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CHAPTER FIVE

Autotrophic-Heterotrophic Interactions and Their Impacts on Biodiversity and Ecosystem Functioning

Shahid Naeem

The living world is, on the protoplasmic level, a single realm; but it is also the realm of immense diversity, of many lines of evolution and more than a million species.
—R. H. Whittaker, 1957

INTRODUCTION

Whittaker (1957) observed that at the most basic level, the biota can be considered a single protoplasmic realm. To transform a geochemical model of ecosystem functioning into a *bio*geochemical model requires adding this "protoplasm," whose metabolic processes modify geochemical processes. A logical starting point for a biogeochemical model is to add a photosynthetic protoplasm, a "green slime," that couples biotic with abiotic carbon cycling. Such a model becomes even more informative when nitrogen, carbon's intimate biogeochemical partner, is included. To treat the "immense diversity" that Whittaker refers to, however, requires additional steps. First, the green slime must be partitioned into trait groups or species clustered by biogeochemical traits. Such trait groups might reflect differences in rates of

nutrient uptake, water use efficiency, CO_2 assimilation, associations with N-fixing symbionts, or other functional characters (Chapin et al. 1996). Exploring the consequences of diversifying a green slime model is an important focus of this volume.

Diversified green-slime models, however, are depauperate representations of global protoplasm, and this chapter evaluates how we might improve biogeochemical models by the inclusion of heterotrophic diversity. Based on the fundamental ecological divisions of autotrophy and heterotrophy, Whittaker (1957) recognized that the global protoplasm was at the least made up of three major classes of species defined by three distinct nutritional modes. These modes were photosynthesis (Plantae), ingestion (Animalia), and absorption (Fungi). It is worth noting that the biological basis for Whittaker's divisions—photosynthetic, absorptive, and ingestive—is based on a fundamental distinction between organisms with and without cell walls. Whittaker lumped the unicellular creatures that exhibited all modes of nutrition into one evolutionary basal group, the Protista, a biotic grab bag that he and Lynn Margulis later divided into the Monera and Potoctista (Whittaker 1959; Whittaker and Margulis 1978). Green slime (i.e., plants and algae), however, represents only one-quarter of described species (Hamond 1992), a fraction that is probably inflated due to underrepresentation of invertebrates, fungi, nonphotosynthetic protists, prokaryotes, and viruses (Stork 1997). The other three-quarters of estimated global protoplasmic diversity consists of heterotrophic species. The exclusion of such a dominant fraction of the biota in a green-slime or producer-only biogeochemical model is likely to limit the utility and predictive power of such a model (this volume, chapter 11 by Holt and Loreau; chapter 12 by Balser, Kinzig, and Firestone).

Theoretical and empirical studies support strong roles for heterotrophs and autotroph–heterotroph interactions in ecosystem functioning. First, the bulk of the earth's biota

and the bulk of biogeochemical processes are driven by heterotrophic species, not autotrophs. Second, only decomposer heterotrophs, primarily species of Archaea, Bacteria, and Fungi, have the biochemical machinery to transform complex organic materials to inorganic forms (Fenchel, King, and Blackburn 1998). This organic–inorganic material transformation is a critical link in biogeochemical cycling without which dead organic materials would accumulate irrevocably (with the exception of slow, abiotic degradative processes, such as weathering or UV degradation) (Schlesinger 1997). Third, heterotrophs may regulate autotrophic biomass (Hairston, Smith, and Slobodkin 1960; Hairston and Hairston 1993; Oksanen, Power, and Oksanen 1995; Naeem and Li 1998). Fourth, heterotrophs regulate rates of cycling (Loreau 1995; Grover and Loreau 1996). And finally, heterotrophs may regulate system stability (De Angelis 1975; Pimm and Lawton 1977; Pimm 1982; De Angelis 1992; Lawler and Morin 1993; De Ruiter, Neutel, and Moore 1995). The roles of heterotrophs are clearly diverse, important, and well known.

FUNDAMENTALS

Some basic principles are reviewed in this section to clarify terminology and objectives of the chapter. This section further serves to provide the framework used for reviewing current evidence for the importance of heterotrophic diversity in ecosystem functioning.

Classes of Trophically Defined Functional Groups

The earth's biota is represented by four basic classes of functional groups. These four groups are based on the ways in which organisms acquire energy (transformation of light or chemical energy) and the forms of carbon they consume (organic or inorganic). This creates the 2 × 2 classification scheme that yields the four fundamental groups. Organisms

