quad (A.5)$$

where

$$A_1 = e_1 \left.\frac{\partial \iota_1}{X_1^*}\right|_* + e_2 \left.\frac{\partial \iota_2}{X_1^*}\right|_*$$

$$A_2 = e_1 \left.\frac{\partial \iota_1}{X_1^*}\right|_* + e_2 \left.\frac{\partial \iota_2}{X_2^*}\right|_*$$

$$B_1 = \iota_1(X_1^*, X_2^*) + \frac{b}{\gamma} X_1^* \left.\frac{d\mu_1}{dR}\right|_*$$

$$B_2 = \iota_2(X_1^*, X_2^*) + \frac{b}{\gamma} X_2^* \left.\frac{d\mu_2}{dR}\right|_*$$

$$C_1 = H^* \left[\frac{\iota_1(X_1^*, X_2^*)}{X_1^*} - \left.\frac{\partial \iota_1}{\partial X_1}\right|_* \right] - q_1 X_1^* \, d\mu_1 \, dR|_*$$

$$C_2 = H^* \left[\frac{\iota_2(X_1^*, X_2^*)}{X_2^*} - \left.\frac{\partial \iota_2}{\partial X_2}\right|_* \right] - q_2 X_2^* \, d\mu_2 \, dR|_*$$

$$D_1 = H^* \left.\frac{\partial \iota_1}{\partial X_2}\right|_* + q_2 X_1^* \left.\frac{d\mu_1}{dR}\right|_*$$

$$D_2 = H^* \left.\frac{\partial \iota_2}{\partial X_1}\right|_* + q_1 X_2^* \left.\frac{d\mu_2}{dR}\right|_*.$$

The quantities B_1 and B_2 are always positive, but the signs of the remaining quantities depend on parameter values, and are once again related to nonlinearities of the herbivore's functional response, and to the strength of intraspecific competition among the plants for the nutrient.

For the special case of a linear functional response, the second stability condition simplifies to

$$\left(\frac{1}{w_1} \left.\frac{d\mu_1}{dR}\right|_* - \frac{1}{w_2} \left.\frac{d\mu_2}{dR}\right|_* \right)\left(\frac{e_2 w_2}{q_2} - \frac{e_1 w_1}{q_1} \right) > 0. \quad \text{(A.6)}$$

The first factor of this expression depends on the relative positions of the plant isoclines for zero growth, as given by eqn (11). Consider first the case (a) where $R_{(1)}^* > R_{(2)}^*$, so that the zero-growth isocline of plant 1 must rise more rapidly than the isocline for plant 2 in order to have an interior equilibrium. Then the first factor of expression (A.6) is positive. For the opposite arrangement of the plant isoclines for zero growth [case (b), $R_{(1)}^* < R_{(2)}^*$], the first factor is negative. In case (a), if the second factor of expression (A.6) is negative, the interior equilibrium is unstable, which corresponds to the MBC for plant 1 having higher elevation than that for plant 2. This leads to the construction of Fig. 4, which illustrates an unstable interior equilibrium and priority effects. In case (b), if the second factor of expression (A.6) is positive, the MBC for plant 2 lies above that for plant

1, and the interior equilibrium is again unstable leading to a priority effect [this leads to the construction of Fig. 3(b)].

The third stability condition is always satisfied for a linear functional response, and therefore in such cases, the stability of the interior equilibrium is completely determined by the second condition. In case (a), where $R_{(1)}^* > R_{(2)}^*$, the interior equilibrium is locally stable if the MBC for plant 1 has lower elevation than that for plant 2. In case (b), where $R_{(1)}^* < R_{(2)}^*$, the interior equilibrium is locally stable if the MBC for plant 1 lies above that for plant 2. This case of coexistence leads to the construction of Fig. 3(a). In both these cases of coexistence, mutual invasibility of food chain equilibria, together with their assumed stability, permits application of the permanence theorem of Hutson & Law (1985). Thus coexistence equilibria are globally stable.

For nonlinear functional responses, the third stability condition can be written

$$H^*(A_1 B_2 D_1 + A_2 B_1 D_2 + A_2 B_2 C_1 + A_1 B_1 C_2)$$

$$- (C_1 + C_2)(A_1 B_1 H^* + A_2 B_2 H^* + C_1 C_2 - D_1 D_2) > 0,$$

$$\text{(A.7)}$$

which admits little interpretation except to repeat that stability is related to nonlinearity of the herbivore's functional response and intraspecific competition among the plants for the nutrient.

