

## CHAPTER 1

# Introduction

Imagine a world in which all primary producers have exactly the same chemistry. In this world, all autotrophs are equally palatable to herbivores, decompose at equal rates, and do not respond phenotypically to changes in the biotic and abiotic environment. There is no evolutionary change in plant chemical traits because there is no heritable variation upon which natural selection can act. Succession after disturbance is characterized only by the accumulation of equally palatable plant biomass. Algal blooms in lakes and oceans represent changes in the quantity, but not quality, of primary production. Our current vegetation-based classification of Earth's biomes is redundant.

The full ecological and evolutionary consequences of living in such a world are hard to imagine in part because we take for granted the enormous chemical variation that exists among the primary producers on Earth. Perhaps we are so familiar with the different autotrophs that characterize our forests, grasslands, and rocky intertidal zones, with the varying palatability of the species we can and cannot eat, that we are desensitized to the profound importance of that variation. As ecologists and evolutionary biologists, we encounter two major (and related) problems when we ignore the importance of variation in the chemistry of primary producers. First, our understanding of ecological and evolutionary processes is incomplete at best and misleading at worst. Second, we will be unable to predict the consequences of losing variation in plant chemical traits from our ecological communities. As human activities cause us to lose members of autotroph communities to extinction, we lose so much more than just scientific names. We lose the phenotypic variation that characterizes those scientific names, and their associated ecological and evolutionary interactions. We simplify the phytochemical landscape.

In this book, I describe how variation in the chemical traits of primary producers is of fundamental importance in ecology, and how that variation can be used as an organizing force for synthesis. Specifically, by focusing on variation in autotroph chemistry on the phytochemical landscape, we can better link studies of trophic interactions to those of ecosystem processes. Autotroph chemistry influences, and is influenced by, nutrient dynamics at the ecosystem level.

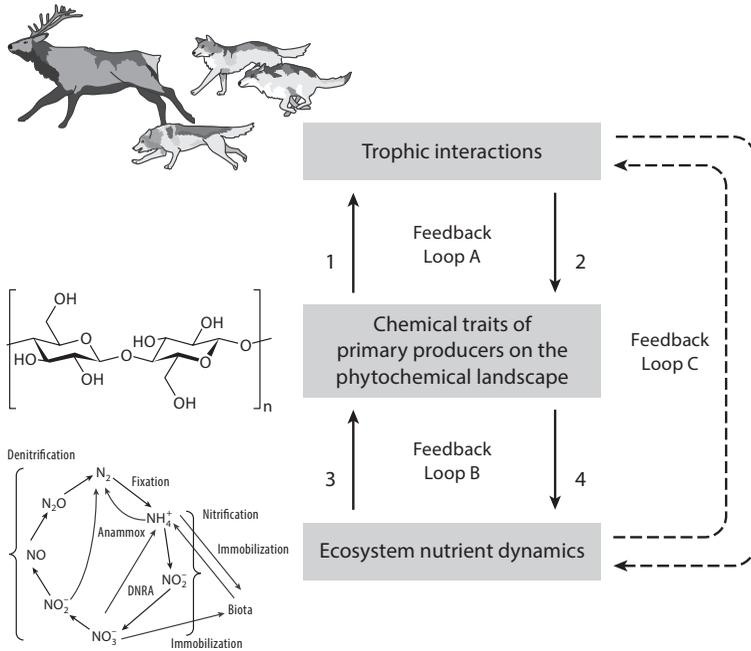


FIGURE 1.1. Links between trophic interactions and nutrient dynamics are mediated by variation in the chemical traits of primary producers on the phytochemical landscape. Trophic interactions such as herbivory and predation vary with the chemical traits of autotrophs (arrow 1). In turn, trophic interactions modify autotroph chemistry (arrow 2) establishing a feedback loop (loop A) between trophic interactions and the chemistry of primary producers. Similarly, nutrient dynamics in the environment influence the chemical traits of autotrophs (arrow 3), which in turn influence the recycling of nutrients (arrow 4), establishing a feedback loop (loop B) between nutrient dynamics and autotroph chemistry. In combination, loops A and B generate a larger feedback loop (loop C) linking trophic interactions with nutrient dynamics through variation on the phytochemical landscape.

