

16: Plants in Trophic Webs

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It is obvious to all students of nature that a paramount question is: who eats whom? Answers are presented as food webs: networks of arrows and boxes. About 20 years ago, the initial, descriptive approach to food webs was replaced by a more abstract and analytical one (e.g. Pimm 1982); the current state of such studies is reviewed by Pimm *et al.* (1991) and Polis & Winemiller (1996) and a critique is provided by Paine (1988). Fascinating though it is, much of this literature is not directly useful to the plant ecologist. Very few food-web studies attempt to represent all species present in a habitat, and plants seem to suffer more from empirical myopia than any other organisms with the possible exception of decomposers. Often, plants are simply lumped into coarse categories – canopy trees versus grasses, phytoplankton versus benthic algae. Processes within these compartments that might influence the rest of the food web, such as the strong intraspecific and interspecific competition suffered by plants (Crawley 1990; see Chapter 15), may be obscured by this kind of aggregation. This competition usually takes place over abiotic resources: light, water and nutrients (Chapter 8). Nutrients are often supplied to plants mainly by decomposition and nutrient recycling, processes that are ignored in many food-web studies (but see DeAngelis 1992). Herbivores fare rather better than plants and decomposers in published food-web studies: many are identified to species, although coarse categories are often used, especially for invertebrates.

These and other deficiencies in the empirical basis of food-web research have stimulated new studies that attempt to catalogue organisms and processes more completely (e.g. Polis 1991). These efforts are an important way forward, but we take another tack in this chapter by adopting a theoretical approach that examines the properties of a small number of trophically connected populations. Rather than studying whole food webs, we focus on food-web ‘modules’ (Fig. 16.1), which allow us to represent important processes realistically. We emphasize the three key processes crucial for understanding plants: (i) herbivory; (ii) the dependence of plant growth on nutrient supply and recycling, and (iii) competition among plants for nutrients. This approach synthesizes the fundamental principles of population biology, first sketched by Hairston *et al.* (1960), with principles of ecosystem ecology concerning nutrient dynamics. Our presentation is graphical and intuitive; more

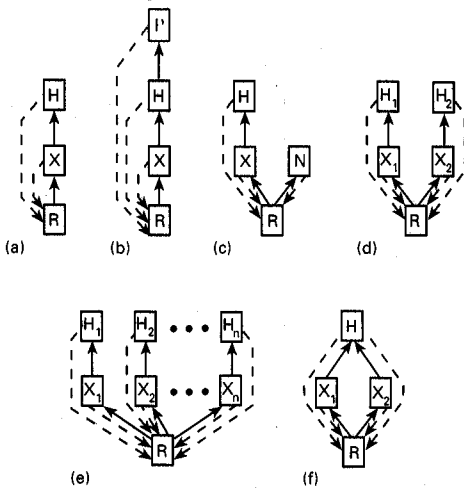


Fig. 16.1 Food-web modules: solid arrows show trophic flows and dashed arrows flows of recycled nutrient. (a) Simple food chain with an abiotic nutrient resource (R), a plant (X) and a herbivore (H). (b) Simple food chain with a nutrient, a plant, a herbivore and a predator (P). (c) Inedible plant module: of two plants, one is edible by the herbivore, and the other (N) is inedible; the two plants compete for the nutrient. (d) Module of two plants (X_1, X_2) competing for the same nutrient, in which each plant is eaten by its own specialist herbivore (H_1, H_2). (e) The specialist-herbivore module can be extended to an indefinite number of coexisting plants and herbivores, if certain conditions are met. (f) Module with a generalist herbivore feeding on two competing plants.

mathematically rigorous treatments are presented elsewhere (Grover 1994; Holt *et al.* 1994).

