

CONCLUSION

Strong interactions between theory and experiments have made significant advances possible on the impacts of biodiversity on ecosystem functioning during the last decade. Thanks to this combination of theory and experiments, we can safely conclude today that biodiversity does have the potential to affect ecosystem functioning to a measurable extent, even in the simple systems and on the small spatial and temporal scales considered in recent experiments, and that some form of complementarity between species driven by niche differentiation or facilitation is responsible for these effects. How many species play a significant role in these effects, which ecosystem processes are affected, and under what conditions, however, are largely empirical questions that are beyond the scope of the present book. I shall continue to explore these issues from a theoretical perspective in the following chapters by considering more complex and more realistic ecosystems that have several trophic levels, change through time, or vary in space.

Whether biodiversity loss will affect large-scale patterns of productivity hinges on the shape and steepness of the local dependence of productivity on diversity. Generally speaking, the relative effects of individual species and species richness may be expected to be greatest at small to intermediate spatial scales, while these biological factors should be less important as predictors of ecosystem processes at regional scales where environmental heterogeneity is greater. While diversity was manipulated as the independent variable in recent experiments, at large scales species diversity itself is a dynamical variable and adjusts to changes in environmental conditions. Theory then suggests that abiotic factors should be the main drivers of variations in ecosystem processes across environmental gradients. The dynamics of biodiversity and ecosystem processes at large scales, however, involves complex spatial processes that can strongly affect these conclusions. I shall return to this issue in chapter 7.

CHAPTER 4

Food Webs, Interaction Webs, and Ecosystem Functioning

A food web describes the network of trophic interactions between species, i.e., who eats whom, in an ecosystem. Since trophic interactions are both the vehicle of energy and material transfers and one of the most significant ways in which species interact, they have always lain at the confluence of community and ecosystem ecology. But they have been approached from different perspectives in different traditions. The energetic view articulated by Lindeman (1942) and developed by ecosystem ecology during the following decades views food webs as networks of pathways for the flow of energy in ecosystems, from its capture by autotrophs in the process of photosynthesis to its ultimate dissipation by heterotrophic respiration. A different approach, rooted in community ecology, was initiated by Elton (1927) and developed by May (1973), Pimm (1982), and many others. This approach focuses on the dynamical constraints that arise from species interactions and emphasizes the fact that too much interaction (whether in the form of a large number of species, a large connectance among these species, or a high mean interaction strength) destabilizes complex ecological systems, including food webs. Food webs have also been studied from a topological perspective: the pattern of trophic interactions in a food web is nonrandomly related to species traits, in particular, body size, which led to the development of size-based models of food-web structure such as the cascade and niche models (Cohen et al. 1990; Williams and Martinez 2000). Perhaps the approach that lies most closely to the interface between community and ecosystem ecology is that based on the trophic cascade concept (Carpenter et al. 1985). Hairston et al. (1960) hypothesized that carnivores control herbivores, thereby releasing plants from control by herbivores, in most ecosystems. This simple idea led to a flurry of studies on the community- or ecosystem-level consequences (though mostly the biomass of the various trophic levels) of the top-down control exerted by higher trophic levels on lower trophic levels.

These different approaches remain poorly integrated with each other. They have also remained largely separated from the recent development of the biodiversity–ecosystem functioning area. As we saw in the previous chapter, most of the recent theoretical and experimental studies on the effects of biodiversity on ecosystem functioning have considered single trophic levels, primary producers for the most part. Although they have contributed to merging community and ecosystem ecology, they have unintentionally disconnected the vertical and horizontal dimensions of biodiversity and ecosystem processes. An important current challenge is to understand how trophic interactions affect the relationship between biodiversity and ecosystem functioning (Duffy et al. 2007). Several experimental and theoretical studies have started to investigate this issue, but the challenges, particularly for theory, are still considerable. Integrating the horizontal and vertical dimensions of biodiversity and ecosystems requires merging the approaches of competition theory (which is concerned with the maintenance of biodiversity within a simple trophic level) and food-web theories (which are concerned with the topological, dynamical, and functional properties of interaction networks). It is high time to lay a bridge between these approaches to foster cross-fertilization and build a broader theoretical framework that has greater relevance to natural ecosystems.

Even more challenging is the need to incorporate nontrophic interactions in ecological theory. Examples of mutualistic interactions (Bronstein 1994), ecosystem engineering (Jones et al. 1994), and trait-mediated indirect interactions (Schmitz et al. 2004; Werner and Peacor 2003) abound in nature. Yet they are most often ignored by ecological theory. One reason for this state of affairs is that simple models do not realistically describe these interactions. The Lotka–Volterra model of mutualism (Gause and Wit 1935), for instance, leads to unlimited population growth “in an orgy of mutual benefaction” (May 1981) when the interaction is too strong. Population explosions due to mutualistic interactions are frequent in random model interaction webs. These unrealistic features occur because the simple models used in community ecology ignore mass-balance constraints arising from the physical law of mass conservation.

In this chapter I extend the theory presented in the previous two chapters to more complex ecosystems that have multiple trophic levels connected by both trophic and nontrophic interactions. I first revisit some of the basic properties of trophic interactions and their consequences for ecosystem functioning by bringing together the energetic approach that focuses on energy flows and efficiencies and the dynamical approach that underlies the trophic cascade. I derive some new predictions about patterns of

productivity and ecological efficiency in food chains and show that trophic interactions tend to make the maximization principles that govern simple competitive systems ineffective. I then review recent theoretical advances in the relationship between biodiversity and ecosystem functioning in food webs with multiple trophic levels. Last, I present a brief overview of a new theoretical approach that integrates nontrophic interactions in ecosystems while at the same time preserving the mass-balance constraints of ecosystem models and the dynamical flexibility of community models.

The synthesis presented in this chapter is still incomplete because it does not deal with complex network topologies as they are often observed in natural food webs (Cohen et al. 1990; Williams and Martinez 2000) and mutualistic networks (Bascompte et al. 2003). But it offers some principles and approaches that should help illuminate the functioning of these more complex systems. The issue of the stability of these systems will be examined specifically in the next chapter.

TROPHIC INTERACTIONS, VERTICAL DIVERSITY, AND ECOSYSTEM FUNCTIONING

The *trophic cascade* concept has traditionally been used to predict and interpret patterns of biomass at different trophic levels as functions of the presence of higher trophic levels and the fertility of the environment (Hairston et al. 1960; Oksanen et al. 1981; Carpenter et al. 1985). The same approach, however, can be used to predict the effects of *vertical diversity*—defined here as the number of trophic levels in an ecosystem—and environmental fertility on ecosystem properties such as the biomass, productivity, and ecological efficiency of the various trophic levels. In this section I deliberately reduce the enormous complexity of food webs and represent them as linear food chains with discrete trophic levels with a view to exploring the functional consequences of vertical diversity in its simplest form. As we shall see, the classical food chain is far from having given up all its secrets yet. Here I derive a number of new predictions that the theory of trophic cascades has not considered traditionally.

Consider a food chain of arbitrary length n , in which each trophic level i obeys a dynamical equation based on a mass or energy budget as in chapter 1 (figure 4.1). Since most ecosystems are thought to be limited by nitrogen or phosphorus, I shall use the mass of the limiting nutrient as my unit of measurement, but the same approach could be used for energy or any other nutrient as long as nutrient recycling is ignored and the energetic

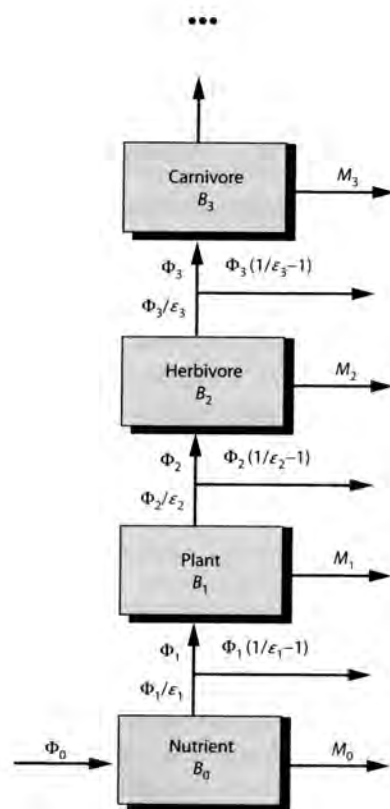


FIGURE 4.1. General model of a linear food chain. Each trophic level has a biomass B_i , a production Φ_i , a production efficiency ε_i , a loss flux M_i that includes basal metabolism and mortality, and a consumption flux to the next higher trophic level equal to the latter's production divided by its production efficiency. Boxes represent nutrient stocks, while arrows represent nutrient flows.

content and stoichiometric composition of the various trophic levels are roughly equal. Equation (1.19) is easily generalized in terms of the basic ecosystem processes of consumption and production at the various trophic levels as follows:

$$\frac{dB_i}{dt} = \Phi_i - M_i - \Phi_{i+1}/\varepsilon_{i+1}, \quad 0 \leq i \leq n. \quad (4.1)$$

In this equation, B_i is the biomass of trophic level i , Φ_i is its production, ε_i is its production efficiency (as defined in chapter 1), M_i is a loss flux that includes basal metabolism and mortality, and the last term represents consumption by the next higher trophic level and is equal to the latter's production divided by its production efficiency (except, of course, for the

last trophic level: $\Phi_{n+1} = 0$). Trophic level 0 is simply the inorganic nutrient, for which I assume that there is a constant input; i.e., $\Phi_0 = I$. This constant input incorporates both endogenous and exogenous sources of inorganic nutrient; at this stage, I am not considering nutrient cycling explicitly. The ecological efficiency of trophic level i , λ_i , is further defined as the ratio of its production to the production of the next lower trophic level (Lindeman 1942):

$$\lambda_i = \Phi_i / \Phi_{i-1}, \quad 1 \leq i \leq n. \quad (4.2)$$

Finally, I assume, as in the classical theory of exploitation interactions, that there is no interference among consumers, so that the production and loss fluxes can be written as

$$\Phi_i = f_i(B_{i-1})B_i, \quad 1 \leq i \leq n, \quad (4.3)$$

$$M_i = m_i B_i, \quad 0 \leq i \leq n, \quad (4.4)$$

where $f_i(B_{i-1})$ is the functional response of trophic level i scaled by ε_i , and m_i is its mass-specific loss rate.

The first question that we can study using this simple, fairly general food-chain ecosystem model is: how does vertical diversity affect ecosystem functioning? In particular, does the addition of higher trophic levels enhance this functioning, does it make the ecosystem more efficient in some way, and, if so, in which way? To answer these questions, assume that the ecosystem reaches a stable equilibrium¹ and that environmental fertility, as measured by nutrient input I , is constant. The effects of vertical diversity on ecosystem properties can then be studied by comparing the biomass, production, and ecological efficiency of the various trophic levels at equilibrium as the number of trophic levels varies. The equilibrium values of biomass and ecological efficiency are provided in table 4.1 for ecosystems that range from 0 (only the inorganic nutrient is present) to 3 (the inorganic nutrient, plants, herbivores, and carnivores are present) trophic levels. In this table and in what follows, $X_{i(n)}^*$ denotes the equilibrium value of variable X at trophic level i in a system with n trophic levels. Note that the production of each trophic level i can be obtained simply by using the following formula derived from equation (4.2):

$$\Phi_{i(n)}^* = I \prod_{j=1}^i \lambda_{j(n)}^*. \quad (4.5)$$

¹It is easy to show that the equilibrium is always stable for small food chains with $n < 2$ (i.e., food chains that contain only an inorganic nutrient and plants) and that it is stable for at least some parameter values for longer food chains with $n \geq 2$, depending on the form of the consumer functional responses.

TABLE 4.1. Equilibrium Values of the Biomass (B) and Ecological Efficiency (λ) of the Various Trophic Levels as the Number of Trophic Levels n Varies from 0 to 3 in the Model Ecosystem Described by Equations (4.1)–(4.4)^a

	$n = 0$	$n = 1$	$n = 2$	$n = 3$
Biomass				
$B_{0(n)}^*$	I/m_0	$f_1^{-1}(m_1)$	$g_2^{-1}(B_{1(2)}^*)$	$g_3^{-1}(B_{1(3)}^*)$
$B_{1(n)}^*$		$\frac{\varepsilon_1}{m_1}(I - m_0 B_{0(1)}^*)$	$f_2^{-1}(m_2)$	No explicit solution
$B_{2(n)}^*$			$\frac{\varepsilon_2}{m_2}[\varepsilon_1(I - m_0 B_{0(2)}^*) - m_1 B_{1(2)}^*]$	$f_3^{-1}(m_3)$
$B_{3(n)}^*$				$\frac{\varepsilon_3}{m_3}[\varepsilon_2[\varepsilon_1(I - m_0 B_{0(3)}^*) - m_1 B_{1(3)}^*] - m_2 B_{2(3)}^*]$
Ecological efficiency				
$\lambda_{1(n)}^*$		$\varepsilon_1 \left(1 - \frac{B_{0(1)}^*}{B_{0(0)}}\right)$	$\varepsilon_1 \left(1 - \frac{B_{0(2)}^*}{B_{0(0)}}\right)$	$\varepsilon_1 \left(1 - \frac{B_{0(3)}^*}{B_{0(0)}}\right)$
$\lambda_{2(n)}^*$			$\varepsilon_2 \left[1 - \frac{m_1}{f_1(B_{0(2)}^*)}\right]$	$\varepsilon_2 \left[1 - \frac{m_1}{f_1(B_{0(3)}^*)}\right]$
$\lambda_{3(n)}^*$				$\varepsilon_3 \left[1 - \frac{m_2}{f_2(B_{1(3)}^*)}\right]$

^a $X_{0(n)}^*$ denotes the equilibrium value of variable X at trophic level i in a system with n trophic levels, f_i^{-1} and g_i^{-1} denote the inverse functions of f_i and g_i , and function g_i is defined by the equation $B_{i(n)}^* = g_i(B_{0(n)}^*) = \varepsilon_i(I - m_0 B_{0(n)}^*)/f_i(B_{0(n)}^*)$.