Similarly, autotroph chemistry influences, and is influenced by, trophic interactions among organisms. The result is a series of feedback loops that link trophic interactions with the cycling of matter, mediated through the nexus of variation in autotroph chemistry on the phytochemical landscape (figure 1.1). These feedback loops represent powerful trait-mediated indirect effects (Werner and Peacor 2003) in which the chemical traits of primary producers link trophic interactions with nutrient cycling. In chapter 2, I introduce in more detail the concept of the phytochemical landscape, while in chapter 3 I describe the diversity of phytochemistry that exists in our ecological systems. In subsequent chapters (chapters 4–7), I provide evidence to support the importance of each of the feedback

loops illustrated in figure 1.1. In chapter 8, I bring the individual feedback loops together into a synthetic whole. Finally, in chapter 9, I discuss priorities for future work and provide some testable predictions that arise from using the concept of the phytochemical landscape to understand the links between trophic interactions and nutrient dynamics.

## 1.1 A MATTER OF PERSPECTIVE

I doubt that there is a single best way to describe an ecological system. As scientists, we carry our experience, our skill sets, and our biases with us as we try to understand the ecological world. We also target our favorite research questions, which naturally influence the perspective that we take when we try to understand the world around us. Because of these diverse experiences, skill sets, biases, and questions, there are many complementary ways in which we can search for pattern and synthesis in ecology (Sternler and Elser 2002, Brown et al. 2004, Schmitz 2008b, Bardgett and Wardle 2010, Loreau 2010, McCann 2011, Cavender-Bares et al. 2012). I mention this explicitly because the approach that I offer here is one among many ways of seeking synthesis in ecology—it arises from my experience and my biases; it's a matter of perspective. My hope is that there is some strength in this perspective, an opportunity for insight that emerges specifically because of the approach that I describe. Other approaches, other perspectives, will offer their own unique insights into ecological processes. I view these varying perspectives as complementary, and not as alternatives. Moreover, figure 1.1 is meant to illustrate how trophic interactions and nutrient dynamics are linked through the nexus of autotroph chemistry. I do not mean to suggest that these feedback processes are the only factors influencing trophic interactions, the chemistry of primary production, and nutrient cycling. Many edaphic, climatic, and biological forces affect the components of figure 1.1, and can act as external influences on the feedback loops that are the focus of this book. These are discussed in chapter 9.

I also want to stress that this book is not about the primacy of plants. I am not suggesting that variation in the chemistry of primary producers in some way “drives” all of the ecological and evolutionary processes on Earth. Indeed, it is absolutely central to the arguments I present here that autotroph chemistry varies in direct response to nutrient dynamics at the ecosystem scale, and varies in response to trophic interactions. It is now abundantly clear that processes such as trophic cascades (Carpenter et al. 1985) (figure 1.1, arrow 2) and soil nitrogen flux (Aber et al. 1989) (figure 1.1, arrow 3) generate variation in the chemical traits of primary producers at landscape scales. These traits then feed back to influence

species interactions and nutrient cycling (figure 1.1, arrows 1 and 4, respectively). Autotrophs are central only in the sense that variation in their chemical traits provides a nexus through which links between trophic interactions and nutrient cycling can take place. Specifically, in no sense am I suggesting that primary producers are more important than herbivores, predators, mutualists, or decomposers in the organization of ecological communities. Rather, I'm suggesting that to understand fully the role of trophic interactions in natural systems, we need to understand how differential consumption generates, and is generated by, variation in the chemistry of primary production.

## 1.2 THE NATURE OF FEEDBACK

Similarly, this is not a book about the relative importance of top-down and bottom-up forces in ecology. Rather, it is a book about feedback processes. Feedback loops play a central role in ecology at all levels of organization (Odum 1953, Royama 1992) and make irrelevant many arguments about primacy. Figure 1.2A shows an extreme example of a perfectly coupled system in which Consumer B consumes only Producer A. The dynamics of B are driven entirely from the bottom up, and the dynamics of A are driven entirely from the top down. The interaction as a whole cannot be characterized as bottom-up or top-down in any meaningful way. Figure 1.2B extends this to a system in which a variable plant trait (nitrogen content) varies in response to both herbivore damage and environmental nitrogen availability. The presence of feedback loops makes it impossible to characterize any part of the system as driven from the top down or the bottom up.