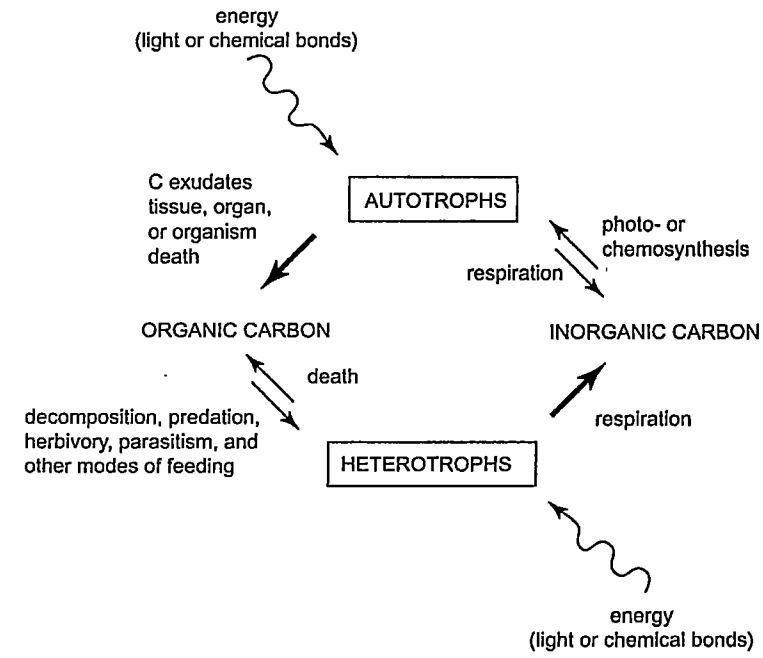

FIGURE 5.1. Fundamental trophic groups.

can be heterotrophs (consumers of organic C) or autotrophs (consumers of inorganic C), which either acquire energy from light (photoautotrophs and photoheterotrophs) or acquire energy from chemical sources (chemoautotrophs or chemoheterotrophs). Figure 5.1 illustrates these fundamental groupings. Of the four possible combinations, the dominant forms in most ecosystems are photoautotrophs (most plants and algae) and chemoheterotrophs (most protozoa, bacteria, fungi, and metazoa).

The value of such a simple classification scheme is that it reduces what may appear to be an intractable degree of trophic complexity typically seen in communities to a tractable set of major players in ecosystem processes. Here we will consider primarily photoautotrophs and chemoheterotrophs. Further classifications of chemoheterotrophs, how-

ever, is necessary for considering additional trophic levels. For simplicity, I will refer to photoautotrophs as *producers*; chemoheterotrophic absorptive, organic–inorganic matter transformers as *decomposers*; and chemoheterotrophic ingestive, organic–inorganic matter transformers as *consumers*. Several ecosystem processes are associated with each of these groups, including decomposition, immobilization, mineralization, production, nutrient uptake, and mortality.

Consumers themselves are conveniently divided into two major groups depending on the basal group from which they acquire their organic carbon sources. The term *basal* stems from the tradition of visualizing pyramids of biomass or pyramids of numbers with consumers at the pinnacle and producers at the base. A more useful representation, however, regards both producers and decomposers as basal groups. For example, a plant fed on by an herbivorous insect fed on by an insectivorous bird fed on by a bird-feeding hawk represents a producer-derived trophic chain of consumers. Decomposer bacteria fed on by bacterivorous nematodes fed on by nematophagous mites fed on by predatory mites represents a decomposer-derived trophic chain. Note that omnivores, or organisms that consume individuals from two or more trophic groups, though important (Diehl 1993), are often ignored to simplify analyses.

The Producer–Decomposer Codependency (PDC)

As basal groups, trophic structure necessarily begins with producers and decomposers, but these two groups are inextricably linked to one another. An important asymmetry, however, exists between these two groups. Organic carbon and organic nutrients are primarily transformed by decomposers while inorganic carbon and inorganic nutrients are transformed by producers, but decomposers can also use (immobilize) inorganic nutrients. This asymmetry leads to an antagonistic mutualism between producers and decomposers that compete for inorganic nutrients but otherwise

need each other (Harte and Kinzig 1993). (Producers have been observed to resorb carbohydrate exudates and nutrients (Killinbeck 1996), but this is currently considered to be a minor part of ecosystem functioning.)

FUNDAMENTAL TROPHIC STRUCTURE

From the above, we can derive the fundamental trophic structure of most ecosystems. At the core reside the producers and decomposers that are the principal drivers of material cycling. From this core emanate chains of consumers, one from the decomposers and the other from the producers. Linear chain length from this core tends to be short, seldom containing three or more groups (Pimm and Lawton 1977; Pimm 1982; Lawler and Morin 1993; Sterner, Bajpai, and Adams 1997). Minimal trophic structure therefore consists of producers and decomposers cycling material between inorganic and organic forms with lateral distributions of materials among consumers that contribute to organic and inorganic matter cycling (figure 5.2). In reality, a more reticulate arrangement (Polis and Strong 1996) or system of trophic guilds (Burns 1989) rather than linear structures might better represent nature. Additionally, omnivores are probably more common than appreciated in multitrophic models (Diehl 1993), but the structure portrayed in figure 5.2 can serve as a useful model for minimal trophic structure.