APPENDIX B

Parameterization of the Numerical Model

We modify a previous model (Grover, 1995), which treated one herbivore, its plant prey, and an inedible competitor of the prey. To represent freshwater plankton, phosphorus is taken as the limiting nutrient (Schindler, 1977), and we take Geller's (1975) data on *Daphnia pulex* as representative of this genus, using his length-dependent allometric formula to calculate parameters for an animal 2 mm long, having a carbon content (b) of $1.9 \, \mu$mol C animal^{-1}. Geller (1975) examined the functional response of *D. pulex* for several algae, from which we calculate parameters for a Holling type II curve (Table B1). Since the highest clearance rate in the limit of zero food concentration ($0.041 \, 1 \, \text{an}^{-1} \, \text{d}^{-1}$) was found for *Scenedesmus acutus*, we take this as an estimate of F, and set $w_j = 1$ for *Scenedesmus*. The remaining w_j are then calculated relative to *Scenedesmus* from clearance rates reported by Geller, in the limit of zero food concentration for these species. Values of handling time (τ_j) are converted from the maximal ingestion rates reported

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TABLE B1

Model parameters for Daphnia pulex *and several algal food species studied by Geller (1975)*

Algal food species	τ_j (d (μmol C)$^{-1}$)	w_j	α_j	r_j(d^{-1})	K_j (μmol P l^{-1})	Reference for r_j and K_j
Scenedesmus acutus	1.2200	1.0000	0.9900	0.9100	0.0200	J. Grover, unpublished
Stichococcus minutus	0.7500	0.6800	0.6100	0.8000	0.0150	cf. small chlorophytes, Grover (1989)
Nitzschia actinastroides	1.6700	0.8800	0.9900	0.3500	0.0023	cf. *N. acicularis*, Grover (1989)
Asterionella formosa	1.2800	0.5600	0.9900	0.5900	0.0060	Tilman (1981)
Stephanodiscus hantzschii	1.0000	0.2000	0.8100	0.8000	0.3100	Van Donk & Kilham (1990)

Values of r_j and K_j were assigned from the references listed, by comparison to similar taxa as noted.

by Geller (1975). Using the allometric relation between *Daphnia* length and metabolic losses suggested by Gurney *et al.* (1990), we set $\delta = 0.165$ d^{-1}.

For algae, population growth usually depends on phosphorus concentration as a rectangular hypebola

$$\frac{r_j R}{K_j + R},\qquad (B.1)$$

where r_j is the maximal growth rate, and K_j is a half-saturation constant (Tilman *et al.*, 1982; Grover, 1989). For the algae studied by Geller (1975), the parameters of this curve are known, or can be inferred from taxonomically and morphologically similar organisms (Table B1). Density-independent losses (ϵ_j) were set to zero for all algae, since these losses are typically small relative to other losses (Reynolds, 1984). Values of q_j vary widely within algal species, depending on physiological and environmental circumstances (Turpin, 1988). A molar carbon: phosphorus ratio of 200 is representative of moderately phosphorus-limited algae (Hecky & Kilham, 1988; Sommer, 1989), corresponding to $q_j = 0.005$ μmol P/μmol C, which we assign to all algae.

Direct measurements of assimilabilities in zooplankton herbivores vary considerably, depending on what is meant by assimilability and upon the methods used. For our purposes, an indirect estimation suffices: when a single food type is saturating, the herbivore population is expected to grow at a maximal rate equal to $\alpha_j/b\tau_j - \delta$. We take 0.26 d^{-1} as the food-saturated population growth rate of *Daphnia pulex*, based on life table studies (Meise *et al.*, 1985), and thus calculate the values of α_j shown. For *Nitzschia* and *Asterionella*, calculated assimilabilities exceed one, so we set them to 0.99, the highest value observed among other algae (for *Scenedesmus*), thereby giving reduced food-saturated growth rates for *Daphnia* populations feeding on these two species. Geller (1975) studied more algae than those listed in Table B1, but for these algae, even complete assimilability did not give *Daphnia* positive growth

rates under food saturation. The high assimilabilities forced on us in this exercise are not unreasonable: metabolic losses that vary in proportion to ingestion are parameterized with α_j, but *Daphnia* is a filter feeder that continually pumps water, so much of its losses may be independent of food intake, and are thus parameterized with δ. Lampert (1978) directly measured quantities close to $1 - \alpha_j$ for many of the same strains used by Geller (1975), and often found values near 0.1.

We take γ, the molar carbon:phosphorus ratio of the *Daphnia*, to be 200 for two reasons. First, this ensures that rates of phosphorus recycling by *Daphnia* are positive ($q_j - \alpha_j/\gamma > 0$ for all algae). Second, the resulting fluxes of regenerated phosphorus are comparable to those found by Olsen & Østgaard (1985) for *D. pulex* feeding on a *Scenedesmus* sp., and those found by Lehman (1980) for other species of *Daphnia* and algae. The value of γ used is higher than reported values based on tissue composition of *Daphnia* spp. (Peters, 1987), and γ is best interpreted as a "demand" ratio for carbon and phosphorus, differing from measured tissue ratios due to the simplistic representation of chemical fluxes in our model.

In parameterizing our model, we calculated α_j in such a way that the benefit-cost ratio (α_j/τ_j) would be constant for all algae, except when it was necessary to constrain $\alpha_j < 1$. For pairs of algae that have equivalent benefit-cost ratios, food chain and food web isoclines for zero growth do not differ, and relations between competitive outcomes and $R_{(H)}^*$ and $H_{(H)}^*$ must follow the patterns pertaining to linear functional responses. However, for five of the six algal pairs analysed in Fig. 8, benefit-cost ratios differed due to truncating α_j at 0.99 for some species. Hence, the food chain and food web isoclines for zero growth of our model algae usually differed. In principle, such differences cause patterns of association between competitive outcomes and $R_{(H)}^*$ and $H_{(H)}^*$ to differ from simple expectations. However, as noted in the main text, such discrepancies appear to be the exception, rather than the norm.