Why does this approach have merit? As the chemical traits of autotrophs respond to both nutrient cycling and trophic interactions, they establish pathways by which unexpected indirect effects emerge (Hunter et al. 2012). For example, figure 1.2C illustrates a pathway by which spatial patterns of environmental nitrogen availability could influence the dynamics between an herbivore host and its agent of disease. Likewise, disease dynamics between host and parasite may feed back to influence the spatial and temporal availability of nutrients in the environment. As disease ecologists learn more about the contingent nature of parasite-host interactions (Duffy et al. 2012, Orlofske et al. 2012), interactions between nutrient dynamics and agents of disease are starting to appear in the literature (Civitello et al. 2013, Lehahn et al. 2014). These kinds of indirect effects, which are experimentally tractable, can be predicted using the perspective shown in figure 1.1.

Feedback loops have other important properties. In the presence of the time lags inherent in ecological systems, feedback loops can generate complex temporal

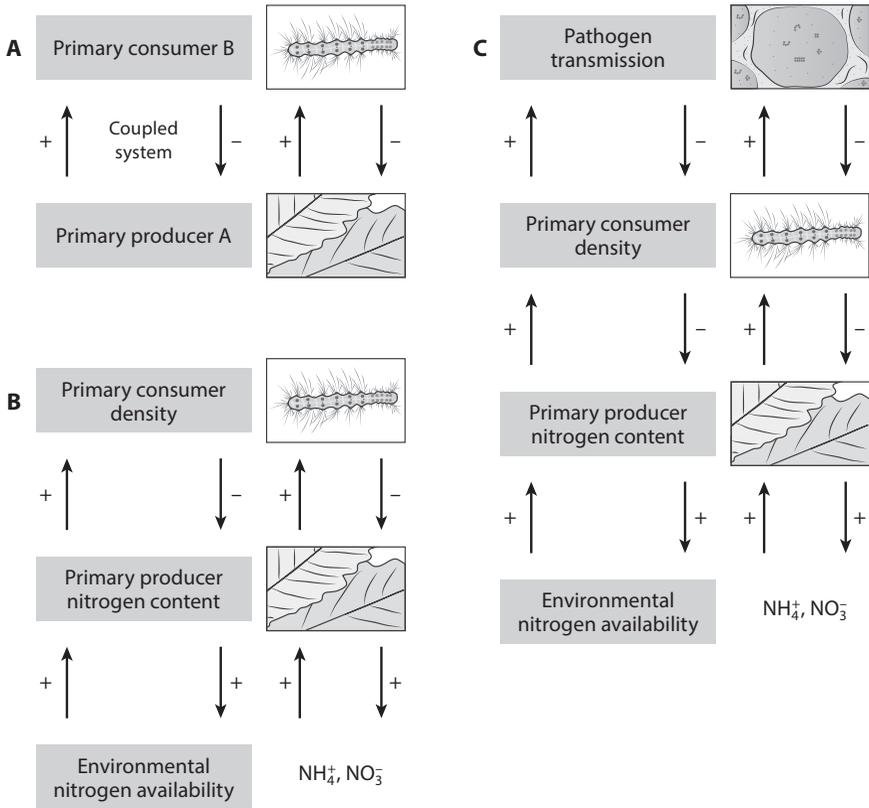


FIGURE 1.2. Bottom-up and top-down forces combine to determine the dynamics of ecological systems. In the simplest 2-level models (A), primary consumer density depends entirely on primary producer density, and vice versa. Extending this to the links between trophic interactions and nutrient dynamics illustrates how primary consumers might reduce the availability of inorganic N (e.g. ammonium  $\text{NH}_4^+$  and nitrate  $\text{NO}_3^-$ ) in ecosystems, while N availability simultaneously feeds back to increase the density of primary consumers (B). Note that variation in both consumer density and N availability may be constrained by the overall negative feedback operating between them (multiply the signs on the arrows to determine the overall effect). Adding complexity (C), it becomes apparent how organisms like pathogens both influence, and are influenced by, the availability of nutrients in ecosystems.