HETEROTROPHIC DIVERSITY AND ECOSYSTEM FUNCTIONING

Given how tightly the producer–decomposer codependency couples the basal groups in ecosystems, it should not be surprising that anything that impinges upon the performance of either group changes ecosystem processes. Consumers feeding on either group will almost certainly change

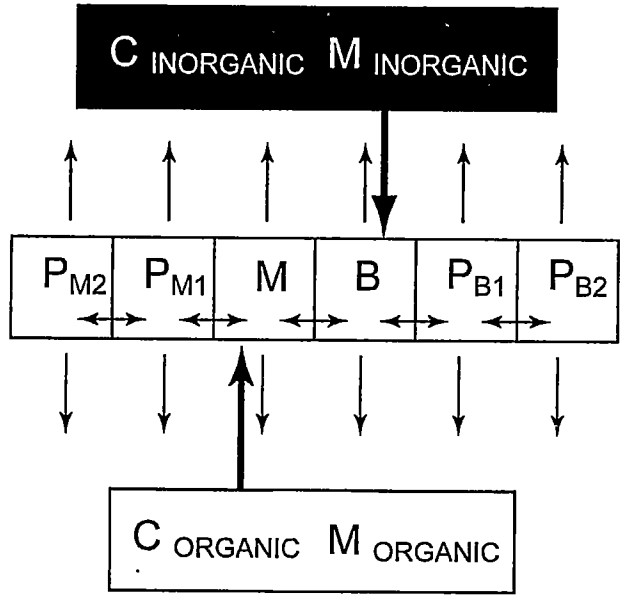

FIGURE 5.2. Fundamental trophic structure. C = carbon; M = microbial decomposers; B = producer biomass; P_{ij} = consumers, where i represents derived from either microbial decomposer biomass (M) or producer biomass (B) in the jth trophic level.

nutrient cycling rates or relative sizes of standing crop, but it is possible that the specific form of the relationship between producer diversity and ecosystem functioning (e.g., an asymptotic relationship) may not be affected by such impacts. A few recent studies, however, suggest that the producer–diversity relationship can be affected by the presence or absence of additional trophic levels. Here, I review several impacts of decomposers and consumers on producers.

Decomposers and Producers Affect Each Other via Carbon Exchange

Observational studies provide abundant evidence for linkages between decomposers and producers mediated by organic carbon exchange. Nonsymbiotic nitrogen fixation, for

example, is often enhanced by producers, presumably by providing the large quantities of energy needed by free-living nitrogen-fixing bacteria via organic carbon exudates (Sprent and Sprent 1990). Although difficult to measure precisely, organic carbon exudates of algae (Berman-Frank and Dubinsky 1999) or terrestrial plants (Wall and Moore 1999) support bacteria and fungi (Hobbie 1992). In aquatic systems such organic carbon exudates can have several effects, including protection from UV damage under high-light/low-nutrient conditions, increasing local concentrations of nutrients by sustaining local populations of bacteria, and protecting against viral infections (Berman-Frank and Dubinsky 1999). As mentioned earlier, however, decomposer absorption of inorganic nutrients lends a measure of antagonism to this seeming mutualism.

Harte and Kinzig (1993) have argued that decomposers control this antagonistic mutualism, but only a handful of ecosystems have been analyzed sufficiently to support their conclusions. Studies of interactions between algae and bacteria, for example, support both positive and negative interactions (Jones 1982). Irrespective of the nature of the interaction, empirical evidence supports a clear link between producers and decomposers via the exchange of organic carbon sources.

Consumers Affect the Biomass of Producers and Decomposers

Community ecologists studying heterotrophs concentrate much of their energies on consumers. Beginning with Hairston, Smith, and Slobodkin (1960), understanding the significance of trophic structure began by examining how trophic structure affects the distribution of biomass among trophic levels (Hairston, Smith, and Slobodkin 1960; Hairston and Hairston 1993). The shape of these distributions are seen as multimodal, virtually square-wave distributions, where biomass abundance along a trophic axis occupies two states. Either the basal group (generally photoautotrophs) and

every second group above it contain the bulk of the biomass ("green worlds") or the opposite is true ("barren worlds"). Long before Hairston, Smith, and Slobodkin, R. E. Lindeman (1942) pointed community ecologists to the fact that biomass distributions among trophic levels were driven by the dynamics of populations feeding upon one another, with a prominent role for the microbes ("ooze") in ecosystems, though his emphasis was on aquatic systems.

Lindeman may have been aware that his construct was a bit forced, because he recognized inconsistencies in his model (Burns 1989), but the tremendous appeal of discrete trophic groups, for their symmetry, heuristic value, and aesthetics, may have led him and contemporary ecologists to continue to favor strict trophic levels over more reticulate, much more realistic structures, such as Burns's (1989) trophic guilds.

Numerous studies have examined the impact of consumers, nutrients, and other factors on the distribution of biomass among trophic levels (Elliot et al. 1983; Liebold and Wilbur 1992; Abrams 1993; Carpenter and Kitchell 1993; Hairston and Hairston 1993; Carpenter et al. 1996). The continuing debate need not concern us here. The important point is that the number of trophic levels can affect the distribution of biomass among producers, decomposers, and consumers (Naeem and Li 1998).

Trophic Structure Influences Rates of Material Cycling

Food web or trophic models are frequently nonecosystem (e.g., Pimm 1982) in the sense that they do not consider nutrient flows. Instead, they focus on population dynamics of consumers and their prey. Such models, however, can be readily modified to accommodate the principles of nutrient cycling and nutrient dynamics (e.g., DeAngelis 1992). When nutrient cycling is included, the impact of consumers may modify rates of cycling (Loreau 1995), can increase local stability (DeAngelis 1992), and can buffer dynamics against

external inputs (Loreau 1994). The inclusion of decomposers can have different effects depending on whether models are donor controlled or Lotka-Volterra (Zheng, Bengtsson, and Ågren 1997). Experimental support of these compelling theories, however, is lacking.