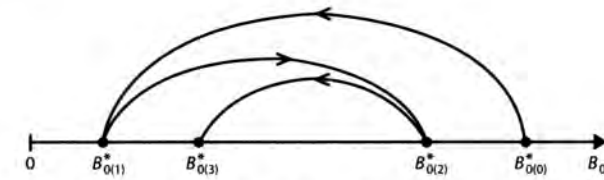


FIGURE 4.2. Effects of increasing food-chain length, n , on the equilibrium amount of inorganic nutrient, $B_{0(n)}^*$, in the linear food chain depicted in figure 4.1. The amount of inorganic nutrient, just like the biomass of any trophic level, is highest when it lies at the top of the food chain, is lowest when it lies just below the top of the food chain, and jumps from low to high and high to low values but converges on an intermediate value as more trophic levels are added.

Despite the fact that not all of these equilibrium values have an explicit solution and some of them are fairly complicated, it is possible to determine how they change qualitatively as more trophic levels are added to the food chain (appendix 4A). The equilibrium biomasses of the various trophic levels satisfy the following inequalities:

$$B_{0(1)}^* < B_{0(3)}^* < B_{0(2)}^* < B_{0(0)}^*, \quad (4.6)$$

$$B_{1(2)}^* < B_{1(3)}^* < B_{1(1)}^*, \quad (4.7)$$

$$B_{2(3)}^* < B_{2(2)}^*. \quad (4.8)$$

These inequalities show a striking general pattern: the biomass of any trophic level is highest when it lies at the top of the food chain (there are no trophic levels above it), is lowest when it lies just below the top of the food chain (there is one trophic level above it), and jumps from low to high and high to low values but converges on an intermediate value as more trophic levels are added (figure 4.2).

Primary production and ecological efficiencies show the same pattern, although quantitatively they vary much less than biomasses:

$$\Phi_{1(2)}^* < \Phi_{1(3)}^* < \Phi_{1(1)}^*, \quad (4.9)$$

$$\lambda_{1(2)}^* < \lambda_{1(3)}^* < \lambda_{1(1)}^*, \quad (4.10)$$

$$\lambda_{2(3)}^* < \lambda_{2(2)}^*. \quad (4.11)$$

Last, production at the second (herbivore) trophic level can either increase or decrease as the third (carnivore) trophic level is added, depending on the form of the functional response of the first (plant) trophic level.

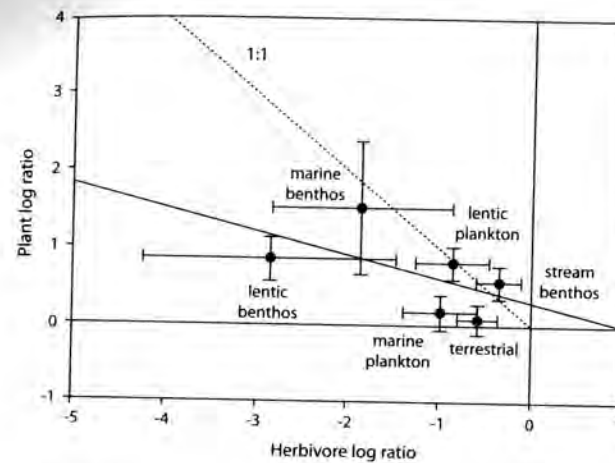


FIGURE 4.3. The effect size (log ratio) of predators on primary producers vs. herbivores in six major ecosystem types. Error bars are 95 percent confidence intervals. The effect of predators is significant if the confidence interval does not overlap zero. The solid line shows the linear regression relating the plant and herbivore effect sizes, while the dotted line shows the 1:1 relationship. Modified from Shurin et al. (2002).

Several general conclusions emerge from this theoretical reexamination of the classical food chain:

1. *The top-down control exerted by the top trophic level cascades down the food chain but becomes progressively weaker, so that lower trophic levels are less and less affected by the addition of further trophic levels at the top.* The biomass of a trophic level varies from high values when this trophic level lies at the top of the food chain, or at an even number of levels below it, to low values when it lies at an odd number of levels below the top, but these oscillations in biomass dampen as more trophic levels are added higher in the food chain. This predicted attenuation of the trophic cascade down the food chain is consistent with experimental data. Experiments that have manipulated carnivore presence show that carnivores generally have a stronger effect on herbivore biomass than on plant biomass (McQueen et al. 1986; Shurin et al. 2002) (figure 4.3). Note that my theoretical predictions consider the effects of adding a variable number of trophic levels on the biomass of a single target trophic level, whereas experiments have considered the effects of adding a single trophic level on the biomass of several lower trophic levels.

Despite this difference, experimental data are at least qualitatively consistent with theoretical predictions.

2. The same cascading but attenuated top-down effects along the food chain hold for ecological efficiencies, but these are much less affected quantitatively than are biomasses. Production is even less affected, and secondary production can even sometimes increase upon addition of a third trophic level. Thus, as a rule, *production should be little affected by trophic cascades*. Unfortunately, I know of no empirical studies that have tested trophic cascades for production.

3. The final, disturbing conclusion is that *vertical diversity does not maximize any ecosystem property*. In contrast to horizontal diversity, which tends to enhance biomass and production in simple competitive systems through functional complementarity among species, vertical diversity tends to bring ecosystems toward a sort of medium functioning. Both the biomasses and ecological efficiencies of the various trophic levels tend to converge to intermediate values as food-chain length increases.

The latter conclusion, however, holds for ecosystem properties measured at the scale of specific trophic levels. What about some more integrative measures of the functioning of the whole ecosystem, such as total ecosystem biomass or total ecosystem production cumulated over all trophic levels? I show in appendix 4A that total ecosystem biomass should on average stay constant as food-chain length increases when the production efficiencies of the various trophic levels are maximal ($\epsilon_i = 1$), and they should decrease under the more realistic conditions where production efficiencies are less than maximal ($\epsilon_i < 1$). This conclusion makes sense since materials and energy are gradually lost along the food chain when there is no internal recycling as in the model considered here. By contrast, total cumulative ecosystem production is expected to increase slightly overall as food-chain length increases, although variations in primary production due to changes in top-down control may override the production increments of the additional trophic levels. We shall see in chapter 6 that nutrient cycling has a much stronger potential to enhance production in ecosystems—not only production cumulated over different trophic levels, which has questionable relevance for both basic and applied purposes, but also production at each trophic level. My purpose here is to explore the functional consequences of vertical diversity per se, and they appear not to be overwhelmingly positive for any measure of ecosystem functioning, except to some extent for total

TABLE 4.2. Direction of the Changes in the Biomass (B), Production (Φ), and Ecological Efficiency (λ) of the Various Trophic Levels at Equilibrium as Environmental Fertility I Increases.^a

	$n = 0$	$n = 1$	$n = 2$	$n = 3$
Biomass				
$B_{0(n)}^*$	+	0	+	— (0 +)
$B_{1(n)}^*$		+	0	+
$B_{2(n)}^*$			+	0
$B_{3(n)}^*$				+
Production				
$\Phi_{1(n)}^*$		+	+	+
$\Phi_{2(n)}^*$			+	+
$\Phi_{3(n)}^*$				+
Ecological efficiency				
$\lambda_{1(n)}^*$		+	— (0 +)	+
$\lambda_{2(n)}^*$			+	— (0 +)
$\lambda_{3(n)}^*$				+

^a $X_{i(n)}^*$ denotes the equilibrium value of variable X at trophic level i in a system with n trophic levels. When several signs are present, the outcome is indeterminate but the signs in parentheses are less probable.

cumulative ecosystem production. We shall continue to explore this intriguing conclusion throughout this chapter.

The second question that we can address using our simple food-chain ecosystem model is: how does *environmental fertility* affect ecosystem functioning for a given number of trophic levels? The classical trophic cascade theory based on logistic plant growth and type-2 consumer functional responses (Oksanen et al. 1981) predicts that the biomass of the trophic levels that lie at the top of the food chain or at an even number of levels below it will respond positively to fertilization, whereas the other trophic levels will not respond to fertilization because they are top-down-controlled. But we may wish to be slightly more general and see if this pattern holds for other functional responses, as well as for production and ecological efficiency. This question can be studied using the derivative of the equilibrium values of the biomass, production, and ecological efficiency of the various trophic levels provided in table 4.1 with respect to parameter I , which measures environmental fertility. The results are presented in appendix 4B and summarized in table 4.2.

Table 4.2 shows that the predictions of the classical trophic cascade theory regarding biomass hold generally, at least for the top three trophic

levels. Note that the stock of inorganic nutrient departs from these predictions since it is expected to often decrease, and sometimes increase, upon nutrient enrichment in the presence of carnivores. An examination of a food chain with four levels would confirm this trend since the responses of the equilibrium stocks of both the inorganic nutrient and primary producers then become indeterminate. These specific results highlight the advantage of studying genuine ecosystem models in which the inorganic nutrient is represented explicitly. Previous models did not consider inorganic nutrients explicitly (Oksanen et al. 1981). In contrast to biomass, production at all levels always increases with fertilization. This emphasizes once more the difference between biomass and production, between stocks and fluxes. As a rule, *production is less affected by top-down forces than is biomass or population density* and responds more to bottom-up influences because of simple mass-balance constraints: an increased inflow at the bottom must necessarily be balanced by an increased outflow in the long run. Part of this outflow is the inflow of the next trophic level, which in turn has an increased outflow, and so on up to the top of the food chain, so that the effect is propagated to the entire system. Despite increased productivity, however, the ecological efficiency of the trophic level just below the top is expected to generally decrease (table 4.2). This occurs because the biomass of this trophic level is top-down-controlled, and hence its production responds relatively less than that of the next lower trophic level.

DOES EVOLUTION OR SPECIES TURNOVER ENHANCE ECOSYSTEM FUNCTIONING IN FOOD WEBS?

We have seen in the previous section that vertical diversity tends to bring ecosystem processes and properties within trophic levels toward some medium, rather than maximum, level in a constant environment. But might this leveling off of ecosystem properties be compensated for by evolution toward more efficient types or species replacement by more efficient species in food webs? Bob Holt and I have shown that species replacement at one trophic level does not necessarily lead to enhanced ecosystem functioning at all levels (Holt and Loreau 2001). There is a fundamental reason why we should expect evolution and species turnover to enhance ecosystem processes only up to a certain point, after which they tend to maintain them at a suboptimal level or even to make them deteriorate.

Evolution through natural selection at one hierarchical level does not occur for the good of all and may even have negative consequences for the

next higher hierarchical level. It is well known that classical Darwinian evolution at the individual level does not necessarily benefit the population as a whole. The same conclusion applies even more to communities and ecosystems, in which the potential for counterintuitive feedbacks and indirect interactions is greater. I shall take a simple classical example to illustrate this point using one of the simplest possible models of a trophic interaction between a prey and its predator, proposed by Rosenzweig and MacArthur (Rosenzweig and MacArthur 1963; Rosenzweig 1971, 1973).

Ignore mass-balance constraints for the time being and assume that the prey, with population size or biomass N , has a population growth that obeys the logistic equation and that the predator, with population size or biomass P , has a type-2 functional response:

$$\begin{aligned}\frac{dN}{dt} &= rN\left(1 - \frac{N}{K}\right) - \frac{cNP}{D + N}, \\ \frac{dP}{dt} &= \frac{\epsilon cNP}{D + N} - mP.\end{aligned}\quad (4.12)$$

In these equations, r is the intrinsic rate of natural increase of the prey, K is its carrying capacity, c is the maximum consumption rate of the predator, D is its half-saturation constant, ϵ is its production efficiency, and m is its mortality rate.

The asymptotic behavior of this prey-predator system can be studied graphically by an isocline analysis (figure 4.4). The null isoclines of the prey and predator are, respectively,

$$\begin{aligned}P &= \frac{r}{cK}[DK + (K - D)N - N^2] \\ N &= \frac{mD}{\epsilon c - m}.\end{aligned}\quad (4.13)$$

The predator isocline is vertical and sets the equilibrium value of the prey population size because of the top-down control exerted by the predator on the prey. The prey isocline is hump-shaped when $K > D$ (the linear term is then positive and is greater than the negative quadratic term for small N) and monotonic decreasing otherwise. It is well known that the equilibrium that lies at the intersection of the two isoclines is stable when it lies in the right, descending part of the prey isocline, whereas it is unstable and gives rise to a stable limit cycle when it lies in the left, ascending part of the prey isocline (May 1973).