We begin with a simple food chain (Fig. 16.1a), based on an abiotic nutrient of concentration R , consumed by a plant of population density X , which is in turn consumed by a herbivore of population density H . Nutrient recycling occurs in two ways: (i) death of plants and herbivores, and (ii) incomplete assimilation of nutrient ingested during herbivory. Throughout, we assume that the microbial processes of decomposition responsible for nutrient recycling are rapid enough so that nutrient lost from populations appears effectively instantaneously in an available form (see Chapter 3). If the habitat is closed, or if it is an open system with inputs that balance outputs, then the total concentration of nutrient (S), both dissolved and bound in organisms, is constant in time. We also assume that the nutrient content (q) of organisms is constant. Therefore, whatever equations we write for the dynamics of the system components, a mass-balance constraint will be obeyed:

$$S = R + q_X X + q_H H \quad (16.1)$$

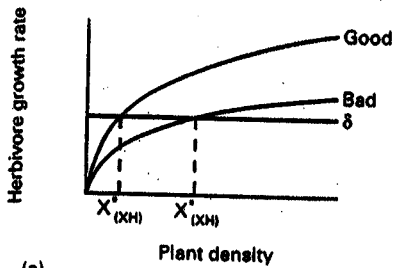
To construct an equilibrium analysis of this simple food chain, we assume that herbivore growth rate increases with food supply and that herbivores experience a constant, density-independent loss rate, δ . This

immediately fixes a plant density representing the food required by the herbivores to balance their losses, producing an equilibrium (Fig. 16.2a). We call this density $X_{(XH)}^*$, where the superscript * denotes dynamic equilibrium and the subscript (XH) denotes that the equilibrium pertains to the food-web module with plant X and herbivore H . Several factors influence the magnitude of $X_{(XH)}^*$. Among these is the herbivore's functional response, the rate at which an individual consumes plant material, which depends on several plant characters affecting attractiveness and ingestibility and on the herbivore's foraging behaviour. The magnitude of $X_{(XH)}^*$ also depends on the plant's nutritional value to herbivores. A 'good' food, one that is highly ingestible and nutritious, has a low value of $X_{(XH)}^*$, because the herbivore can balance a given loss rate with a low density of that food (Fig. 16.2a). With poor foods, a higher plant density is required for the herbivore to balance the same loss rate (Fig. 16.2a).

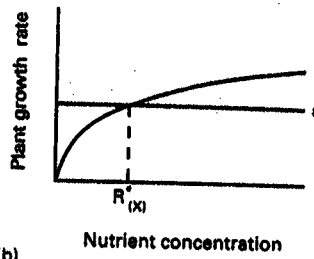
With the equilibrium plant density thus fixed, we then find the equilibrium nutrient concentration and herbivore density graphically, in the plane of nutrient concentration (R) versus herbivore density (H). The first tool we need is a zero net growth isocline, or simply isocline, describing the set of points (R, H) for which the plant population is at equilibrium. Suppose that plant growth rate increases with nutrient concentration and that plants experience a fixed, density-independent loss rate, ϵ . Then without herbivores, plants require a nutrient concentration $R_{(X)}^*$ (where the subscript (X) means a food-web module with only the plant present) to balance their losses and achieve an equilibrium (Fig. 16.2b; see Chapter 8). With herbivores present, plants suffer a higher loss rate and thus require a nutrient concentration higher than $R_{(X)}^*$. Therefore the plant isocline in the RH plane is a forward-sloping curve (Fig. 16.2c): above and to the left of the curve plant density decreases (too little nutrient and too many herbivores); below and to the right, plant density increases (few herbivores, plenty of nutrient). The more preferred a plant is by the herbivore, the greater its losses will be at a given herbivore density, and the more steeply the nutrient concentration required for equilibrium will increase with herbivore density. Therefore, a preferred plant has a lower isocline than a less preferred one (Fig. 16.2c), other things being equal.