Heterotrophic Diversity Affects Levels and Stability of Ecosystem Processes

Naeem and Li (1997, 1998) used microbial microcosms to explore the relationship between heterotrophic diversity and ecosystem functioning. Each microcosm in this study contained freshwater protist media, a single green algal species (*Chlamydomonas reinhardtii*) as the producer base, and at least three species of freshwater bacteria (*Serratia marcescens*, *Bacillus subtilis*, and *Bacillus cereus*), which served as decomposers. The only factor that varied was the composition of the consumer community, which consisted entirely of species of protists that fed either on the decomposers, the producers, or both (table 5.1). This study demonstrated that variation in consumer (omnivorous, autotrophic-, or decomposer-derived) species richness showed a strong, negative association with standing autotrophic biomass (figure 5.3). Three principles emerged from this study. First, autotrophic biomass declines in the presence of decomposers, possibly due to competition for nutrients between producers and decomposers. Second, bacterivores increase autotrophic biomass, possibly by suppressing bacteria. Third, consumers that do not feed on decomposers either directly decrease standing autotrophic biomass by herbivory or indirectly decrease standing autotrophic biomass by consuming bacterivores. This is a variation on the Hairston, Smith, Slobodkin theme.

In their second experiment, Naeem and Li (1997) demonstrated that the reliability of heterotrophic suppression of autotrophic biomass was dependent on how many heterotrophic species were found per functional group. The same

TABLE 5.1. Species Composition of Microbial Microcosms Used in Experiments

Species Richness	Bacterivores			Omnivores			Carnivores		
	CHIL	COLP	SPIR	PA	PC	PM	EUPL	APROT	CHAO
1	X								
1		X							
1							X		
1								X	
1									X
2	X			X					
2	X					X			
2		X					X		
2	X	X							
3	X			X		X			
3	X	X					X		
3	X			X					X
3	X					X			X
3	X			X				X	
3	X					X		X	
4	X	X		X		X			
4	X	X		X			X		
4	X	X				X	X		
4	X			X		X			X
5	X	X		X		X			X
5	X	X		X			X		X
5	X	X		X		X	X		
7	X	X	X	X		X	X	X	X

Notes: All microcosms contained *Chlamydomonas reinhardtii* (photoautotroph, unicellular alga), *Serratia marcescens*, *Bacillus subtilis*, and *Bacillus cereus* (decomposers, bacteria). Species are abbreviated as follows: Detritivores: CHIL = Chilomonas sp., COLP = *Colpidium* sp., SPIR = *Spirostomum* sp. Consumers of either autotrophs or detritivores or both (omnivores): PA = *Paramecium aurelia*, PC = *P. caudatum*, PM = *P. multimicronucleatum*. Predators of consumers: EUPL = *Euplotes* sp., APROT = *Amoeba proteus*, CHAO = *Chaos carolinensis*. Containers were sterile, disposable, polystyrene petri-dishes. Media consisted of sterile Carolina Biological Supply protozoan media and three sterilized wheat seeds.

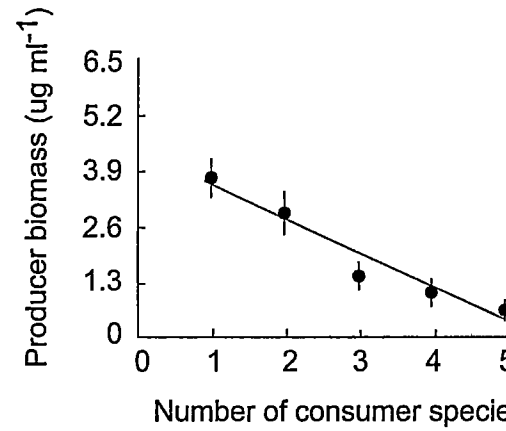

FIGURE 5.3. The relationship between consumer heterotrophic species richness and standing producer biomass. Circles represent means and error bars represent one SE of unicellular algal biomass measured in microbial microcosms. The number of heterotrophic species refers to the number of either decomposer-derived or producer-derived heterotrophic species of protists (flagellates or ciliates). This figure illustrates that increases in consumer protistan diversity, here measured as species richness, can reduce standing algal biomass in a predictable manner to very low levels. See Naeem and Li (1998) for details. After (Naeem and Li 1998).

microcosm design was employed, but the number of functional groups and number of species per functional group was varied systematically. The number of trophically defined functional groups varied from a minimum of two (bacteria and algae) to a maximum of five (bacteria, algae, bacterivorous protists, omnivorous protists, and carnivorous protists). The number of species per functional group (except for carnivorous protists, where maintaining a third species within the microcosm was not possible) varied from one to three. Local extinction occurred in most microcosms, ensuring that replacement by substitutable species within functional groups could occur. The experiment was replicated at two different light levels and two to three different nutrient levels to provide a more robust test of the patterns observed.