Now, assume that evolution occurs within the predator population by natural selection. Individual predators that have the highest net growth rate will be selected for, and a higher net growth rate can be achieved by either increasing parameter ϵ or c or decreasing parameter D or m . All these

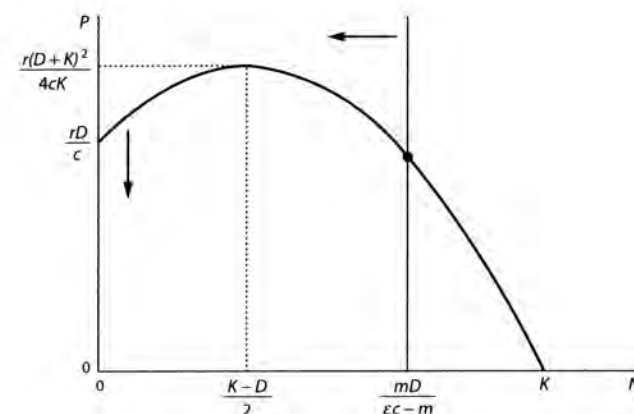


FIGURE 4.4. Effects of predator evolution on the equilibrium population sizes of prey and predators in the Rosenzweig-MacArthur model. The ecological equilibrium point lies at the intersection of the hump-shaped prey null isocline and the vertical predator null isoclines. Predator evolution shifts the predator isocline to the left, and the left part of the prey isocline downward. As a result, the equilibrium prey population size decreases, while the equilibrium predator population size first increases and then decreases.

changes will have the effect of shifting the predator isocline to the left: the predator becomes more efficient at exploiting the prey and hence depresses the prey population further. If natural selection acts on parameter c or D that determines prey consumption by the predator, the prey isocline will also be affected, such that its maximum shifts to the right and its y -intercept declines (figure 4.4). All these changes have two obvious effects on the prey-predator interaction: (1) they decrease the prey population size, and (2) they tend to destabilize the system since the equilibrium can become unstable if it is brought to the left of the hump of the prey isocline.

Their effect on the predator population is slightly more complex. If we start from a situation in which the predator is relatively inefficient, such that its isocline lies far on the right of the hump of the prey isocline, evolution will gradually shift its isocline to the left, which at first increases its population size (the equilibrium point at the intersection of the two isoclines moves up). If, however, evolution toward greater efficiency continues further, the predator isocline will eventually move past the hump (which itself may shift to the right), at which point the predator population starts decreasing. Since the y -intercept of the prey isocline moves downward simultaneously, both the predator and prey populations ultimately tend to zero. In fact, this point will never be reached since the system will become

increasingly unstable, generating fluctuations of increasing amplitude, as the predator becomes more efficient at exploiting the prey. Thus, stochastic extinction will occur before the deterministic extinction of the two interacting populations can ever take place.

The general conclusion, however, is clear: evolution toward more efficient predators at first benefits the predator population, but, past a threshold, it decreases both the prey and predator populations, ultimately driving them to extinction. Species turnover, in which more efficient predators replace less efficient ones by successive invasions from outside the ecosystem, leads to exactly the same result. It is hard to find a clearer example of how *evolution in food webs can be detrimental to the functioning, and even the very existence, of the ecosystem*. Of course, the prey too will evolve in response to the deterioration of its selective environment, leading to coevolution of the two partners and possibly stabilization of the interaction. But there is no reason to expect this coevolution to lead to optimal functioning, whatever the criterion one wishes to choose to define optimal functioning. Darwinian extinction, i.e., the process by which individual natural selection leads to population extinction, might be a widespread, if often ignored, phenomenon. Webb (2003) provides a classification of the various dynamical mechanisms that can generate Darwinian extinction.

This simple example reveals a general property of trophic interactions: the potential for *overexploitation*. Overexploitation occurs when increasing the exploitation of a resource leads to a decreased yield to the consumer. Overexploitation does not occur (at least at equilibrium) when resources are inorganic or inert because such resources do not self-reproduce but are renewed by independent factors (whether through recycling within the ecosystem or through inputs from outside the ecosystem). Increasing the exploitation rate of these resources does not affect their renewal and hence can only increase consumption up to a level where it matches resource renewal. As a result, overexploitation of inorganic resources by primary producers is unlikely, except as a transient phenomenon. In contrast, living resources have the fundamental property of being self-reproducing. Exploiting them beyond a certain threshold reduces their population size to such an extent that their collective production, and hence also the production available for their exploitation, decreases, leading ultimately to the decline of the exploiter populations. Some of the best-known examples of overexploitation involve our own species since humans have driven a number of large-sized mammals to extinction or near extinction because of hunting, and a similar fate is threatening a growing number of large-sized fishes because of increasing fishing efforts. Infectious disease ecology is another area

where overexploitation is widespread and conspicuous. Infectious diseases often decimate host populations and subsequently fade out for lack of susceptible hosts. The commonness of overexploitation in many other natural systems, however, is still poorly known.

HORIZONTAL DIVERSITY, VERTICAL DIVERSITY, AND ECOSYSTEM FUNCTIONING

The previous chapters showed that horizontal diversity tends to enhance resource exploitation and hence also generally production and biomass, within a trophic level. Therefore, we might intuitively expect horizontal diversity to counteract the disruptive effect of vertical diversity on ecosystem functioning. This should be true in particular at the bottom of the food web. If inorganic resources are not fully exploited by primary producers because of the pressure exerted by higher trophic levels, other species should be able to invade the system and use the resource leftovers, thus restoring a higher primary production and biomass. As it turns out, things are not so simple because there are strong constraints on coexistence in exploitation systems.

ASSEMBLY RULES AND ECOSYSTEM FUNCTIONING IN A FOOD WEB WITH PLANTS AND SPECIALIST HERBIVORES

The constraints that arise from species interactions in exploitation systems are particularly clear in the case of specialist plant-herbivore food chains supported by a single, homogeneous limiting nutrient. Grover (1994) showed that strict rules govern community assembly in this case. In his analysis, he made some restrictive assumptions about mortality rates (which were all equal to a common dilution rate, as in a chemostat) and nutrient recycling, but his results are robust to relaxation of these assumptions. To understand the functional consequences of these constraints on coexistence, consider the general food-chain model described in the first section but assume that there is an arbitrary number of such food chains, each of which is limited to two trophic levels, i.e., plants and herbivores (figure 4.5). The dynamical equations of the system depicted in figure 4.5 are

$$\begin{aligned} \frac{dB_0}{dt} &= I - m_0 B_0 - \sum_j f_{1j}(B_0) B_{1j} / \varepsilon_{1j}, \\ \frac{dB_{1i}}{dt} &= f_{1i}(B_0) B_{1i} - m_{1i} B_{1i} - f_{2i}(B_{1i}) B_{2i} / \varepsilon_{2i}, \\ \frac{dB_{2i}}{dt} &= f_{2i}(B_{1i}) B_{2i} - m_{2i} B_{2i}, \end{aligned} \quad (4.14)$$

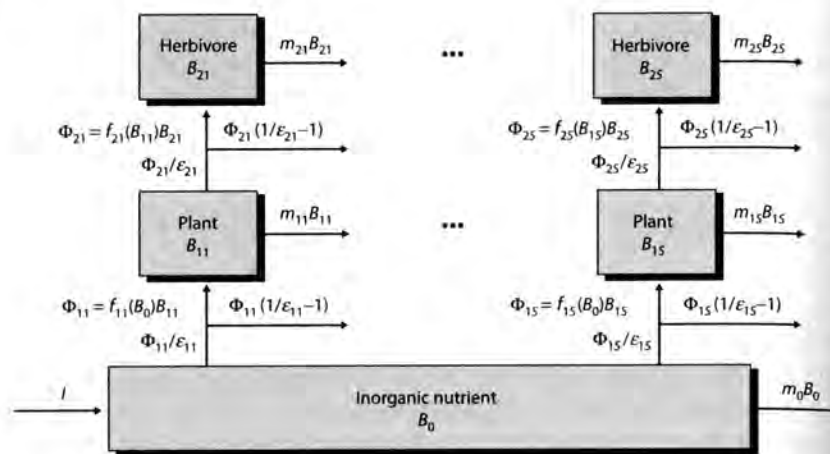


FIGURE 4.5. A simplified nutrient-limited food web made up of S specialist plant-herbivore food chains. Boxes represent nutrient stocks, while arrows represent nutrient flows.

where variables and parameters have two subscripts, the first of which indicates the trophic level, and the second, species identity.

In this system, the stock of inorganic nutrient obeys strict constraints at equilibrium (appendix 4C). Let $B_{0(*)}^*$ denote the equilibrium value of the stock of inorganic nutrient in the presence of a community with composition $(.)$ and write this composition using the subscripts of the species present². Figure 4.6 illustrates the multiple inequalities that must be satisfied when there are up to two plant and herbivore species. It is straightforward to generalize these inequalities to an arbitrary number of food chains.

Since there is a single limiting resource in this system, competition among plants obeys the R^* rule in the absence of herbivores (chapter 2): the plant species with the lowest B_0^* drives all other species to extinction. Here I have arbitrarily defined species 1 as the most competitive one ($B_{0(0,11)}^* < B_{0(0,12)}^*$). The addition of herbivores to a food chain increases B_0^* because the loss of plant biomass to herbivores must be compensated for by a higher plant growth rate at equilibrium, which itself requires a higher resource availability. Consequently, plant 1 can invade and extirpate all food-web configurations from which it is absent since these are characterized by a nutrient availability that exceeds its B_0^* . Plant 2 cannot invade a

²Thus, for instance, $B_{0(0,11,21)}^*$ is the equilibrium inorganic nutrient stock (first subscript 0) in a simple food chain that comprises the inorganic nutrient (subscript 0 in parentheses), plant species 1 (subscript 11 in parentheses), and herbivore species 1 (subscript 21 in parentheses).

system in which only plant 1 is present, but it can invade a system with a food chain made up of plant 1 and herbivore 1 provided its B_0^* is lower than that of food chain 1. This invasion, however, does not lead to the competitive exclusion of plant 1, and hence of herbivore 1, because plant 1 is a better competitor. Thus, as emphasized by Grover (1994), the constraints shown in figure 4.6 not only determine the potential for *species coexistence* but also the precise *assembly sequence* in which the community can assemble itself through successive species introductions. The unique sequence of introductions that leads to a community of two plants and their specialist herbivores limited by a single nutrient is the following: (1) plant 1 (2) herbivore 1 (3) plant 2 (4) herbivore 2. To be feasible, this sequence requires a trade-off between the ability of plants to compete for resource exploitation and their ability to resist herbivory, such that stronger competitors are most suppressed by their herbivores, thereby leaving enough nutrient available to weaker competitors.

During this community assembly process, the level of the basal inorganic resource alternatively decreases and increases at each introduction but converges on an intermediate value, a pattern that is strikingly similar to the assembly of a single food chain (figure 4.2). The inorganic nutrient stock in turn determines total resource consumption by plants: at equilibrium, the first of equations (4.14) implies that inorganic nutrient consumption (the summation term on the right-hand side of the equation) equals $I - m_0 B_0^*$. Therefore, inorganic nutrient consumption is lower when B_0^* is higher, and vice versa. And since primary production and plant biomass depend directly on inorganic nutrient consumption, unless there are special trade-offs among plant traits, they should be expected to generally show a pattern symmetrical to that of the inorganic nutrient stock (figure 4.6). Thus, we are led to the conclusion that *horizontal diversity has qualitatively the same effect on ecosystem properties as does vertical diversity* in food webs made up of plants and specialized herbivores. Each new plant species added to such food webs has qualitatively the same effect as does an additional consumer trophic level in a linear food chain, and each new herbivore species has qualitatively the same effect as does a second additional trophic level that controls the first.

The ups and downs of nutrient availability correspond to different food-web configurations, however. Therefore, it is also useful to analyze the effects of increasing species diversity in the two configurations separately. When the food web includes a plant that is not controlled by its specialist herbivore (figure 4.6, left), simultaneously increasing plant and herbivore diversity along the assembly sequence leads to an increased available nutrient

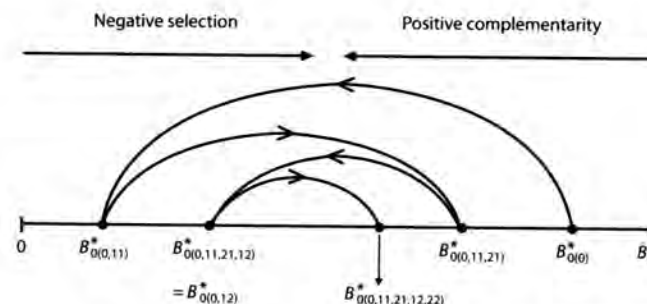


FIGURE 4.6. Coexistence conditions and assembly rules for the nutrient-limited food web with plants and specialist herbivores depicted in Figure 4.5. The unique sequence of introductions that leads to an equilibrium community of two plants and their specialist herbivores is the following: (1) plant 1; (2) herbivore 1; (3) plant 2; (4) herbivore 2. The amount of inorganic nutrient alternatively decreases and increases at each introduction but converges on an intermediate value, just as in a single food chain (figure 4.2). Adding a plant-herbivore pair to a system that contains an unconsumed plant generates a negative selection effect that deteriorates nutrient exploitation (left), while adding a plant-herbivore pair to a system in which all plants are controlled by their specialist herbivore generates a positive complementarity effect that enhances nutrient exploitation (right).

stock, and hence to a less efficient nutrient exploitation. In contrast, when all plants are controlled by their specialist herbivores (figure 4.6, right), simultaneously increasing plant and herbivore diversity leads to a decreased available nutrient stock and hence to a better nutrient exploitation. Thus, the effects of species diversity on nutrient consumption, and hence also generally on plant biomass and primary production, are expected to be opposite in the two alternating parts of the assembly process, and these contrasting responses are entirely due to differences in the configuration of the food web in the two parts. Plant-herbivore food chains are less efficient at using the inorganic nutrient than are plants alone. Adding a plant-herbivore pair to a system that contains an unconsumed plant can only be achieved, while maintaining equilibrium coexistence, if the herbivore consumes the most competitive plant, which counteracts selection toward a greater competitive ability in plants and reduces the ability of the system as a whole to exploit the limiting nutrient. On the other hand, if the system contains only plant-herbivore food chains, adding another food chain—as long as the inorganic nutrient input is large enough to support it—does not affect the plants that are already present because their biomass is top-down-controlled by the herbivores. Thus, increasing the diversity of full

plant-herbivore food chains can only increase the plants' total biomass and collective efficiency at exploiting the inorganic nutrient.