The second tool we need comes from considering the mass balance of the nutrient. Setting X to its equilibrium value, and rearranging

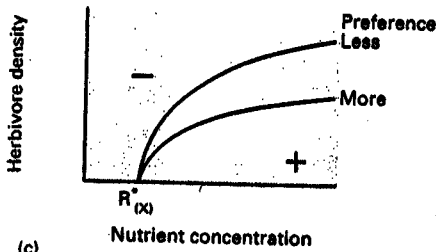
Fig. 16.2 (*opposite*) Graphical analysis of a simple food chain with a nutrient, a plant and a herbivore. (a) Per capita growth rate of the herbivore population is an increasing function of plant density. At equilibrium with a given loss rate (δ , horizontal line), the herbivore requires a lower density of a good (i.e. nutritious) plant ($X_{(XH)}^*$, determined by the intersection of the growth curve with line δ). (b) Per capita growth rate of the plant population is an increasing function of nutrient concentration. In the absence of herbivores, plants experience a loss rate ϵ , which determines an equilibrium nutrient requirement, $R_{(X)}^*$. (c) Isocline of zero net growth for the plant population in the plane of nutrient concentration and herbivore density, given that the herbivore's net growth is



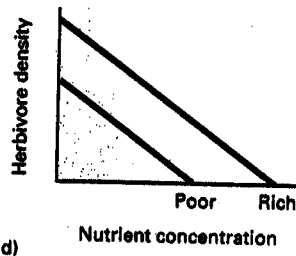
(a)



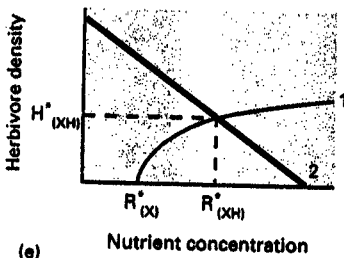
(b)



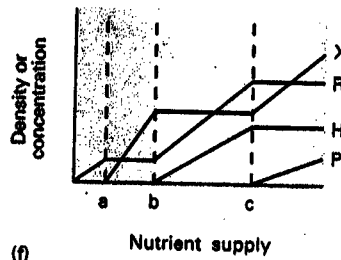
(c)



(d)



(e)



(f)

also zero. The plant isocline intersects the axis of nutrient concentration at $R_{(X)}^*$, the plant population's nutrient requirement in the absence of herbivory. The isocline of a plant more preferred by the herbivore lies below that of a less preferred plant. (d) Mass-balance constraints in the plane of nutrient concentration and herbivore density, given that the herbivore's net growth is zero. Nutrient-rich habitats have higher constraint lines than nutrient-poor habitats. (e) Equilibrium of the simple food chain is determined graphically by the intersection of the plant isocline with the mass-balance constraint. (f) Equilibrium densities of plants, herbivores and predators in simple food chains vary in a predictable way with the habitat's nutrient supply. In the poorest habitats, up to point a, there is insufficient nutrient to support plants or other populations, and nutrient concentration (R) simply increases with supply. From point a to point b, nutrient supply is high enough to support plants but not herbivores, and increasing nutrient leads to higher plant density (X), although nutrient concentration is controlled by plants. From point b to point c, nutrient supply is high enough to support herbivores, whose population density (H) increases with nutrient supply, as does nutrient concentration, while plant density is controlled by herbivores. In the richest habitats, above point c, nutrient supply is high enough to support predators, whose population density (P) increases with nutrient supply and who control herbivore density, while plant density also increases with nutrient supply; nutrient concentration is controlled by plants (Oksanen *et al.* 1981).

Equation 16.1, we get the equation of a straight line in the XH plane:

$$H = \frac{1}{q_H} (S - q_X X_{(XH)}^*) - \frac{1}{q_H} R \quad (16.2)$$

whose elevation is proportional to total nutrient supply S , but whose slope is independent of nutrient supply. Therefore, rich and productive habitats (high S) have higher mass-balance constraints than poor and unproductive habitats (Fig. 16.2d). The intersection of the plant isocline and the mass-balance constraint represents the equilibrium of the two-step food chain, with nutrient concentration $R_{(XH)}^*$ and herbivore density $H_{(XH)}^*$ (Fig. 16.2e).