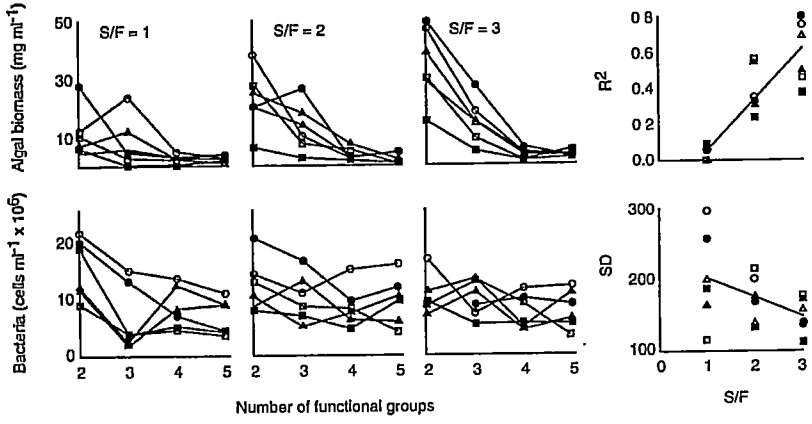

FIGURE 5.4. The pattern of production is affected by the number of species per trophically defined functional group of protistan consumer species. Top, left: Algal production (biovolume) at the end of the experiment as a function of functional group richness. Top, right: The R^2 of linear regressions of $\log_{10}$ (algal production) against numbers of protistan species per trophically defined functional group in microbial microcosms. This figure shows that predictability of algal production increases sharply as numbers of species (S) per functional group (F) increases. Note decline in production is a function of functional group richness, which is similar to results obtained in earlier experiments (figure 5.3). Bottom, left: Bacterial biomass at the end of the experiment as a function of number of functional groups in microcosm. Bottom, right: The standard deviation of microbial production plotted against species per functional group. This figure shows that bacterial production varies less, or is more predictable, when S/F increases. Open symbols are high-light replicates while closed symbols are low-light. Circles are full-strength media, triangles are half-strength, and squares are one-quarter nutrients. Each symbol represents the mean of four replicates. After Naeem and Li (1997).

The same decline in producer biomass with increasing trophic diversity was observed in this study as in the earlier experiment (figure 5.3), but the more species per functional group, the more predictable the response (figure 5.4). This experiment provided general support for the principle of ecosystem reliability (Naeem 1998; Rastetter et al. 1999). A similar multitrophic-level study (McGrady-Steed, Harris, and Morin 1997), which did not directly manipulate

trophic structure but examined ecosystem functioning more closely, found that both resistance to invasion and ecosystem predictability increased with increasing diversity.

Like decomposers, consumer species richness may also influence consumer biomass, but this possibility is relatively unexplored. To my knowledge, the only explicit manipulation of consumer diversity is Norberg's (2000) study, which directly manipulated cladoceran, zooplankton species richness and demonstrated an idiosyncratic response of zooplankton biomass to species richness. This study was a microcosm study and had fewer than four species (Norberg 2000), but it does suggest that consumer diversity may affect consumer biomass.

Heterotrophs Modulate Producer Diversity Effects

Recent studies of producer diversity have shown that diversity and production are positively associated with a number of ecosystem processes (Naeem et al. 1994; Naeem et al. 1995; Naeem et al. 1996; Tilman et al. 1996; Hooper and Vitousek 1997; Tilman et al. 1997; Tilman, Lehman, and Thomson 1997; Hooper 1998; Hooper and Vitousek 1998). Such studies argue for a role of biodiversity in biogeochemical processes even though only one study. (Naeem et al. 1994) manipulated the diversity of more than one trophic level. Recent evidence is accumulating, however, that heterotrophs interact with producers and modify the impacts of variation of producer diversity on ecosystem processes. For example, both mycorrhizal fungal diversity (Van der Heijden et al. 1998) (figure 5.5A) and insects (Mulder et al. 1999) modify producer diversity effects on ecosystem production (figure 5.5D). CO_2 flux, a product of producer, decomposer, and consumer metabolic activities, showed a positive relationship to microbial species diversity in freshwater microcosms (figure 5.5B). Finally, variation in producer diversity that did not yield aboveground responses did exhibit microbial responses, such as a positive relationship between

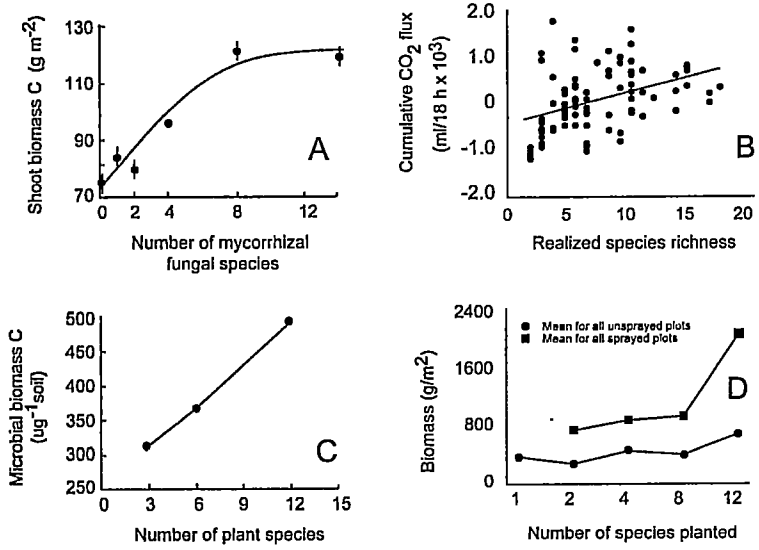

FIGURE 5.5. Examples of how heterotrophs interact with producer diversity. After (A) McGrady-Steed, Harris, and Morin 1997; (B) Chapin et al. 1998; (C) Van der Heijden et al. 1998; (D) Mulder et al. 1999.

microbial biomass (most likely entirely due to decomposer microbes) and plant species richness (Chapin et al. 1998) (figure 5.5C).