dynamics (May 1974). Ecologists still struggle to explain much of the temporal variation in species abundances and ecological processes that we observe in nature. But we should expect temporal variation to emerge in systems such as those illustrated by figure 1.2C. Critically, time lags in the responses of primary producer chemistry to trophic interactions or nutrient dynamics could generate complex temporal dynamics, including cycles and deterministic chaos (Royama

1992). It is a fundamental feature of many phytochemical traits that they are plastic, changing markedly in response to interactions with the biotic and abiotic environment. The timescales of such changes vary from a few seconds to years within individual autotrophs (Liechti and Farmer 2002), and to millennia within whole terrestrial plant communities (Petit et al. 1997). It is a prediction of the perspective described here that temporal variation in trophic interactions and ecosystem processes emerges in part from (a) feedback loops that include variation in autotroph chemistry, and (b) time lags in the responses of autotroph chemistry to abiotic and biotic interactions.

### 1.3 WHICH AUTOTROPHS AND WHICH TRAITS?

For simplicity, I use some shorthand throughout this book. I use the word “plant” or “autotroph” to include all primary producers, including autotrophic bacteria and archaea, and autotrophic members of the paraphyletic Protista (including diatoms, dinoflagellates, chlorarachniophytes, euglenids, brown algae, and the members of the Plantae that are not characterized as land plants). That being said, the ecological importance of variation in their chemical traits is much better known for some groups (e.g., land plants, cyanobacteria) than for others; the better-known groups will necessarily provide many of the examples in the book. Although the great majority of ecological processes presented here operate in both terrestrial and aquatic environments (chapter 9), there are some specific to each. I discuss relevant differences between terrestrial and aquatic habitats as they arise in each chapter.

I occasionally use the shorthand *autotroph quality* when focusing on the effects of biochemical traits on consumers or microbes. Autotroph quality is a tricky term because quality is a function of the user, not of the plant trait itself. For example, my daily consumption of caffeine and theobromine (in coffee and chocolate, respectively) would be lethal to most organisms, including many mammals (Gans et al. 1980). These particular alkaloid secondary metabolites have no inherent quality beyond their effects (positive or negative) on particular consumers (Scholey et al. 2010, Messerli 2012). However, there are a suite of chemical traits expressed by primary producers that appear to have significant and generalizable effects on nutrient cycling, trophic interactions, or both (Classen et al. 2007a). These traits include mineral nutrient concentrations and ratios (elemental stoichiometry), secondary metabolites (alkaloids, phenolics, terpenoids, etc.), and structural compounds such as lignin, cellulose, and suberin. These are the chemical traits on which I focus here. Some of them are particularly important in mediating interactions between consumers and nutrient cycling because they have broad biological activity. For example, depending on local chemical conditions,

hydrolysable tannins can form complexes with proteins, form complexes with iron, and participate in redox reactions (Hartzfeld et al. 2002). Such chemical interactions are important across a broad spectrum of biological processes from nutrient absorption in the gut of mammalian herbivores to the decomposition of terrestrial plant litter.

The chemistry of primary producers varies across a broad range of temporal and spatial scales. In space, autotroph chemistry varies among tissues within single individuals, among individuals (including phytoplankton cells), among species within communities, among landscapes, and among biomes (Denno and McClure 1983, Hunter et al. 1992). This spatial variation generates a complex phytochemical landscape on which trophic interactions and nutrient dynamics take place. The phytochemical landscape might be imagined as a contour map of primary producer chemistry that varies from high to low mineral nutrient content, high to low toxicity to herbivores, and high to low recalcitrance to heterotrophic microbes that mineralize organic chemical compounds into inorganic forms. The phytochemical landscape has both chemical richness and chemical diversity and, as in traditional landscapes, patches of autotroph chemistry are differentially connected to one another through the flow of materials (chapters 2 and 9).

Moreover, the phytochemical landscape is not static over time. Autotroph chemistry can change within individuals over just a few seconds following herbivory (Zagobelny et al. 2004). Additionally, the phytochemical landscape changes over weeks and years as the result of selective foraging (Pastor and Naiman 1992) and over centuries during the course of ecological succession and recovery from disturbance (Bishop 2002). Finally, the differential fitness of individuals that vary in chemical traits results in evolutionary change in the chemistry of primary producers on the phytochemical landscape (Ehrlich and Raven 1964), with consequences for subsequent trophic interactions and nutrient dynamics (Classen et al. 2007a). Variation in autotroph chemistry at all of these spatial and temporal scales are simultaneously causes and consequences of ecological interactions linked by feedback processes.