These two quantities increase with nutrient supply, and if the herbivore density in a rich habitat is sufficiently high we can expect predators to invade, giving a longer food chain (Fig. 16.1b). If predators are food-limited in the way that we previously imagined for herbivores, then herbivore density at equilibrium, now denoted $H_{(XHP)}^*$, will be controlled by the predators at some value less than $H_{(XH)}^*$. Because herbivores now suffer predation losses, their food requirement increases, hence $X_{(XHP)}^* > X_{(XH)}^*$, and the decrease in herbivory reduces the nutrient concentration required by plants, hence $R_{(XHP)}^* < R_{(XH)}^*$. Simple food chains, including longer ones, follow a pattern of 'top-down' control, as suggested by Hairston *et al.* (1960) and since elaborated (Oksanen *et al.* 1981). Each trophic level is alternately controlled by predation or competition for limiting resources. According to this theory, habitats arrayed along a gradient from nutrient-poor to nutrient-rich will contain an increasing number of trophic levels (Fig. 16.2f), and in every habitat dynamic control of population density propagates from the highest trophic level to the basal, a top-down process dubbed the 'trophic cascade' by Paine (1980). The theory of the trophic cascade has been enormously influential, especially in limnology. However, there are examples from aquatic systems (DeMelo *et al.* 1992) and terrestrial systems (Sih *et al.* 1985; Schoener 1989) where food-chain theory appears to be inadequate. One possible reason for this inadequacy is heterogeneity within the trophic level labelled 'plants' – up to this point, we have assumed that all plants are equal.

We explore the consequences of differences between plants later; first, we consider another factor that might obscure the patterns predicted by food-chain theory, namely its reliance on equilibrium analyses. In productive habitats, the plant-herbivore equilibrium can be unstable if the herbivore's growth rate saturates with plant density, as in Fig. 16.2a (Rosenzweig 1971). This is likely, since the ability of a herbivore to consume vegetation cannot increase indefinitely as plant density increases. In most models of two-step food chains, a stable limit cycle develops when the plant-herbivore equilibrium is unstable (DeAngelis 1992). With more trophic levels, there are more possible sources of instability (predator-prey interactions) and, moreover, a wide range of non-equilibrium dynamics can result from the response of food

chains to environmental variability. The extent to which such dynamic instability contributes to observed variability in natural populations is unclear. Moreover, spatial heterogeneity, much of it created by plants themselves, can counter tendencies to instability in trophic interactions (Murdoch & Oaten 1975; Taylor 1990), allowing application of an equilibrium approach, though perhaps only at certain spatial scales.

Setting aside the question of non-equilibrium dynamics (see Chapter 14), not all kinds of plants are equally edible to herbivores. As a plant becomes less edible, its isocline in the RH plane rotates counter-clockwise (Fig. 16.2c). For the limiting case of a completely inedible plant (denoted N , Fig. 16.1c), the plant isocline becomes a vertical line (Fig. 16.3a), regardless of herbivore density; such a plant requires a nutrient concentration of $R_{(N)}^*$ to balance its losses. Under certain technical assumptions, the inedible plant (N), edible plant (X) and

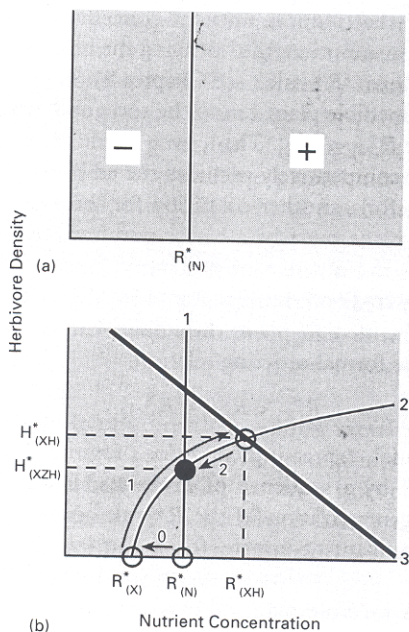


Fig. 16.3 Graphical analysis of adding an inedible plant to a simple food chain of nutrient, plant and herbivore. (a) Isocline of the inedible plants in the plane of nutrient concentration and herbivore density is a straight line parallel to the herbivore density axis. The isocline intersects the nutrient concentration axis at the nutrient concentration required by the inedible plant to balance its losses, $R_{(N)}^*$. Right of the isocline, the density of inedible plants increases; left of the isocline, it decreases. (b) Inedible and edible plants coexist with the herbivore when the inedible plant isocline (1) intersects the edible plant isocline (2) below its intersection with the mass-balance constraint of the constituent food chain (3). The equilibrium of the inedible plant module is determined by the intersection of the plant isoclines (solid circle). The equilibria of the constituent subsystems of this module are shown as open circles, and are invulnerable by other species as indicated by the arrows and explained in the text.