The most complex effects are shown in a recent freshwater microbial microcosm study (Naeem, Hahn, and Schuurman 2000), where varying decomposer diversity (bacterial species richness) and varying producer diversity (algal species richness) were both shown to affect producer and decomposer biomass production (figure 5.6). That is, both the main effects (producer and decomposer diversity) and the interaction between the two were significant using a two-way ANOVA ($P < 0.05$) (Naeem, Hahn, and Schuurman 2000). More importantly, variation in decomposer diversity nearly doubled (1.82 times) the range of producer biomass observed in microcosms where only producer diversity was varied. These studies suggest that variation in producer diversity by itself is insufficient to account for variation in pro-

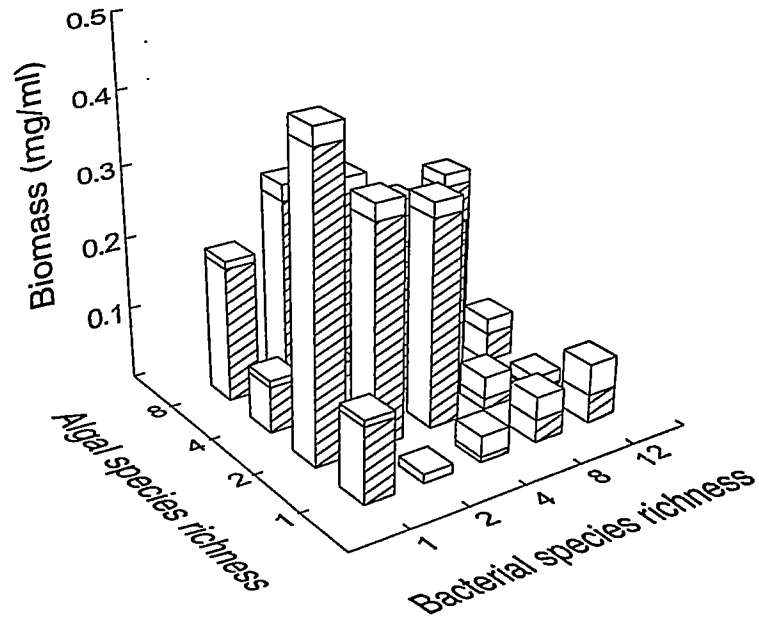

FIGURE 5.6. The relationship between biomass production and simultaneous variation in producer and decomposer diversity. Boxed top portions of columns represent bacterial (decomposer) biomass while lower portions represent algal (producer) biomass in 50 ml freshwater microbial microcosms after four weeks. After Naeem, Hahn, and Schuurman 2000.

duction due to biodiversity loss. Decomposer and consumer diversity, and the *interaction* between these and producer diversity, may generate differences in ecosystem processes.

Summary of Empirical Findings

From the above, the best-documented impacts of heterotrophs on producer-driven biogeochemical processes concern the interactions between decomposers and producers and the impacts of trophic chains on these basal trophic groups. The theoretical and empirical studies surveyed above, though an eclectic and scant assemblage of studies, point to a variety of possible effects that heterotrophs may

have on producer-driven processes. These effects provide motivation for modifying the basic producer-only model that is the focus of this book. They also provide some hints of what sorts of effects one might expect. These include much greater variation in model predictions of producer biomass and ecosystem processes tied to autotrophic production and decomposition rates due to a variety of simple effects (e.g., competition between decomposers and producers for inorganic nutrients) to complex effects (e.g., interactions between variation in producer and decomposer diversity). The next section offers some suggestions for multitrophic-level model development.

IMPLICATIONS FOR AUTOTROPH-ONLY MODELS

Useful autotroph–heterotroph model development requires extracting the fundamental, common set of features typical of multitrophic systems from the mountain of detail concerning the various ways heterotrophic species affect producers. From the brief review of trophic groups above, the simplest yet most realistic model would contain the following universal elements:

1. photoautotrophs (producers)
2. decomposers
3. a two-link chain of decomposer-derived consumers
4. a two-link chain of producer-derived consumers

The basic model used in this volume (presented in chapter 8) simplifies the treatment of material by tracking only C, N, and H_2O (W) as these materials are cycled among the organic and inorganic pools. C is compartmentalized into refractory (fast) and recalcitrant (slow) fractions. The inclusion of heterotrophic effects would minimally require the inclusion of decomposers and consumers. This would partition the living biomass into several compartments, each of

which needs to account for N and C cycling and water effects on growth.