This contrast between the two food-web configurations shows that the two main biodiversity effects at the plant trophic level, the selection effect and the complementarity effect, are driven by different factors and may conflict when plant coexistence is mediated by a consumer trophic level. The *selection effect* in plants is driven by competition for a single limiting resource, which tends to maximize resource consumption. In contrast, the *complementarity effect* cannot arise from niche differences among plants in the way they use resources since the model assumes that there is a single, homogeneous limiting resource without any means of partitioning it. Here, complementarity among plants arises from *avoidance of herbivore-mediated or "apparent" competition* (Holt 1977) because they have different specialized consumers. This new form of functional complementarity that arises from trophic interactions has a positive effect on plant ecosystem processes when all plants are involved in trophic interactions. But plants can always gain greater access to the shared limiting resource if they escape trophic interactions with the upper trophic level. Therefore, this form of complementarity is unable to compensate for the intrinsically detrimental effect that trophic interactions have on plant ecosystem processes, and it conflicts with selection toward greater resource acquisition among those plants that escape trophic interactions and compete for the limiting resource.

These conclusions are important because they provide insights into some basic biodiversity effects that operate in food webs and their mechanisms. But they do not necessarily apply to all natural ecosystems. Model (4.14) makes, implicitly or explicitly, strong assumptions about the nature of species interactions and the assembly process. By assuming a single, homogeneous limiting nutrient, the model ignores any form of functional complementarity that arises from resource partitioning or facilitation among plants, for which there is now ample theoretical and experimental support as shown in chapter 3. By assuming that the system reaches equilibrium at each step of the assembly sequence, the above analysis ignores the possibility that new species may invade during transient dynamics, and hence that biodiversity loss or gain may not follow a neat assembly sequence.

BIODIVERSITY AND ECOSYSTEM FUNCTIONING IN FOOD WEBS

Elisa Thébault and I (Thébault and Loreau 2003, 2006; Loreau and Thébault 2005) developed a model that partly relaxes some of the restrictive assumptions involved in Grover's (1994) assembly rules and that is more suitable for a general analysis of the relationship between biodiversity

and ecosystem functioning in food webs. First, our model considers consumers whose dietary niche breadth can vary from specialist to generalist and thereby relaxes the assumption that each plant species is controlled by a unique specialist herbivore. It also includes carnivores as a third trophic level, although most of its interesting features can be analyzed with only two trophic levels. Second, the model allows some degree of coexistence and resource partitioning among plants through limited access to the limiting nutrient in local resource depletion zones around the rooting system of each plant, following the formalism developed by Huston and DeAngelis (1994) and me (Loreau 1996, 1998a). Our analysis, however, focused mainly on the case where nutrient transport in the soil is relatively fast, and hence where the potential for plant coexistence through this mechanism is limited, to emphasize the specific role trophic interactions play in the relationship between biodiversity and ecosystem functioning. Last, our analysis of the model considered the expected response of ecosystem properties following random species loss or gain to mimic recent biodiversity experiments and study the effects of species diversity independently of species identity. Consequently, we relaxed the assumption that changes in species richness can occur only as a result of a strict, sequential community assembly process since this strong assumption is irrelevant in the case of biodiversity loss and community disassembly.

Our model is depicted graphically in figure 4.7. The corresponding dynamical equations are obtained easily by setting the rate of change of each compartment equal to the sum of inflows to that compartment minus the sum of outflows from that compartment. Here, R is the nutrient stock in the soil nutrient pool with volume V_R , L_i is the nutrient stock in the set of individual resource depletion zones, (with total volume V_i) of plants from species i , and P_i , H_i , and C_i are the nutrient stocks of plant, herbivore, and carnivore species i , respectively. Biomasses are again assumed to be simply proportional to nutrient stocks here. $\sigma_i = V_i/V_R$ is the relative volume occupied by plant species i in the soil³. The limiting nutrient is supplied in inorganic form with an amount I per unit time, is lost at a rate q per unit time, and is transported between individual resource depletion zones and

³The variables in figure 4.7 are nutrient stocks in order to make mass balance explicit and obtain direct measures of stocks and biomasses. Earlier models (Loreau 1996, 1998) were expressed in terms of nutrient concentrations. The model described by figure 4.7 is equivalent to these earlier models after nutrient concentrations are multiplied by the appropriate volumes to obtain nutrient stocks. The original model presented in Thébault and Loreau (2003), however, had two types of variables: nutrient concentrations for the inorganic nutrient and nutrient stocks for the living compartments.

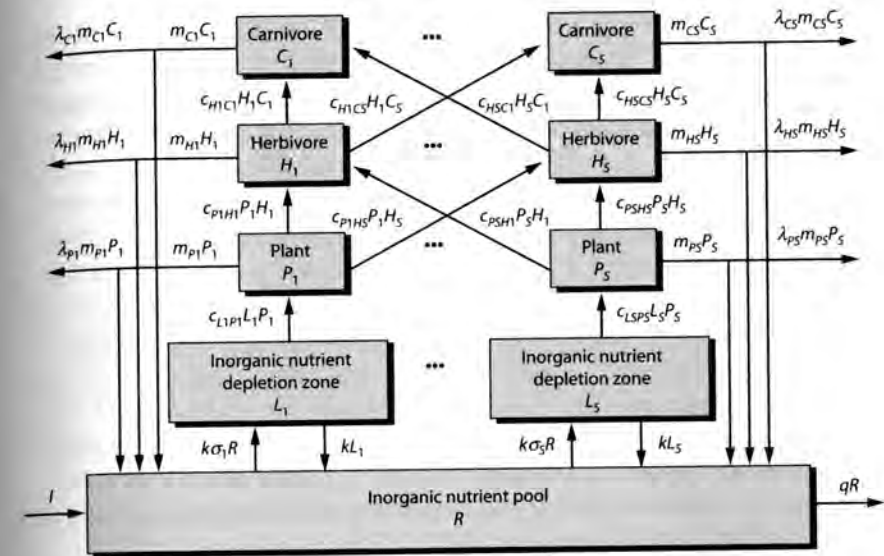


FIGURE 4.7. A complex nutrient-limited food web made up of S plants, S generalist herbivores, and S generalist carnivores. Plants have limited access to inorganic nutrient in individual resource depletion zones. Boxes represent nutrient stocks, while arrows represent nutrient flows.

the soil nutrient pool at a rate k per unit time. Plant species i consumes the inorganic nutrient at a rate c_{LiP_i} , herbivore species j consumes plant species i at a rate c_{PiH_j} , and carnivore species j consumes herbivore species i at a rate c_{HiC_j} . The nutrient is released from biomass by natural death and metabolic activity at rates m_{P_i} , m_{H_i} , and m_{C_i} in plants, herbivores, and carnivores, respectively. Part of the nutrient thus released is recycled within the local ecosystem; λ_{P_i} , λ_{H_i} , and λ_{C_i} represent the fractions of nutrient coming from plants, herbivores and carnivores, respectively, that are not recycled and hence are lost from the system. Resource-consumer interactions are here assumed to follow the law of mass action (i.e., consumer functional responses are assumed to be linear), and production efficiencies are assumed to be 100 percent for the sake of simplicity. Lower production efficiencies do not change the results qualitatively; they affect only the shape of the nutrient or biomass pyramid of the ecosystem, i.e., the distribution of nutrient across the various trophic levels. The number of species is in principle S per trophic level, but it may differ between trophic levels in some food-web configurations.

The main effect of carnivores in this model is to control the herbivores they prey upon and thereby to release plants from the top-down control of

herbivores. This creates a situation that is qualitatively similar to that in which some plants are unconsumed by herbivores. Therefore, I consider here only cases in which carnivores are absent for simplicity. I also present results only for total plant biomass, total herbivore biomass, and total ecosystem biomass (sum of total plant and herbivore biomasses) as ecosystem properties for comparison with experimental studies. Total plant biomass is likely to be a poor approximation of primary production when consumed by higher trophic levels, but total biomasses at producer and consumer trophic levels are often used for convenience as ecosystem properties in experiments on the relationship between species diversity and the functioning of both single-trophic-level and multitrophic ecosystems (Duffy et al. 2003; Finke and Denno 2005). In the simple scenarios analyzed here, all plants are assumed to have equal nutrient turnover rates m_{p_i} , in which case primary production can be shown to be proportional to total ecosystem biomass. Thus, total ecosystem biomass can be used as a convenient surrogate for primary production.

Using this model, we examined how changes in species richness influence ecosystem properties at equilibrium for different food-web structures under conditions that allow all plant and herbivore species to coexist. We also considered different scenarios of biodiversity changes: either plant species richness and herbivore species richness vary in parallel or herbivore species richness varies alone. Changing plant richness alone leads to unfeasible food-web configurations in our model because there cannot be more herbivore species than plant species at equilibrium. To analyze expected ecosystem responses to changes in species richness, we calculated, at each diversity level, the expected value of plant and herbivore biomass across all possible species compositions or, equivalently, in randomly assembled communities, as is often done in experiments.

The most striking conclusion of our analysis is that *the effects of species richness on ecosystem properties are critically dependent on the structure of the food web*. First, as expected from the previous analysis of specialist plant-herbivore food webs in a homogeneous environment, the *presence of plants that are released from top-down control by herbivores*, either because they are inedible or because their herbivores are themselves controlled by carnivores, strongly affects the relationships between diversity and biomass. When each plant is consumed by a specialist herbivore, the mean total plant biomass increases linearly with species richness (figure 4.8, left) because each plant species is controlled by its own herbivore and is unaffected by the addition of other species. The corresponding complementarity effect (as defined in chapter 3) is positive, while the selection effect is

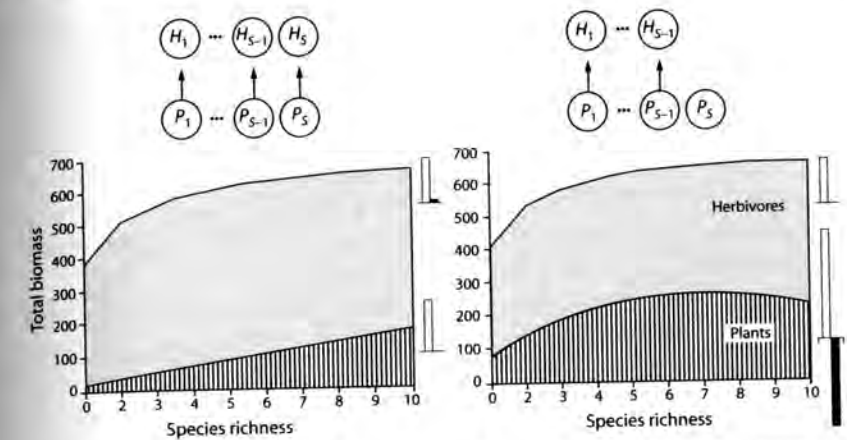


FIGURE 4.8. Expected total plant biomass (hatched area) and total herbivore biomass (gray area) as functions of plant species richness, for a food web with specialist herbivores and either no inedible plant (left panel) or one inedible plant (right panel) in the model depicted in figure 4.7 but without carnivores. The upper curve shows total ecosystem biomass (sum of total plant and herbivore biomasses). Total herbivore biomass is the difference between the upper and lower curves (gray area). Herbivore species richness varies parallel to plant species richness to keep the same food-web configuration along the diversity gradient. Top panels show the food-web configurations analyzed in the corresponding column. Small histograms on the right of the panels show the strengths of the complementarity effect (in white) and the selection effect (in black) for the highest diversity treatment (10 plant species). These effects are measured on the same scale as the y-axis, except for plant biomass in case of a food web with one inedible plant, where they are reduced by a factor of 2. Modified from Loreau and Thébaud (2005).

zero. As discussed in the previous section, this complementarity is generated by a very different mechanism than in simple competitive systems: here it does not arise from resource partitioning or facilitation but from avoidance of herbivore-mediated competition through differentiation in plants' natural enemies.

In contrast, when the same food web comprises a plant that is either inedible or protected from top-down control by a carnivore, the mean total plant biomass does not increase linearly and can even decrease at high diversity (figure 4.8, right). In this case, the biomass of the inedible plant is controlled by resource availability, which decreases when plant richness increases. This also leads to a negative selection effect because the inedible plant, which tends to be dominant is most affected by an increase in diversity. Note that, in this scenario, since our analysis considers the expected

biomass across all possible species compositions, some assemblages do not contain the inedible plant, which explains why the mean total plant biomass increases with diversity over at least part of the diversity gradient. If the inedible plant were included automatically in all assemblages, total plant biomass would decline monotonically with diversity, as predicted by the assembly rule analyzed in the previous section. This illustrates the fact that specific scenarios of biodiversity loss or gain may deviate significantly, and even qualitatively, from the expected response.