herbivore (H) will theoretically coexist if it is possible to construct a sequence of invasions leading to the full community (Hutson & Law 1985). At each invasion, we imagine that an infinitesimally small population of the invader is trying to increase, while residents are at equilibrium. Suppose that total nutrient supply exceeds the nutrient requirement of either plant growing alone (i.e. $S > R_{(X)}^*$ and $S > R_{(N)}^*$), so that either plant can invade an empty habitat. If the edible plant invades first, and then equilibrates at a density exceeding the herbivore's equilibrium food requirement, then the herbivore can also invade (pathway 1, Fig. 16.3b), eventually reaching the equilibrium density $H_{(XH)}^*$ (Figs 16.2e and 16.3b). This happens if nutrient supply is high enough. The inedible plant can now invade if the associated nutrient concentration, $R_{(XH)}^*$, exceeds its equilibrium nutrient requirement, $R_{(N)}^*$ (pathway 2, Fig. 16.3b). Verbally, this last condition says that the inedible plant is a better resource competitor than the edible plant, when the latter is burdened by herbivory. That is, a good resource competitor is one that reduces nutrient concentration to a low level, through its own consumption, thus denying the resource to other plants (this is the well-known ' R^* rule'; see Chapter 8).

However, the inedible plant cannot be too good a resource competitor. Suppose that $R_{(N)}^* < R_{(X)}^*$. Then, even when herbivores are absent, the inedible plant competitively excludes the edible plant, according to the R^* rule. Therefore, another condition for three-species coexistence is that the edible plant must be a better resource competitor than the inedible plant, in the absence of herbivory (this is the palatability/competitive ability trade-off; see Chapters 13 & 15). Then, if the habitat is dominated by the inedible plant, the edible plant can invade (pathway 0, Fig. 16.3b). The formal ordering relation

$$R_{(X)}^* < R_{(N)}^* < R_{(XH)}^* \quad (16.3)$$

is an 'assembly rule', expressing conditions required for assembly of a food-web module by a sequence of invasions; Equation 16.3 can be interpreted as a generalization of the R^* rule applying to competitive dominance when plants compete for a nutrient in the absence of herbivores.

Of course, an inedible plant with no natural enemies is an unexploited resource. Suppose that a new herbivore arrives on the scene (immigrates or evolves), specializing on the inedible plant (Fig. 16.1d). This has the effect of increasing the equilibrium nutrient requirement of the previously inedible plant above its previous requirement, $R_{(N)}^*$, to compensate for losses to herbivory. So long as this increased requirement is not too large, all four species can coexist at equilibrium. The process of adding another inedible plant, followed by a specialist herbivore that eats it, can be continued indefinitely (Fig. 16.1e), so long as certain ordering relations are satisfied generalizing Equation 16.3 (Grover 1994). Verbally, each new species can invade if (i) plants invade

in order of decreasing ability to compete for nutrient in the absence of herbivory, and (ii) each plant's herbivore invades before another plant is added. If a species violating these rules tries to invade, one of two things happens: either it is excluded from invasion by the residents, or it successfully invades but disrupts the relations allowing residents species to coexist, so that a cascade of extinctions take place. In the specialist-herbivore module, herbivores of the most competitive plants are 'keystone' species, whose role is crucial to community organization and which can be identified from the assembly rules. Releasing highly competitive plants from the burden of herbivory allows them to exclude other plants, and their herbivores.