Decomposers

The simplest approach to incorporating decomposers is to redefine decomposition rates in terms of microbial processes and minimally treat decomposer diversity as two "species" of decomposers. In the common ecosystem model, this is accomplished by assuming that each plant produces at least two classes (fast and slow) of organic C, the C:N ratio being the critical determinant of rate of decomposition of either class. Decomposers could be minimally divided into two groups, one group would be those that specialize on recalcitrant organic material but at a cost to growth, while the second group makes use of the labile fraction with higher growth rates, which is done in chapter 12 (Balser, Kinzig, and Firestone). From the principle of producer–decomposer codependency, we assume microbes are primarily carbon limited.

Trophic Levels

Two trophic levels should be added to each basal group. Herbivores (P_{B1}) and carnivores (P_{B2}) feed on plants while bacterivores (P_{M1}) and predators of bacterivores (P_{M2}) are added (figure 5.2). To consider the impact of trophic groups on microbes we can assume that both forms of microbial decomposers are edible and have the same C:N ratio. This is accomplished by different rates of metabolic loss of C, where M_s respires more C. Herbivores are considered in chapter 11 (Holt and Loreau).

Material Pools

The inclusion of two specialist classes of microbial decomposers (above) requires a specific treatment of N as two classes of compounds. The common ecosystem model approach used in this volume divides N into two forms: N_f

associated with organic matter that decomposes quickly and N_s associated with organic matter that decomposes slowly. Ultimately both forms accumulate in the inorganic N pool by mineralization. One problematic twist is that microbes can convert inorganic N into microbial biomass (immobilization), a factor that is regulated by C availability.

Nitrogen is complicated. In addition to terms for deposition and leaching in the basic model, we need to add terms that reflect the contributions by mineralization from consumers and decomposers. The consumer terms are readily added by assuming that respiration is related to mineralization. Additional modifications involve the inclusion of decomposer immobilization of inorganic N and the replacement of rates of decomposition by decomposer conversion, as with C. Thus, N would be a function of gain due to deposition, loss due to leaching, loss due to plant uptake, gain due to heterotrophic mineralization, and loss due to immobilization. Loss due to denitrification is minimal, but for wet, anaerobic soils, tracking loss by this route would be important. Balser, Kinzig, and Firestone (chapter 12) employ this approach in their analyses.

DISCUSSION

Two common perspectives among modelers is to either consider heterotrophic diversity as fat on the autotrophic backbone of ecosystems or, in sharp contrast, consider autotrophs as merely fodder for ecosystem processes conducted primarily by heterotrophs. Neither perspective works well because autotrophs and heterotrophs are mutually codependent (Harte and Kinzig 1993; Naeem, Hahn, and Schuurman 2000). Levels, dynamics, and the stability properties of ecosystem functioning are governed by both autotrophic diversity and heterotrophic diversity, as well as the complex interactions between the two.

Trophic differences among species represent the basis for

evolutionary divergence among the plants, fungi, animals, and microbes, so it should be no surprise that ecosystems are strongly affected in different ways by such different species. These groups, defined by different modes of nutrition, are biologically distinct (e.g., possess or lack cell walls, can or cannot produce specific exo- or endoenzymes) and are not substitutable.

From this survey of empirical studies, several principles emerge. First, decomposers are locked in an "antagonistic mutualistic" relationship with producers (Harte and Kinzig 1993), which leads to inseparable responses of these groups to environmental variation. Second, consumers affect rates of movement of materials among different pools (Loreau 1995; Grover and Loreau 1996). Third, consumers determine the distribution of biomass among trophic groups (Hairston, Smith, and Slobodkin 1960; Del Giorgio and Gasol 1995; Naeem and Li 1998). Fourth, stability and reliability, both of systems and populations, are affected by trophic structure and numbers of species within trophic groups (Pimm and Lawton 1977; Lawler and Morin 1993; McGrady-Steed, Harris, and Morin 1997; Sterner, Bajpai, and Adams 1997). Finally, interactions may exist between diversity at one level and diversity at another (Fig. 5:6) (Harte and Kinzig 1993; Naeem, Hahn, and Schuurman 2000).

Theoretical and empirical evidence suggest some possible outcomes of such an autotroph–heterotroph model. First, the addition of trophic groups most likely enhances overall rates of cycling by increasing flows of biomass to the dead organic pool and increasing rates of mineralization. These enhanced rates will be accompanied by lower standing crops of autotrophic and decomposer biomass, but higher rates of biogeochemical processes. Whether or not this enhancement of rates will translate into differences in the biodiversity–ecosystem functioning relationship remains to be seen.

Second, given the biogeochemical linkages among tro-

phic groups, the impacts of varying producer diversity on ecosystem functions, such as enhanced production and nutrient drawdown (Naeem et al. 1994; Naeem et al. 1995; Naeem et al. 1996; Tilman, Wedin, and Knops 1996; Hooper and Vitousek 1997; Tilman et al. 1997; Tilman, Lehman, and Thomson 1997; Hooper 1998; Hooper and Vitousek 1998), are likely to have feedbacks through other trophic levels. The mechanistic basis for these feedbacks is likely to be the exchange of organic carbon between producers and decomposers.