In both cases, total herbivore biomass (difference between the upper and lower curves in figure 4.8) can show complex relationships with diversity. In the scenarios examined in figure 4.8, it decreases at high diversity when all plants are edible, and it also decreases at intermediate species richness when the food web comprises an inedible plant. Total ecosystem biomass (upper curves in figure 4.8) and primary production, however, increase monotonically with diversity until saturation, just as in systems with a single trophic level. Thus, the *nature of population control* (top-down vs. bottom-up) in an ecosystem can profoundly affect the responses of ecosystem properties to changes in species richness. Heterogeneity within trophic levels and the presence of inedible species are important to consider as they modify top-down control and trophic cascades in food webs (Leibold 1989; Abrams 1993).

Food-web connectivity, as measured by the diet breadth of herbivores, is another factor that has a strong impact on the relationship between diversity and ecosystem properties (figure 4.9, top). When all plants are consumed and herbivores are generalists, the mean total plant biomass no longer increases linearly with diversity and can even decrease at high diversity levels. In this case, the biomass of each plant species is still controlled by herbivores, but it decreases with the addition of other herbivore species because plant consumption increases. This in turn can result in decreased total plant biomass. The mean total herbivore biomass is generally higher when herbivores are generalists than when they are specialists, but it also increases less with diversity and can decrease at high diversity. Competition between generalist herbivores is strong, and resource-use complementarity among them is lower, as indicated by the smaller complementarity effect. Total ecosystem biomass and primary production can also decrease at high diversity when herbivores are generalists.

The *trophic position* of the species being lost or gained also plays a critical role. Changes in the diversity of the consumer trophic level alone (figure 4.9, bottom) have very different effects than do simultaneous changes at the plant and herbivore trophic levels (figure 4.9, top). The mean total

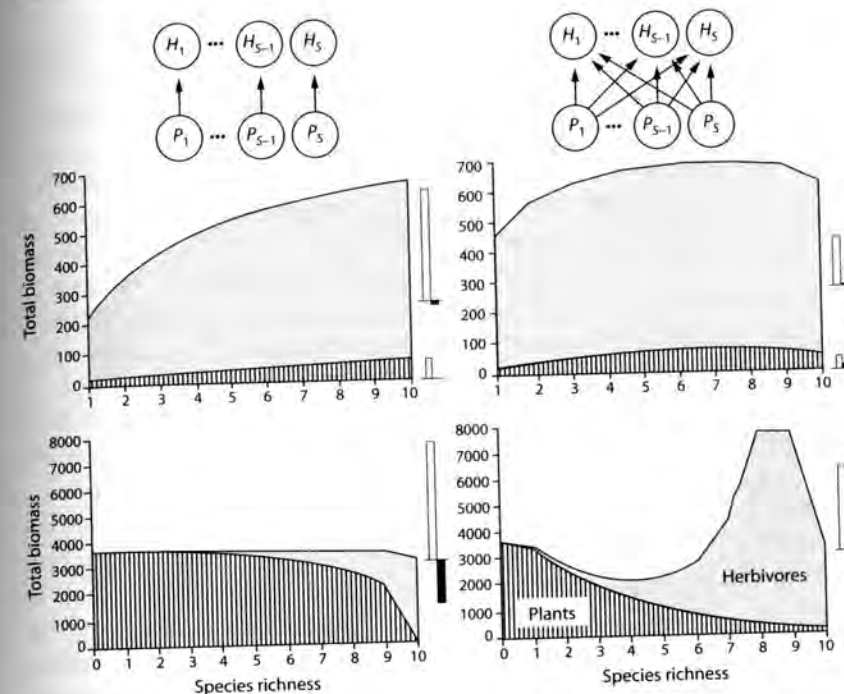


FIGURE 4.9. Expected total plant biomass (hatched area) and total herbivore biomass (gray area) as functions of species richness, for a food web with specialist herbivores (left panels) and a food web with generalist herbivores (right panels) in the model depicted in figure 4.7 but without carnivores. The upper curve in each panel shows total ecosystem biomass (sum of total plant and herbivore biomasses). Total herbivore biomass is the difference between the upper and lower curves (gray area). Species richness varies either at the two trophic levels simultaneously (top panels) or at the herbivore trophic level only while plant species richness is held constant at 10 species (bottom panels). Small histograms on the right of panels show the strengths of the complementarity effect (in white) and the selection effect (in black), measured on the same scale as the y-axis, for the highest diversity treatment (10 herbivore species). Modified from Loreau and Thébaud (2005).

plant biomass then always decreases upon herbivore addition, whether herbivores are specialists or generalists. But it decreases faster at low diversity when herbivores are generalists because the consumption of each plant is then higher. The mean total herbivore biomass always increases with diversity when herbivores are specialists, but it can decrease at high diversity when herbivores are generalists (figure 4.9, bottom right). Again, when herbivores are generalists, resource-use complementarity is smaller, which

can result in a decrease in total herbivore biomass at high diversity and a smaller complementarity effect. The strong increase in total herbivore biomass at an intermediate diversity of herbivores when they are generalists may be explained by a strong increase in herbivore consumption together with more favorable conditions for herbivore-mediated plant coexistence.

Using very different models of predator-prey interactions, Ives et al. (2005) and Casula et al. (2006) have further explored the effects of *nonadditive interactions* between consumers on the total density or biomass of both consumers (predators) and resources (prey). Nonadditive interactions arise when consumers either decrease (antagonism) or increase (synergism) the per capita capture rates of other consumer species because of nontrophic effects such as mutual interference (antagonism) and facilitation (synergism). Ives et al. (2005) included these interactions in the form of a single parameter a that modulates the per capita capture rate of consumers. If a is negative, increasing the density of a consumer species decreases the per capita capture rate of another consumer species, thus generating antagonism. The converse is true if a is positive, which leads to synergism. Their model shows patterns very similar to ours when consumers are generalists and only consumer species richness is varied (compare figure 4.9, bottom right, and figure 4.10, left panels): total resource density or biomass decreases, and total consumer density or biomass shows a hump-shaped pattern as initial consumer species richness increases. Synergistic interactions between consumers only strengthen these patterns, while antagonistic interactions weaken them and may sometimes turn a humped-shaped pattern of consumer density into a monotonic increase (figure 4.10, bottom left). This occurs because antagonistic interactions inhibit the extinction of resource species in their model (figure 4.10, top right), thereby weakening the negative effect of consumers on resources at high consumer richness. Resource extinction, however, is not required to generate such hump-shaped patterns. These also emerge in our model in spite of the fact that we considered only food webs in which there was no species extinction. Declines in consumer biomass or density at high consumer diversity arise from resource overexploitation, which is a more general phenomenon than outright extinction. Last, intraguild predation has effects very similar to those of antagonistic interactions because it also acts to reduce the impact of consumers on resources (Ives et al. 2005).

In conclusion, horizontal diversity does not simply oppose the effect of vertical diversity on ecosystem functioning. The interactions between horizontal diversity and vertical diversity are complex and lead to complex relationships between biodiversity and ecosystem properties. Horizontal

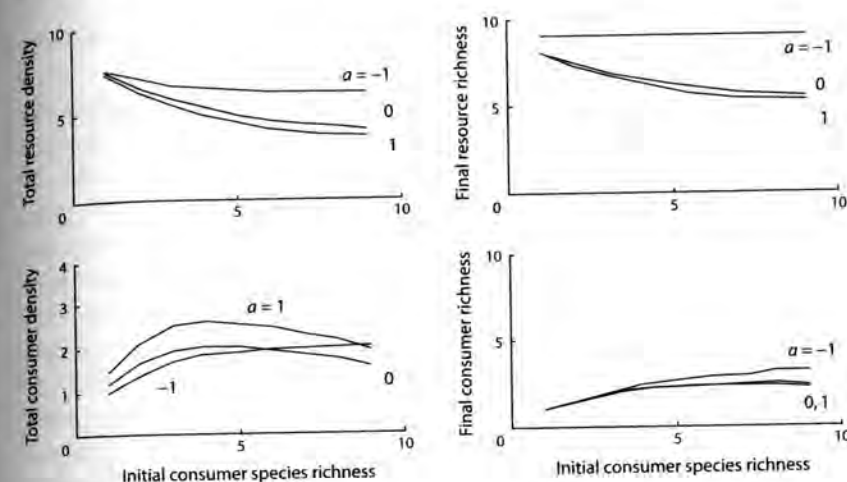


FIGURE 4.10. Effects of nonadditive interactions on the relationships between total resource density (top left), total consumer density (bottom left), final resource species richness (top right), final consumer species richness (bottom right), and initial consumer species richness in a predator-prey model. Consumers have additive effects on the per capita population growth rate of resources when $a = 0$, nonadditive antagonistic effects when $a < 0$, and nonadditive synergistic effects when $a > 0$. Modified from Ives et al. (2005).

diversity still contributes to enhance some ecosystem processes to some extent, but its effects are strongly dependent on the trophic level at which diversity varies and on the structure of the food web, in particular, its connectivity and the nature of population control (top-down vs. bottom-up). Nonlinear responses are common, except for special food-web structures, and negative effects at a very high diversity are possible because of collective overexploitation of resources by a diverse assemblage of efficient consumers. The prevalence of resource overexploitation in nature, however, is unknown and might be more limited than suggested by the models. Horizontal diversity does not prevent upper trophic levels from reducing the efficiency with which the ecosystem as a whole exploits the basal resource compared with a system with a single trophic level.

Despite the complexity introduced by trophic interactions, the relationships between biodiversity and ecosystem properties are predictable provided environmental conditions and food-web structure are known. Our model makes several predictions that deserve to be tested experimentally to gain better knowledge of the impacts of biodiversity changes on ecosystem functioning under natural conditions. Although a few experiments have been performed, they are still too limited to draw general conclusions regarding

the functional effects of interactions between horizontal diversity and vertical diversity in food webs (Duffy et al. 2007).

Experimental changes in the diversity of a single trophic level within the context of a multitrophic system are slightly more frequent. Experimental manipulations of consumer diversity often showed enhanced resource exploitation and increased consumer biomass (Duffy et al. 2003, 2007), just as in single-trophic-level systems (chapter 3). There has been no evidence so far for the negative effects of consumer diversity that are predicted by the model under conditions conducive to resource overexploitation. This lack of evidence, however, might be due to the fact that recent experiments generally have not provided the necessary conditions for these effects to occur, in particular, sufficient time for prey abundance to adjust to changes in consumer diversity and feed back on consumer abundance. Antagonistic interactions among predators, which limit the potential for overexploitation, also appear to be relatively frequent (Schmitz 2007).

The converse effects of prey diversity on prey consumption by consumers have been studied much more frequently, although controlled experimental manipulation of prey diversity has been rare. Our model makes a straightforward prediction about these effects: since the presence of inedible plants allows part of the plant trophic level to escape consumption, herbivores are expected to have a smaller effect on plant biomass as plant diversity increases. Plants have a larger total biomass when some plant species experience no or reduced consumption (compare left and right panels in figure 4.8). Hillebrand and Cardinale (2004) performed a meta-analysis of a large number of experiments that manipulated the presence of invertebrate or vertebrate grazers while also measuring the magnitude of grazer effects on algal biomass and the diversity of algal assemblages. They found a consistent pattern of decreased consumer effects on algal biomass (i.e., consumer effects become less negative) as algal diversity increases (figure 4.11), in agreement with theoretical predictions.

Complete inedibility of some prey species, however, is not necessary for these effects to occur. Provided some mechanism other than top-down control by predators maintains prey diversity, differential susceptibility to predation coupled with differential dominance may often be sufficient to decrease predator effects on prey biomass. This is the basis for what is known as the dilution effect in the literature on disease ecology. The *dilution effect* occurs when increased species diversity reduces disease risk (Keesing et al. 2006). Striking examples of this effect include increased rice resistance to blast disease following increased rice genetic diversity (Zhu et al. 2000) and reduced risk of human exposure to Lyme disease as vertebrate host

FOOD WEBS

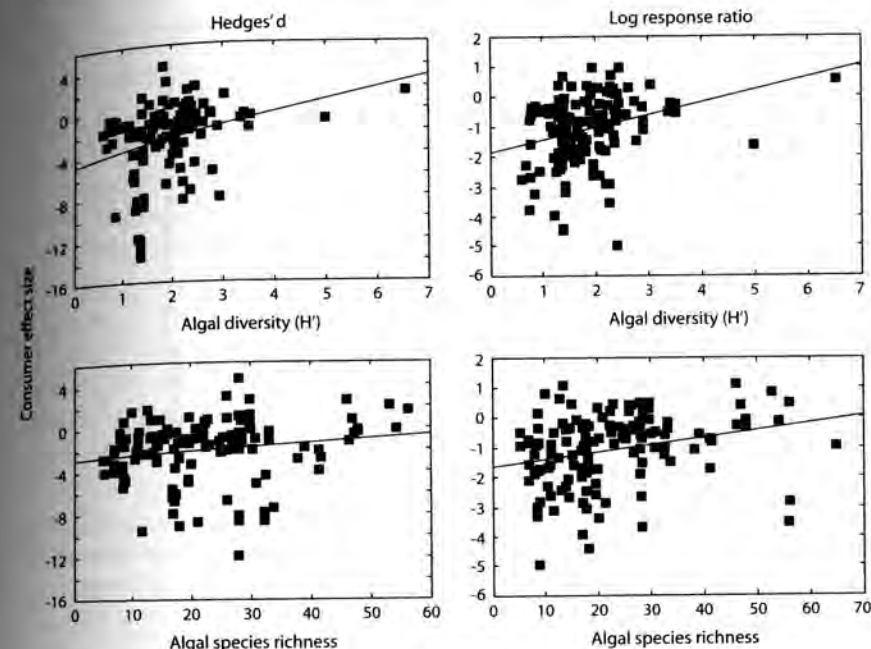


FIGURE 4.11. Consumer effect sizes on algal biomass vs. algal diversity in experiments that manipulated the presence of invertebrate or vertebrate grazers. Effects sizes are Hedges's *d* (left panels) or log response ratio (right panels). Algal diversity is measured by Shannon's diversity index (top panels) or species richness (bottom panels). Modified from Hillebrand and Cardinale (2004).

diversity increases (Ostfeld and Keesing 2000). The mechanism underlying the latter example is relatively well known and has been studied theoretically: as vertebrate host diversity decreases, the host species that transmit the disease most effectively (in this case, mice and deer) become dominant, thereby increasing disease risk. Although a model with random species loss would predict decreased Lyme disease risk on average as more species are lost, all realistic extinction scenarios predict that mice and deer will be the last species to go extinct, yielding an opposite trend toward increased Lyme disease risk as more species are lost (figure 4.12).