Some insects may play the role we have sketched, of specialist herbivores that hobble a plant's competitiveness (Crawley 1989), but the world also has generalist herbivores and plenty of predators to eat them. Food-web theory is not yet able to specify assembly rules for communities with arbitrarily complex trophic connections. Nevertheless, we expect that more complex communities also have assembly rules that predict the outcome of species addition and deletion, and allow identification of keystone species. The assembly rules we have encountered so far, such as Equation 16.3, are based on quantities, such as $R_{(X)}^*$ and $R_{(XH)}^*$, that summarize a great deal of biology: the physiological and morphological characters determining plants' uptake of nutrients, growth and reproduction, their edibility and nutritional value to herbivores, herbivore foraging behaviour, life history and demography (see Chapter 13). We expect that more complex trophic webs will be characterized by similar critical quantities but that their assembly rules will become more complicated and contingent, as the foraging behaviours and ecological quirks of more and more herbivores and predators must be accounted for.

Taking a few steps in this direction, we now sketch some of the rules that apply to a food-web module with two plants and a generalist herbivore (Fig. 16.1f). In Fig. 16.2c, we drew isoclines for two plants differing in their preference to a herbivore. Likely causes of reduced herbivore preference are low nutritional value and morphological or chemical defences against herbivores (see Chapters 10 & 13). Such defences usually come at a cost of energy and nutrients (Chew & Rodman 1979, Bergelson & Purrington 1996), making the less preferred plant less competitive when herbivores are absent. Therefore, Fig. 16.2c would be more accurate if the preferred plant's isocline had a lower R intercept than the less preferred plant's, i.e. $R_{(1)}^* < R_{(2)}^*$, where the subscripts 1 and 2 represent preferred and less preferred plants, respectively. Then, since the isocline of the preferred plant has a lower slope than that of the less preferred plant, there will be an intersection of the two plants' isoclines, potentially representing an equilibrium in which they coexist (Fig. 16.4a-c). Either because of plant defences that reduce nutritional value, or because it is adaptive for herbivores to prefer