Third, variation in diversity in one trophic level is likely to modulate the impacts of variation in another trophic level. For example, if increasing producer diversity increases the efficiency of light, water, and nutrient exploitation in a limited space, then increasing decomposer diversity may lead to similar increases in trophic exploitation of resources. Increases in decomposer diversity and producer diversity would intensify the competition for and reduce the standing level of inorganic nutrients.

It is important to note that there is little question that decomposers and consumers are important in regulating ecosystem functioning, but the importance of biodiversity within these groups, the focus of this chapter, is much more difficult to assess. One possibility is that decomposer communities are less sensitive to variation in their biodiversity compared to variation in producer and consumer biodiversity. Exoenzymatic capabilities are widespread among microbial taxa in decomposer communities, and mutation and gene exchange, coupled with high reproductive rates and large population sizes, suggests that biodiversity loss may not correlate strongly with loss of functional diversity. Functional capabilities may be widespread among taxa or may return quickly even if lost due to habitat destruction. It is possible that recovery is much faster in decomposer than producer and consumer communities because microbes typically exhibit order-of-magnitude higher rates of ecological

and evolutionary processes. Freshwater and marine systems driven by microbial producers as well as microbial decomposers may set these ecosystems apart from metaphytan-driven terrestrial ecosystems. For this reason, focusing on consumers may prove more valuable for predicting ecosystem response to biodiversity loss.

The inclusion of trophic groups in biodiversity–ecosystem function studies has begun, but this area of research clearly needs expansion. Both current experimental research and theory (Balser, Kinzig, and Firestone, chapter 12; Holt and Loreau, chapter 11) support potential roles for heterotrophs in modifying biodiversity–functioning relationships, but the role of heterotrophic diversity itself is still unclear. What are the roles of decomposer diversity? What are the roles of autotrophically derived consumers? What are the roles of decomposer-derived consumers? What is the role of trophic structure either in decomposer or autotrophic-derived food chains? Finally, what are the interactions among these factors? The promise of insights into these and other issues strongly encourages multitrophic approaches to understanding the ecological consequences of changing patterns in biodiversity.

Biodiversity experiments that manipulate plant diversity are difficult, and simultaneously manipulating heterotrophs and producers makes this already difficult line of ecological research even more difficult. Perhaps the most straightforward approach is a "brute-force" simultaneous manipulation of plant, insect, and microbial diversity in a well-replicated series of experimental plots. Such an experiment would require several hundred replicates for examining functional group richness and perhaps thousands of replicates for examining species richness within both autotrophic and heterotrophic functional groups. Though inelegant, it would provide answers to the questions raised above.

There are, however, more focused and tractable experiments one could conduct. For example, field experiments

that manipulate functional group richness of heterotrophic diversity on simple autotrophic communities, such as guilds of specialist insect herbivores on single, clonal host species, may prove valuable as a starting point. One could test whether autotrophic production is affected by the number of functional groups (e.g., sucking insects, chewing insects, predatory, parasitoid, or other trophically defined groups) or the number of species per functional group. The sampling effect, heterotrophic niche complementarity, and tests of stability and reliability of mineralization, community respiration, or biomass production (heterotrophic or autotrophic) could be measured as response variables in such experiments.

Decomposer communities are more difficult to manipulate under field conditions, but soil could either be partially sterilized by varying amounts of chloroform fumigation, selective bactericides and fungicides, or microwave treatment. Alternatively, completely sterilized soil could be reinoculated with live soil plugs from different habitats (high-diversity treatment) or single habitats (low-diversity). Quantification of microbial diversity could be accomplished by a variety of methods (Zelles et al. 1995; Borneman and Triplett 1998; Torsvik et al. 1998) to ensure that treatments were effective. Bacterivorous and fungivorous microarthropod communities may be similarly manipulated by use of fauna-infected litter or soil plugs placed in sterilized soil.

Uncovering interactions between diversity at one trophic level and diversity at another level can follow the design we employed in our microbial microcosm research (Naeem, Hahn, and Schuurman 2000), but this is not an elegant solution. A more effective solution might be to partition trophic manipulations to better explore the linkages. For example, establishing plant communities at different diversity levels in sterilized soil that had been previously maintained at different levels of decomposer diversity would provide a way to isolate decomposer diversity effects from autotrophic

diversity effects. Such "conditioned" soil would exhibit the effects of carbon-depleted decomposer communities on nutrient pools. Theoretically, the most diverse communities would have exhausted the most diverse set of carbon sources, thereby leading to larger inorganic nutrient pools than might be found in soils that had depauperate decomposer communities. Plants would respond favorably to soil that had been exposed to high-diversity decomposer communities, and higher-diversity plant communities may respond even more favorably by exhibiting higher production.

Conceptually, constructing effective experimental designs is not difficult, but logistically, due to the combinatoric explosion of necessary replicates to explore variation in even modest amounts of diversity, multitrophic biodiversity–functioning experiments are likely to require larger scale efforts than ecology has traditionally employed in field experiments. Microcosm and mesocosm experiments are ready solutions, but field experiments are necessary as robust tests of microcosm findings. Elegant solutions to the logistic problems of multitrophic diversity–functioning experiments may emerge from theoretical explorations such as those by Balser, Kinzig, and Firestone (chapter 12) and Holt and Loreau (chapter 11). Perhaps, as this volume suggests, theory may provide focus and testable hypotheses for empirical study.