NONTROPHIC INTERACTIONS, BIODIVERSITY, AND ECOSYSTEM FUNCTIONING

While understanding the effects of trophic interactions on biodiversity and ecosystem functioning is challenging, an even greater challenge is to

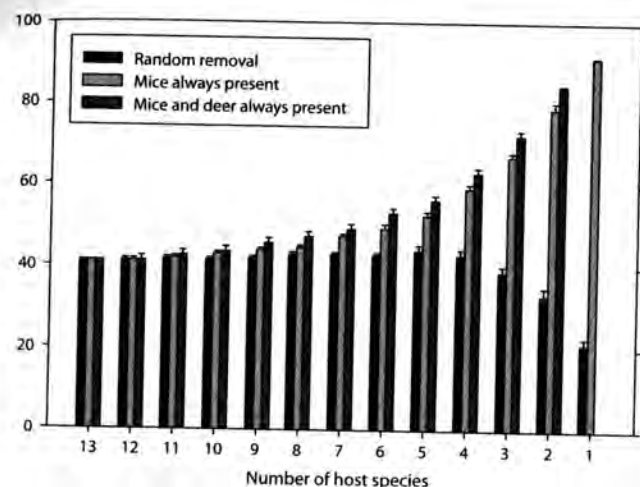


FIGURE 4.12. Results of simulations assessing the effects of reduced species richness on Lyme disease risk as measured by nymphal tick infection prevalence. Data are means \pm 1 SE of 100 replicates. Three scenarios of species extinction are shown: (1) random species removal; (2) white-footed mice were present in all communities, but otherwise removal was random; and (3) mice and white-tailed deer were present in all communities, but otherwise removal was random. Reprinted from Ostfeld and LoGiudice (2003).

understand how *nontrophic interactions* affect biodiversity and ecosystem functioning. Trophic interactions and food webs have been studied abundantly from the early days of ecology, but nontrophic interactions have traditionally been neglected, especially by ecological theory (Bruno et al. 2003). The only exception is interference competition, since classical competition theory based on the Lotka–Volterra model does not differentiate between interference and exploitation competition. Recent mechanistic developments of competition theory, however, have mainly focused on exploitation competition, which is an indirect interaction resulting from the direct trophic interactions between consumers and their shared resources. I briefly discussed some specific effects of nontrophic interactions among consumers on the relationship between total resource or consumer biomass and consumer species richness in the previous section. Here I consider a wider range of nontrophic interactions that can potentially affect any species and any nontrophic interaction in ecosystems.

Recent experiments suggest that nontrophic interactions, such as facilitation, may play an important role in ecosystem functioning (Mulder et al. 2001; Cardinale et al. 2002; Rixen and Mulder 2005) and that different

kinds of species interactions do not act in isolation but co-occur within the same community (Callaway and Walker 1997). Evidence for the importance of trait-mediated indirect interactions is also accumulating (Werner and Peacor 2003; Schmitz et al. 2004). Models of mutualism are often fairly specific and consider only one kind of species interaction. Simple models of mutualism also have the unrealistic property of leading to unlimited population growth under some conditions because they do not respect the principle of mass conservation. To explore interactions between community and ecosystem properties, ecological theory needs flexible, general ecosystem models that are able to include all types of direct species interactions (interference competition, mutualism, exploitation, commensalism, amensalism), as well as their indirect effects, while at the same time satisfying mass-balance constraints.

Following the pioneering work of Arditi et al. (2005), Alexandra Goudard and I recently developed an *interaction-web* model that meets this need (Goudard and Loreau 2008). Our model expands upon the food-web model presented in the previous section by adding nontrophic interactions in the form of nontrophic modifications of trophic interactions—that is, each species is allowed to modify the trophic interaction between any two species (figure 4.13). There are two main differences between this model and the food-web model described in the previous section. First, our interaction-web model includes a production efficiency, ϵ_x , for each species x . The amount of consumed nutrient that is not used in production is assumed to be recycled within the ecosystem. Second, and more fundamentally, the rate of consumption of species x by species y , c_{xy} , is now the product of a trophic component, the predation rate a_{xy} , and a nontrophic component, the nontrophic coefficient ν_{xy} :

$$c_{xy} = \nu_{xy} a_{xy}. \quad (4.15)$$

This nontrophic coefficient captures all the modifications of the trophic interaction between species x and y that are caused by the nontrophic effects of the $3S$ species (S species at each trophic level) in the ecosystem (including species x and y themselves). Each species z is allowed to modify the trophic interaction between species x and y ; the size of this nontrophic effect depends on its biomass, X_z , and an interaction modification coefficient, μ_{xyz} :

$$\nu_{xy} = \prod_{z=1}^{3S} (1 + X_z)^{\mu_{xyz}}. \quad (4.16)$$

The function that describes nontrophic effects [equation (4.16)] was chosen such that it satisfies several conditions. First, it is a strictly increasing function of both the intensity of interaction modification, μ_{xyz} , and

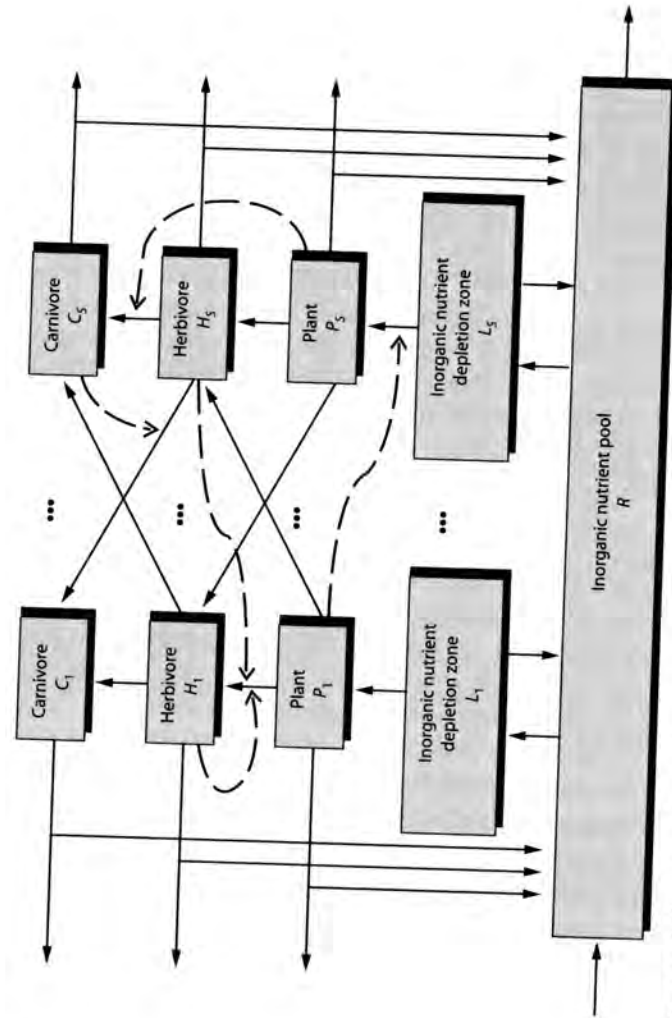


FIGURE 4.13. A complex nutrient-limited interaction web made up of S plants, S generalist herbivores, and S generalist carnivores, in which each species may modify trophic interactions between any two species through nontrophic effects. Plants have limited access to inorganic nutrient in individual resource depletion zones. Boxes represent nutrient stocks, thin solid arrows represent nutrient flows, and thick dashed arrows show examples of possible interaction modifications.

biomass, X_z . Second, if either $\mu_{xyz} = 0$ or $X_z = 0$, then $(1 + X_z)^{\mu_{xyz}} = 1$, and species z does not affect the trophic interaction between species x and y . In the absence of any interaction modification, $\nu_{xy} = 1$, and the consumption rate reduces to a simple trophic predation rate; i.e., $c_{xy} = a_{xy}$. Third, the function for nontrophic effects is strictly positive, so that the sign of the consumption rate does not change. The intensity of interaction modification, μ_{xyz} , can be either positive or negative while keeping the nontrophic coefficient, ν_{xy} , and hence the consumption rate, c_{xy} , positive. This ensures that, whatever the sign of the nontrophic effects of other species, the nutrient flow between species x and y is not reversed, and the food-web structure of the system remains intact. Last, interaction modification coefficients are symmetrical ($\mu_{xyz} = \mu_{yxz}$) to maintain mass balance.

In the presence of interaction modifications, the consumption rate c_{xy} can be smaller or larger than the corresponding trophic predation rate a_{xy} depending on whether the nontrophic coefficient ν_{xy} is smaller or larger than 1 [equation (4.15)], which in turn depends on whether the various species have negative or positive interaction modification coefficients μ_{xyz} [equation (4.16)]. Consequently, each species can either increase or decrease the population growth rate of any other species through nontrophic effects, so that all types of species interactions (competition, mutualism, exploitation, commensalism, amensalism) are incorporated in the model, including intraspecific density dependence (if μ_{xzz} or $\mu_{zyz} \neq 0$). Thus, our model describes a full interaction web. It also satisfies mass balance: interaction modifications change the material flow between a resource and a consumer, but what is gained by the consumer is lost by the resource, and vice versa, so that there is mass conservation overall.

We used this model to analyze the relationships between community and ecosystem properties that emerge from the assembly dynamics of complex ecosystems through successive species invasions from a regional species pool. Here I highlight a few of the main results that came out of this study. First, despite continuous species replacement due to invasion of new species, community and ecosystem properties stabilize relatively quickly in a *quasistationary regime*. In this regime, local species richness increases almost linearly with regional species richness (i.e., the number of species in the regional pool) despite the presence of strong species interactions. This confirms the prediction that species interactions generally do not limit local species diversity but only reduce it relative to the regional species pool (Loreau 2000a).

Second, a number of ecosystem properties, such as total biomass, plant biomass, carnivore biomass, plant production, herbivore production, carnivore production, and inorganic soil nutrient use, generally increase with

regional species richness and hence also with local species richness. The positive effects of species diversity on these ecosystem properties, however, tend to level off at high levels of regional species richness in the presence of nontrophic interactions (figure 4.14). Surprisingly, biomass and production are typically lower in the presence of nontrophic interactions—i.e., in interaction webs—than in their absence—i.e., in simple food webs. Herbivore biomass is usually unaffected by species richness, which suggests a top-down control of carnivores on herbivores.

At first sight, one would expect facilitative and mutualistic interactions to be fostered by the presence of nontrophic effects, and these positive interactions to make the ecosystem more efficient. This is indeed what Arditi et al. (2005) found overall with their model. So, why do nontrophic interactions counterintuitively tend to reduce biomass and production at all trophic levels in our model? The answer is paradoxical: *they do so precisely because resource exploitation becomes more efficient*. The frequency and strength of nontrophic interactions can be easily manipulated in our interaction-web model by varying two parameters in the regional species pool: nontrophic connectance (the proportion of realized nontrophic effects among all possible nontrophic effects) and maximal nontrophic intensity (the maximum absolute value of the interaction modification coefficients). Increasing either of these parameters does increase the frequency of nontrophic species interactions, including mutualistic interactions, but concurrently it increases the mean resource exploitation ability of each species. This increased resource consumption leads to overexploitation, intense competition, and reduced resource-use complementarity at consumer trophic levels, which cascades down the food web and eventually results in decreased biomass and production at all trophic levels.

Two main differences between our model and that of Arditi et al. may explain why this outcome was not apparent in their study. First, they used relatively low levels of trophic connectance among species from different trophic levels, whereas we allowed all species to be generalist consumers. As we saw in the previous section, consumer generalism can greatly increase the potential for resource overexploitation. Second, nontrophic interaction modifications combined additively in their model, whereas they combine multiplicatively in our model [equation (4.16)]. As a result, nontrophic effects can increase resource consumption more strongly in our model, thereby further enhancing the potential for resource overexploitation. It is currently difficult to assess which of the two models is closer to reality for lack of appropriate empirical data. The two models highlight different potential outcomes that might occur in different ecosystems.