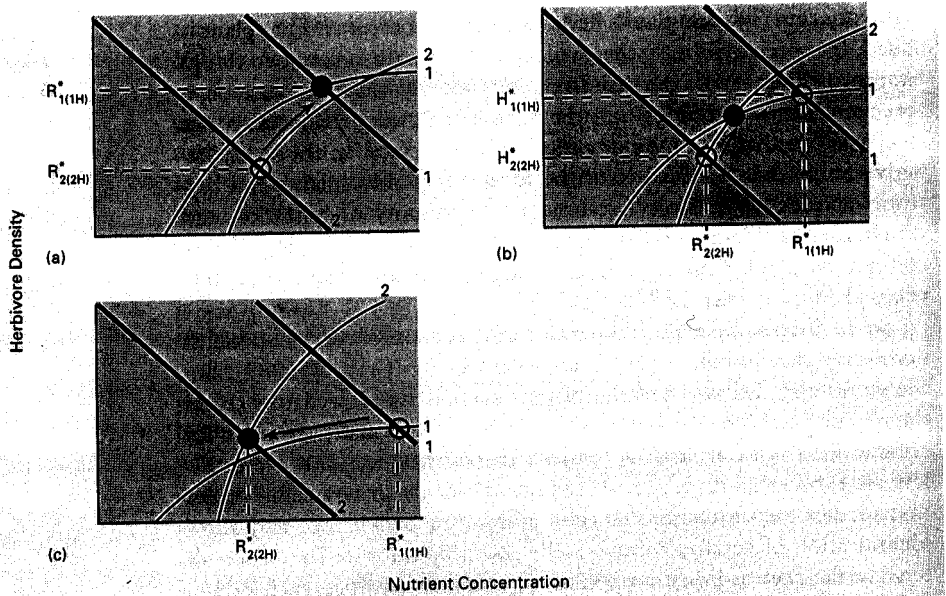


Fig. 16.4 Graphical analysis of the generalist herbivore module. In each graph, the isoclines and mass-balance constraints of simple food chains based on plants 1 and 2 are superimposed. (a) Nutrient-poor habitats. The intersection of the plant isoclines is above the highest of the two plants' mass-balance constraints. The equilibrium of the food chain containing the less preferred plant 2 (open circle) is inviable by the preferred plant (arrow), but the equilibrium of the food chain with the preferred plant 1 (solid circle) is not inviable by the less preferred plant 2. Plant 1 owes its victory to apparent competition. (b) Moderate habitats. The intersection of the plant isoclines falls between the two plants' mass-balance constraints (solid circle). The equilibria of the simple food chains (open circles) are each inviable by the missing plant (arrows) and coexistence occurs, due to a trade-off between resource and apparent competition. (c) Rich habitats. The intersection of the plant isoclines is below the lowest of the two plants' mass-balance constraints. The equilibrium of the constituent food chain containing the preferred plant 1 (open circle) is inviable by the less preferred plant (arrow), but the equilibrium of the food chain with the less preferred plant 2 (solid circle) is not inviable by the preferred plant 1. Plant 2 owes its victory to resource competition.

nutritious plants, plant 1 is likely to be a better food for the herbivore, so that less of it is required to support the herbivore than is required of plant 2 (Fig. 16.2a). That is $X_{1(1H)}^* < X_{2(2H)}^*$, where the simple food chains based on the two plants are distinguished by the subscripts (1H) and (2H). The nutrient cost of defences against herbivores could also result in a higher nutrient content for the less preferred plant ($q_1 < q_2$). These two hypotheses imply that plant 1 has a higher mass-balance constraint than plant 2 (Equation 16.2).

If the habitat is relatively nutrient-poor, then plant 1's mass-balance constraint lies below the intersection of the plants' isoclines (Fig. 16.4a). Because the band of the RH plane lying between the two

plants' mass-balance constraints represents the feasible space for a three-species equilibrium (Holt *et al.* 1994), both plants cannot coexist with the herbivore in a nutrient-poor habitat. Instead, when plant 1's food chain is at equilibrium, the corresponding point in the RH plane falls in a region where plant 2 has negative net growth; plant 1 excludes plant 2. However, when plant 2's food chain is at equilibrium, the corresponding point in the RH plane falls in a region where plant 1 has positive net growth; therefore, plant 1 invades. The competitive victory of plant 1 is signalled by the fact that it supports more herbivores at equilibrium than does plant 2 ($H_{1(1H)}^* > H_{2(2H)}^*$). The outcome of competition follows an ' H^* rule' because the generalist herbivore module involves apparent competition, the indirect interaction between the two plants mediated by the herbivore that eats them both (Holt 1977). In this type of competition, it is ability to support a generalist natural enemy that counts, rather than ability to depress resource availability.

For somewhat richer habitats, the band of feasible space lying between the plants' mass-balance constraints rises to encompass the intersection of the plant isoclines (Fig. 16.4b). Invasion analysis shows that when plant 1's food chain is at equilibrium, the corresponding point in the RH plane falls in a region where plant 2 has positive net growth; therefore, it invades. When plant 2's food chain is at equilibrium, the corresponding point in the RH plane falls in a region where plant 1 also has positive net growth; so plant 1 also invades. This mutual invasibility implies coexistence of the two plants that is mediated by the herbivore. Coexistence rests on the trade-offs and constraints dictating that plant defences are costly in terms of the resource over which competition occurs. The less defended, preferred plant supports more herbivores in its own food chain than does the less preferred plant ($H_{1(1H)}^* > H_{2(2H)}^*$). Balancing plant 1's advantage in apparent competition is plant 2's advantage in resource competition ($R_{2(2H)}^* < R_{1(1H)}^*$), which results from a reduced nutrient demand, achieved by reducing losses to herbivory through defence.