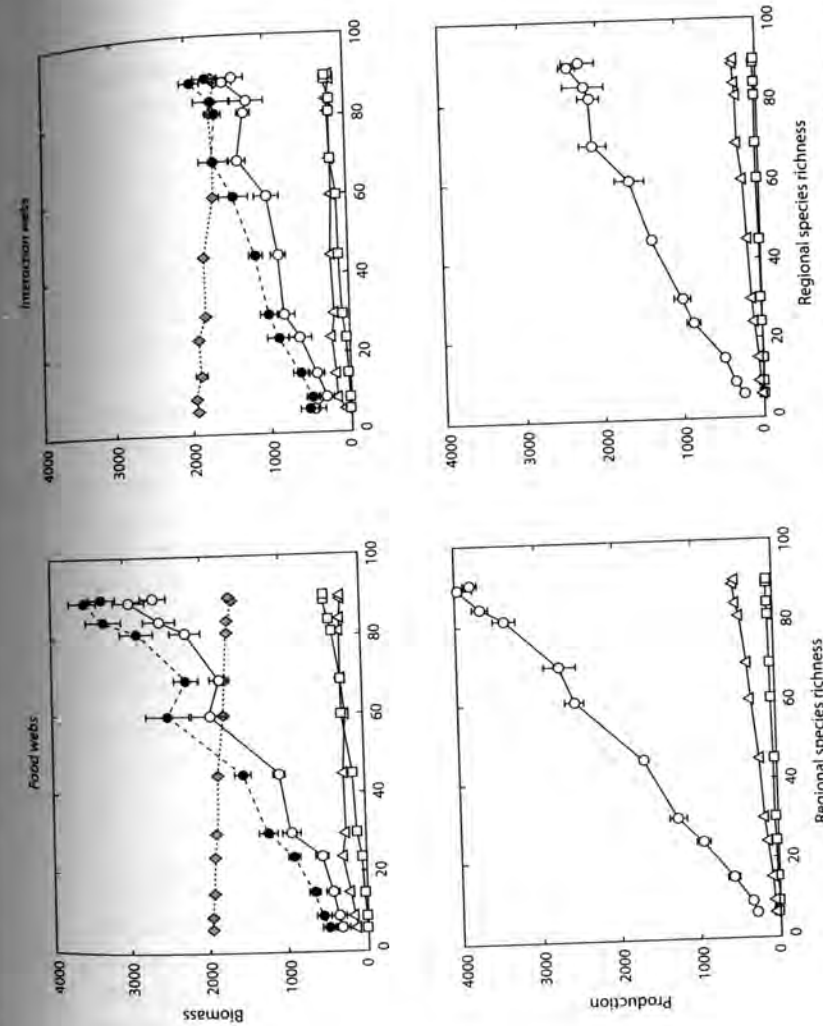


FIGURE 4.14. Biomass and production vs. regional species richness in the interaction web depicted in figure 4.13, in the absence (left panels) or presence (right panels) of nontrophic interactions. Results are means ± 1 SD in the quasi-stationary regime for total biomass (\circ), total herbivore (Δ), and total carnivore (\square) biomass and production. Dotted lines represent the amount of inorganic nutrient (\diamond). Modified from Goudard and Loreau (2008).

Thus, while positive species interactions such as facilitation and mutualism are one of the biological mechanisms that contribute to generate functional complementarity, and hence positive relationships between species diversity and total biomass and production within single trophic levels (chapter 3), their impact in multitrophic systems is more complex because they tend to increase the resource exploitation ability of species at all trophic levels. Consequently, they can enhance the efficiency with which limiting resources are used and transferred along the food chain, thereby contributing to enhance ecosystem functioning, but they can also exacerbate the negative effects of trophic interactions when consumers are generalists, including the potential for overexploitation, intense resource and apparent competition, and reduced functional complementarity at consumer trophic levels. Since a higher species diversity provides more opportunities for both trophic and nontrophic interactions, it can also exacerbate these negative effects and result in weaker, or even negative, relationships with total biomass or production at high diversity.

It is important to keep in mind, however, that our model did not explore all possible forms of nontrophic interactions or all possible scenarios for the topology and strength of these interactions. In particular, it focused on nontrophic modifications of resource consumption rates and assumed no restriction on either consumer generalism or maximal consumption rates. Other scenarios and other forms of nontrophic interactions that affect other demographic and functional parameters are likely to yield different results. But our model reveals the real potential for counterintuitive effects arising from nontrophic interactions, which are too often assumed *a priori* to be positive.

CONCLUSION

The general conclusion that emerges from this chapter is that trophic and nontrophic interactions make the relationships between biodiversity and ecosystem functioning more complex in ecosystems with multiple trophic levels than in the simple competitive systems that have been usually studied experimentally. Theory predicts that vertical diversity does not maximize ecosystem properties at the scale of trophic levels but instead makes them converge on intermediate values through damped oscillations as food-chain length increases. More integrative measures of ecosystem functioning, such as total ecosystem biomass, may even decrease as food-chain length increases. Overexploitation of biological resources is another factor that can

cause deterioration of the functioning of diverse, strongly interacting ecosystems. Although horizontal species diversity is still expected to enhance ecosystem properties under a range of conditions, it can also reduce them when it promotes overexploitation. The fact that recent experiments have generally found positive effects of species diversity on total biomass and resource use at all trophic levels (chapter 3) does not invalidate these theoretical predictions because most of these experiments have manipulated the diversity of a single trophic level and have probably not created conditions conducive to resource overexploitation.

The models I have discussed, however, do not imply that the relationships between biodiversity and ecosystem functioning should always be complex in nature. Mutual interference, intraguild predation, and spatial heterogeneity may dampen top-down effects of consumers on their resources and thereby reduce the potential for overexploitation. Trade-offs between species traits are ubiquitous and can strongly affect the impacts of biodiversity on ecosystem processes. For instance, trade-offs between a consumer's ability to exploit a wide range of prey species and its ability to exploit any particular prey efficiently are likely. Our models so far have also assumed a constrained trophic structure with a limited number of distinct trophic levels (plant, herbivore, and carnivore), but omnivory and ontogenetic diet shifts are also common in nature. The effects of all these factors deserve more thorough investigation based on empirical data to predict the expected relationships between biodiversity and ecosystem properties in different types of ecosystems.

One of the most robust properties of food webs and interaction webs is that species additions or deletions can trigger abrupt changes in the structure and functioning of ecosystems. Such abrupt changes occur, for instance, when an entire trophic level is added or removed, or when an inedible species is added or removed. In both cases, the nature of the factors that control the various trophic levels may change, with major effects on the allocation of energy, materials, and biomass among them. This property makes trophic and nontrophic species interactions an important source of surprises and uncertainty in a rapidly changing world.

It seems fair to say that theory has still barely scratched the surface of complex interaction webs. One of the main strengths of the mechanistic approach followed in this chapter is that it allows simple principles to be revealed based on the operation of a limited set of elementary processes. But its corresponding limitation is that it cannot explore the full range of the possible. In particular, I have considered only systems that are limited by a single nutrient, an assumption that severely constrains species coexistence

and ecosystem processes. It is my hope that the principles derived based on these constraints will help in understanding the properties of more complex ecosystems. But a more integrative approach that takes into account multiple limiting factors, multiple mechanisms of coexistence, and more realistic configurations of species interactions will be needed to fully account for the complexity and functioning of natural ecosystems. Merging the perspectives of food webs, nontrophic interaction webs, biodiversity, and ecosystem functioning remains an exciting challenge that is key to understanding and predicting future changes in natural and managed ecosystems and the services they provide to humans.

APPENDIX 4A EFFECTS OF VERTICAL DIVERSITY IN A FOOD CHAIN

The effects of vertical diversity on the biomass, production, and ecological efficiency of the various trophic levels at equilibrium in the model food chain described by equations (4.1)–(4.4) can be studied by comparing the equilibrium values provided in table 4.1 and using the feasibility and invasion conditions for the various trophic levels. This analysis assumes that all equilibria are feasible and stable, which requires that environmental fertility I be high enough to support the top trophic level but not too high to avoid consumer satiation and destabilization of the system.

1. ONE TROPHIC LEVEL ($N = 1$)

The persistence of the first trophic level ($B_{1(1)}^* > 0$) requires

$$B_{0(1)}^* < \frac{I}{m_0} = B_{0(0)}^* \quad (4A.1)$$

2. TWO TROPHIC LEVELS ($N = 2$)

Invasion by the second trophic level of a food chain with a single trophic level at equilibrium ($dB_2/dt > 0$ when $B_2 \approx 0$) requires

$$\begin{aligned} f_2(B_{1(1)}^*) - m_2 &> 0, \\ B_{1(1)}^* &> f_2^{-1}(m_2) = B_{1(2)}^* \end{aligned} \quad (4A.2)$$

g_2 (table 4.1) is a decreasing function of $B_{0(2)}^*$, hence its inverse, g_2^{-1} , which determines $B_{0(2)}^*$, is a decreasing function of $B_{1(2)}^*$. Therefore, because of inequality (4A.2),

$$B_{0(1)}^* < B_{0(2)}^* \quad (4A.3)$$

The persistence of the second trophic level ($B_{2(2)}^* > 0$) also requires

$$B_{0(2)}^* < \frac{I}{m_0} = B_{0(0)}^* \quad (4A.4)$$

Combining (4A.3) and (4A.4) yields

$$B_{0(1)}^* < B_{0(2)}^* < B_{0(0)}^* \quad (4A.5)$$

Based on the expressions for the ecological efficiencies at equilibrium (table 4.1), this inequality implies that

$$\lambda_{1(2)}^* < \lambda_{1(1)}^* \quad (4A.6)$$

Last, since Φ_1^* is proportional to λ_1^* [equation (4.5)], one also has

$$\Phi_{1(2)}^* < \Phi_{1(1)}^* \quad (4A.7)$$

Although the biomass, production, and ecological efficiency of the first trophic level all decrease upon addition of the second trophic level [inequalities (4A.2), (4A.6), and (4A.7)], it is easy to show that its production and ecological efficiency decrease less than does its biomass. Indeed, $\Phi_1 = f_1(B_0)B_1$ [equation (4.3)]. Since B_0 and B_1 vary in opposite directions, the production, and hence also the ecological efficiency, of the first trophic level vary less than does its biomass.

3. THREE TROPHIC LEVELS ($N = 3$)

An analysis based on the same principles can be performed when there are three trophic levels, ultimately leading to the full inequalities (4.6)–(4.11).

The only indeterminacy concerns secondary (herbivore) production. From equation (4.5),

$$\Phi_2 = I\lambda_1\lambda_2 \quad (4A.8)$$

Since λ_1 and λ_2 vary in opposite directions upon addition of the third trophic level, Φ_2 can potentially vary in both directions. Note, however, that at equilibrium λ_1 and λ_2 are simple functions of the mass of inorganic nutrient, B_0 , irrespective of the number of trophic levels. Thus, secondary production at equilibrium, Φ_2^* , is also a continuous function of B_0^* :

$$\Phi_2^* = \varepsilon_1\varepsilon_2(I - m_0B_0^*)\left[1 - \frac{m_1}{f_1(B_0^*)}\right] \quad (4A.9)$$

$$\frac{d\Phi_2^*}{dB_0^*} = \frac{\varepsilon_1\varepsilon_2}{f_1^2(B_0^*)}\{m_1f_1'(B_0^*)(I - m_0B_0^*) - m_0f_1(B_0^*)[f_1(B_0^*) - m_1]\} \quad (4A.10)$$

In this equation, the term $I - m_0B_0^*$ is positive and measures the net supply of inorganic nutrient available for consumption by the first trophic

level (chapter 1), while the term $f_1(B_0^*) - m_1$ is also positive and measures the net productivity of the first trophic level available for consumption by the second trophic level. Thus, the variation of Φ_2^* as a function of B_0^* depends on the relative magnitude of the consumption flows by the first two trophic levels. It also depends on the form of the functional response of the first (plant) trophic level as determined by f_1 and its derivative f_1' . If the ecosystem reaches an equilibrium such that B_0^* is sufficiently low and lies in the steeply ascending part of the plant functional response, Φ_2^* will tend to vary in the same direction as does B_0^* ; i.e., it will tend to decrease upon addition of the third trophic level. In contrast, if the ecosystem reaches an equilibrium such that B_0^* is sufficiently high and plant nutrient uptake is near saturation, $f_1'(B_0^*)$ will be close to zero, and Φ_2^* will vary in a direction opposite to B_0^* ; i.e., it will increase upon addition of the third trophic level.

4. WHOLE-ECOSYSTEM PROPERTIES

The dynamics of the total nutrient stock, $B_T = \sum_{i=0}^n B_i$, in the ecosystem is obtained simply by summing equations (4.1) across all trophic levels, yielding

$$\frac{dB_T}{dt} = I - \sum_{i=1}^n \left(\frac{1}{\varepsilon_i} - 1 \right) f_i(B_{i-1}) B_i - \sum_{i=0}^n m_i B_i. \quad (4A.11)$$

Assume first that all trophic levels have maximal production efficiencies, i.e., $\varepsilon_i = 1$. The second term on the right-hand side of equation (4A.11) is then zero. Solving this equation at equilibrium yields

$$\sum_{i=0}^n m_i B_i^* = I. \quad (4A.12)$$

The summation term on the left-hand side of this equation can be expressed in terms of the means and covariance of m_i and B_i^* across trophic levels. Therefore,

$$B_T^* = n \cdot \overline{B^*} = \frac{I}{\bar{m}} - \frac{n \cdot \text{cov}(m, B^*)}{\bar{m}}. \quad (4A.13)$$

When the mass-specific loss rates of all trophic levels are equal ($m_i = m$), the total nutrient stock is simply $B_T^* = I/m$, a constant that is independent of food-chain length. But in principle it can be larger or smaller than this constant when the mass-specific loss rates of the various trophic levels differ, depending on the sign of the covariance between m and B^* .

Now relax the unrealistic assumption that all trophic levels have maximal production efficiencies and let $\varepsilon_i < 1$. The second term on the right-hand side of equation (4A.11) then becomes negative. Using the same derivation as above, it is straightforward to see that the total nutrient stock at

equilibrium is then necessarily smaller than that provided by equation (4A.13) because of the additional negative term that has to be subtracted from the right-hand side of this equation. As a result, the total nutrient stock generally decreases as food-chain length increases (unless there is a large negative covariance between m and B^*).

Since total ecosystem biomass at equilibrium is simply $B_T^* - B_0^*$ and the inorganic nutrient stock B_0^* alternates between smaller and larger values depending on the number of trophic levels in the system, total ecosystem biomass is expected to show the same overall decreasing trend with food-chain length as does the total nutrient stock.

Total cumulative ecosystem production across all trophic levels at equilibrium, $\Phi_T^* = \sum_{i=1}^n \Phi_i^*$, can be obtained as follows. Since model (4.1) tracks nutrient stocks and flows and plants generally fully use the amount of limiting nutrient they take up, $\varepsilon_1 \approx 1$. Hence primary production $\Phi_1^* = I - m_0 B_0^*$, and the ecological efficiency of plants $\lambda_1^* = (I - m_0 B_0^*)/I$. Production at higher trophic levels is then readily obtained using equation (4.5). Summing production over all trophic levels yields

$$\Phi_T^* = (I - m_0 B_0^*) \left(1 + \lambda_2^* + \lambda_2^* \lambda_3^* + \dots + \prod_{i=2}^n \lambda_i^* \right). \quad (4A.14)$$

When the ecological efficiencies of all consumer trophic levels are equal, $\lambda_i^* = \lambda^*$, and food-chain length is large enough ($n \rightarrow \infty$), this equation simplifies to

$$\Phi_T^* = \frac{I - m_0 B_0^*}{1 - \lambda^*}. \quad (4A.15)$$

Since consumer ecological efficiencies are typically on the order of 2 percent to 10 percent, equations (4A.14) and (4A.15) show that total cumulative ecosystem production is expected to increase slightly overall as food-chain length increases. Variations in the inorganic nutrient stock, B_0^* , due to changes in top-down control, however, may override the production increments of the additional trophic levels.

APPENDIX 4B EFFECTS OF NUTRIENT ENRICHMENT IN A FOOD CHAIN

The effects of nutrient enrichment on the biomass, production, and ecological efficiency of the various trophic levels at equilibrium in the model food chain described by equations (4.1)–(4.4) can be studied by taking the derivative of the equilibrium values provided in table 4.1 with respect to environmental fertility I .

When the number of trophic levels $n = 0$ or 1, the results are straightforward and reported in table 4.2. When $n = 2$, the derivative of $B_{0(2)}^*$ with respect to I is obtained by implicit differentiation of the following equation derived from the dynamical equation for the inorganic nutrient at equilibrium:

$$I - m_0 B_{0(2)}^* - \frac{B_{1(2)}^* f_1(B_{0(2)}^*)}{\varepsilon_1} = 0, \quad (4B.1)$$

Since $B_{1(2)}^*$ is constant, implicit differentiation of this equation yields

$$\frac{dB_{0(2)}^*}{dI} = \frac{\varepsilon_1}{\varepsilon_1 m_0 + B_{1(2)}^* f_1'(B_{0(2)}^*)}, \quad (4B.2)$$

which is positive.

The sign of the variation of all the other variables follows immediately, except that of $\lambda_{1(2)}^*$, whose derivative is

$$\frac{d\lambda_{1(2)}^*}{dI} = \frac{\varepsilon_1 m_0 B_{1(2)}^* [B_{0(2)}^* f_1'(B_{0(2)}^*) - f_1(B_{0(2)}^*)]}{I^2 [B_{1(2)}^* f_1'(B_{0(2)}^*) + \varepsilon_1 m_0]}. \quad (4B.3)$$

The sign of $d\lambda_{1(2)}^*/dI$ depends on the form of the plant functional response, f_1 . If the plant functional response is linear, as in a Lotka-Volterra interaction (type 1), $f_1' = f_1/B_0$ and $d\lambda_{1(2)}^*/dI = 0$. If the plant functional response is concave down (type 2, or the second part of type 3), $f_1' < f_1/B_0$ and $d\lambda_{1(2)}^*/dI < 0$. If it is concave up (the first part of type 3), $f_1' > f_1/B_0$ and $d\lambda_{1(2)}^*/dI > 0$. Since plant functional responses are usually of type 2, $\lambda_{1(2)}^*$ is expected to decrease more often than increase after nutrient enrichment.

When $n = 3$, there is no explicit solution for the equilibrium biomasses of trophic levels 0, 1, and 3. A logical argument, however, allows us to conclude that $\Phi_{1(3)}^*$, $B_{1(3)}^*$, and $B_{3(3)}^*$ necessarily increase with I . If I increases, either $B_{0(3)}^*$ or $B_{1(3)}^*$ (or both) must increase to compensate for this increased nutrient input, and hence primary production, $\Phi_{1(3)}^*$, which is an increasing function of $B_{0(3)}^*$ and $B_{1(3)}^*$, must increase. This increased inflow at the first trophic level must in turn be balanced by an increase in the sum of the outflows, i.e., plant mortality and secondary production. Since $B_{2(3)}^*$ is top-down-controlled and stays constant, this implies that $B_{1(3)}^*$ increases. As a result, $B_{3(3)}^*$, which is positively related to $B_{1(3)}^*$, also increases.

The sign of the variation of $B_{0(3)}^*$ can be determined by implicit differentiation of the following equation derived from the dynamical equation for the first trophic level at equilibrium:

$$B_{1(3)}^* f_1(B_{0(3)}^*) - m_1 B_{1(3)}^* - \frac{B_{2(3)}^* f_2(B_{1(3)}^*)}{\varepsilon_2} = 0. \quad (4B.4)$$

Implicit differentiation of this equation yields, after some algebra,

$$\frac{dB_{0(3)}^*}{dI} = \frac{dB_{1(3)}^*}{dI} \left\{ \frac{B_{2(3)}^* [B_{1(3)}^* f_2'(B_{1(3)}^*) - f_2(B_{1(3)}^*)]}{\varepsilon_2 B_{1(3)}^* f_1'(B_{0(3)}^*)} \right\}. \quad (4B.5)$$

The sign of $dB_{0(3)}^*/dI$ depends on the form of the herbivore functional response, f_2 . If the herbivore functional response is linear (type 1), $f_2' = f_2/B_1$ and $dB_{0(3)}^*/dI = 0$. If it is concave down (type 2, or the second part of type 3), $dB_{0(3)}^*/dI$ has the opposite sign to $dB_{1(3)}^*/dI$ and hence is negative. If it is concave up (the first part of type 3), $dB_{0(3)}^*/dI$ has the same sign as $dB_{1(3)}^*/dI$ and hence is positive. Since herbivore functional responses are more likely to be concave down than concave up because of digestion limitations at high food availability, $B_{0(3)}^*$ is expected to decrease more often than increase after nutrient enrichment.

The sign of the variation of the other variables follows immediately from the above results.

APPENDIX 4C

ASSEMBLY RULE FOR TWO-LEVEL FOOD WEBS WITH SPECIALIST HERBIVORES

This appendix shows that the assembly rule depicted in figure 4.6 holds for the model food web described by equations (4.14).

In the case of a single food chain, this system is identical that studied in appendix 4A. Thus, for the food chain composed of plant 1 and herbivore 1, we have, from equation (4A.5),

$$B_{0(0,11)}^* < B_{0(0,11,21)}^* < B_{0(0)}^*. \quad (4C.1)$$

If plant 2 is added to this food chain without its specialist herbivore, it is limited only by the inorganic nutrient and hence eventually controls the inorganic nutrient stock at its own B_0^* value:

$$B_{0(0,1,21,12)}^* = f_{12}^{-1}(m_{12}) = B_{0(0,12)}^*. \quad (4C.2)$$

On the other hand, plant 1 is top-down-controlled by herbivore 1 just as in the simple food chain:

$$B_{11(0,11,21,12)}^* = f_{21}^{-1}(m_{21}) = B_{11(0,11,21)}^*, \quad (4C.3)$$

while herbivore 1 is bottom-up-controlled by the nutrient left over by plant 2:

$$B_{21(0,11,21,12)}^* = \frac{[f_{11}(B_{0(0,12)}^*) - m_{11}] \varepsilon_{21} B_{11(0,11,21)}^*}{m_{21}}. \quad (4C.4)$$

The persistence of herbivore 1 requires

$$\begin{aligned} f_{11}(B_{0(0,12)}^*) - m_{11} &> 0, \\ B_{0(0,12)}^* &> f_{11}^{-1}(m_{11}) = B_{0(0,11)}^*. \end{aligned} \quad (4C.5)$$

Whatever the food-web configuration, mass balance for the inorganic nutrient also imposes

$$m_0 B_0^* + \sum_j f_{1j}(B_0^*) B_{1j}^* / \varepsilon_{1j} = I. \quad (4C.6)$$

The left-hand side of this equation is a monotonic increasing function of B_0^* . Since plant 2 introduces an additional term in this function while B_{11}^* is unchanged compared with the system without plant 2 [equation (4C.3)], one necessarily has

$$B_{0(0,11,21,12)}^* < B_{0(0,11,21)}^*. \quad (4C.7)$$

Combining (4C.1), (4C.5), and (4C.7),

$$B_{0(0,11)}^* < B_{0(0,11,21,12)}^* = B_{0(0,12)}^* < B_{0(0,11,21)}^* < B_{0(0)}^*. \quad (4C.8)$$

If we now add herbivore 2 to this system comprising plant 1, herbivore 1, and plant 2, both plants are top-down-controlled by their specialist herbivore at the same level as in a simple food chain, and both herbivores are bottom-up-controlled by the inorganic nutrient:

$$B_{2(0,11,21,12,22)}^* = \frac{[f_{1j}(B_{0(0,11,21,12,22)}^*) - m_{1j}] \varepsilon_{2j} B_{1(0,1,2j)}^*}{m_{2j}}, \quad (4C.9)$$

which imposes

$$B_{0(0,11,21,12,22)}^* > f_{1j}^{-1}(m_{1j}) = B_{0(0,1j)}^* \quad (4C.10)$$

for both $j = 1$ and 2 .

Using again the mass-balance constraint (4C.6) and the fact that B_{11}^* is unchanged compared with the system with food chain 1, one also has

$$B_{0(0,11,21,12,22)}^* < B_{0(0,11,21)}^*. \quad (4C.11)$$

Combining (4C.8), (4C.10), and (4C.11), we finally get the multiple inequality depicted in figure 4.6.

Generalizing this inequality to more than two food chains is straightforward since the constraints that arise from herbivore persistence and mass balance remain the same. Thus, adding a third food chain requires that the equilibrium values of the inorganic nutrient stock with and without the third herbivore be comprised between the corresponding values for the system with two food chains, just as the second food chain requires them to be comprised between the corresponding values for a single food chain.

Stability and Complexity of Ecosystems: New Perspectives on an Old Debate

Research into the potential consequences of changes in biodiversity on ecosystem functioning and on the delivery of ecosystem services has been prominent in fostering cross-fertilization between community ecology and ecosystem ecology during the last decade. This research has shown that biodiversity loss can have adverse effects on the average rates of ecosystem processes such as primary production and nutrient retention in temperate grassland ecosystems (chapter 3). Most of the evidence for this conclusion, however, comes from relatively short-term theoretical and experimental studies under controlled conditions, which do not address the long-term sustainability of ecosystems. The last chapter (chapter 4) extended this body of theory to more complex food webs and interaction webs but focused again on their functioning under equilibrium conditions.

It is of considerable interest to further understand how biodiversity loss will affect long-term temporal patterns in ecosystem functioning. Will ecosystem functional properties and services become more variable and less predictable as species diversity is reduced? Are species-rich ecosystems more capable of buffering environmental variability and maintaining ecosystem processes within acceptable bounds than species-poor ecosystems? These are fundamental questions that have considerable implications for our ability to understand, predict, and manage ecosystems in a changing world. In this chapter I synthesize recent theory that seeks to answer these questions.

As a matter of fact, these questions address in a new form a long-standing debate in ecology about the relationship between the complexity and stability of ecological systems. The study of this relationship has had a long and controversial history (May 1973; Pimm 1984, 1991; McCann 2000). It is therefore useful to understand the ins and outs of this debate before attempting to provide fresh answers to these questions. Accordingly, I first briefly summarize the central components of this debate to identify