For relatively rich habitats, the band of feasible space lying between the plants' mass-balance constraints rises above the intersection of the plant isoclines (Fig. 16.4c). Coexistence of the two plants is thus no longer feasible. Invasion analysis shows that when plant 1's food chain is at equilibrium, the corresponding point in the RH plane falls in a region where plant 2 has positive net growth; therefore, plant 2 invades. However, when plant 2's food chain is at equilibrium, the corresponding point in the RH plane falls in a region where plant 1 has negative net growth; plant 2 excludes plant 1. The competitive victory of plant 2 is signalled by an R^* rule: at equilibrium, plant 2 depresses nutrient concentration to a lower level than plant 1 ($R_{2(2H)}^* < R_{1(1H)}^*$). Therefore, in rich habitats, with high herbivore densities, investment in defence against herbivory pays off, and it does so by reducing the population-level requirement for nutrient.

For this case (Fig. 16.4a-c), which we consider likely, herbivore-mediated coexistence of competing plants occurs in moderately rich habitats, where apparent competition trades off against resource competition. If we reverse the positions of either the isoclines or the mass balance-constraints in Fig. 16.4b, we get cases in which each of the constituent food chains in the generalist herbivore module can exclude the missing plant. The three-species equilibrium at the intersection of the plant isoclines is then unstable. This requires a constellation of plant and herbivore characters that seem unlikely to us, but we caution that so far we have implicitly assumed that the herbivore functional response is linear. With non-linear functional responses, graphical analysis is more complex, since the plant isoclines cannot be constrained to single curves in the RH plane. Moreover, we have not done justice to the full range of possibilities suggested in the rich literature on trade-offs and constraints in plants' abilities to compete for resources and resist herbivory (reviewed by Louda *et al.* 1990; Bryant *et al.* 1991; Pacala & Crawley 1992). With a broader view, some of the cases we dismiss here as unlikely may look more plausible.

It is premature to sketch any formal theory for more complex trophic architectures involving predators as well as plants and their herbivores. However, predation is always in some sense a dependent variable, erected on the foundation of plants which extract abiotic resources from the habitat. Therefore, plants will exert a number of effects that propagate from the bottom up (Price 1992). Once there are consumers present in a food web, however, the possibility always exists for strong top-down effects reminiscent of those suggested by food-chain theory (above). Top-down effects need not necessarily arise only from the top trophic level, but could now arise from lower within food webs (Menge & Sutherland 1976). Other effects reverberating up and down the trophic web arise from the interactions of population and nutrient dynamics (Bryant *et al.* 1991; DeAngelis 1992).

Up to this point we have treated plants and herbivores as if they were plankton, and have taken no account of the spatial heterogeneity that is universal in terrestrial systems (Oksanen *et al.* 1996). Much of this spatial heterogeneity is created by the plants themselves (Price 1992). Plants exist in patches composed of different species, and individual plants consist of various different tissues, each of which is potentially a patch of resource or a habitat for some animal. The spectrum of spatial variability presented by plants makes possible a wide range of indirect interactions, since plants provide both cover from, and cues to, predators that attack the animals feeding on or living on a plant (Price *et al.* 1980; Sih *et al.* 1985). Such spatial heterogeneity allows a diversity of consumers to rely on a single plant species (Hutchinson 1959; Lawton 1983). Because plants are fixed in single positions for long periods of time, relative to the generation times of many animals, animals can evolve spatial behaviours such as territoriality, habitat selection and

migration (Holt 1987; Ostfeld 1992) in response to a mosaic of plants. The physical structure created by plants thus amplifies the possibility for idiosyncrasies of particular species to become important, and it may be a major cause of the diversity of terrestrial life (Hutchinson 1959; Price 1992; see Chapter 15).

Notwithstanding the complexities and contingencies that such considerations entail, ecologists need to develop a robust and predictive understanding of nature. If at all possible, our theory must retain both simplicity and generality. Simple advice on management of our threatened world is the most likely to be heeded. Much of what we present here is inspired by findings from the field of limnology. So is our conclusion. From studying lakes, we know that trophic dynamics are important, and that human intervention, whether at the top or the bottom of the trophic web, has strong, potentially disastrous effects. Despite the complexity of life within lakes, simple and general principles for their management are emerging, based largely on an understanding of trophic webs (but not without controversy; Carpenter & Kitchell 1992; DeMelo *et al.* 1992). To the extent that a lake is a microcosm (Forbes 1887), we may urgently hope for global progress.