#### 1.4 TRAIT VARIATION AND TRAIT DIVERSITY

There are two related yet separate ways by which variation in the chemical traits of primary producers can influence trophic interactions and nutrient cycling. First, key chemical traits in autotrophs can influence (and respond to) trophic interactions or nutrient dynamics. For example, damage by caterpillars to the leaves of many broad-leaved trees results in the induction of polyphenolic

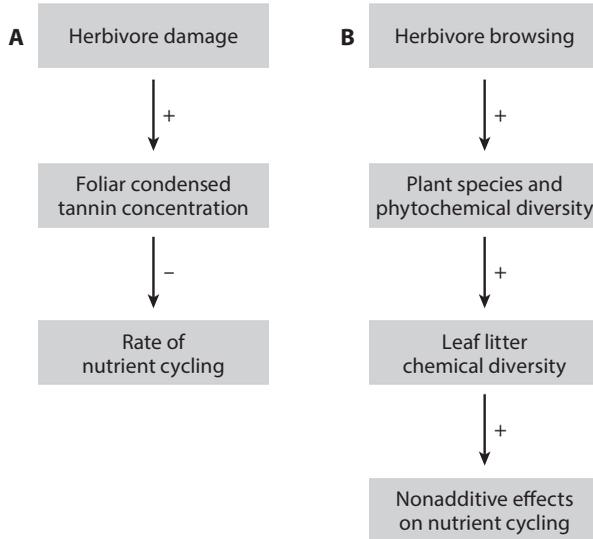


FIGURE 1.3. Both phytochemical trait variation (A) and phytochemical trait diversity (B) mediate the links between trophic interactions and ecosystem processes. For example, herbivore damage can influence variation in the condensed tannin chemistry of tree leaves and litter, thereby modifying the rate at which nutrients are released from that litter (A). Additionally, herbivores may increase the diversity of chemical traits expressed in plant communities, thereby facilitating nonadditive effects during litter decomposition (B). See chapter 6 for further details.

compounds in leaves and decreases in foliar nitrogen (N) levels (Rossiter et al. 1988, Tao and Hunter 2011). In turn, high concentrations of polyphenols and high lignin:N ratios in leaf litter can reduce rates of litter decomposition and nutrient cycling in soils (Madritch and Hunter 2002). In this example, variation in autotroph chemical traits (N, polyphenols) provides a pathway of interaction between insect herbivores and nutrient cycling (Hunter et al. 2012) (figure 1.3A). This is an example of how chemical **trait variation** can link trophic interactions and ecosystem processes.

Additionally, plant **trait diversity** within communities can influence both trophic interactions and nutrient cycling (figure 1.3B). Here, trait diversity refers to the richness of different chemical traits that are expressed simultaneously by communities of autotrophs on the phytochemical landscape. The expanding literature that links species diversity and ecosystem function (Cardinale et al. 2006) is in part a reflection of this. In this body of literature, “species diversity” is an easily measurable variable that serves as a proxy for the complex latent variables that actually determine functional phenotypic differences among taxa (Edwards et al. 2013). The quantification of Latin binomials (species diversity or richness)

is convenient shorthand for the variation in phenotype, including variation in phytochemistry, which actually mediates ecological processes (Whitham et al. 2003). Whether described as species diversity, functional diversity, or phenotypic diversity, it is apparent that autotroph trait diversity can influence both trophic interactions (Haddad et al. 2009) and nutrient cycling (Kominoski et al. 2007). Similarly, Latin binomials represent phylogenetic relationships among species that share common ancestors and common ancestral traits. Consequently, a trait-based approach may better serve to explain relationships among the phylogenetic diversity of primary producers, species interactions, and ecosystem processes wherein the assembly of autotroph communities is viewed as the assembly of chemical phenotypes (Asner et al. 2014).

## 1.5 WHICH TROPHIC INTERACTIONS?

In figure 1.1, arrows 1 and 2 illustrate the feedback loop between trophic interactions and the chemistry of primary producers. What kinds of trophic interactions influence, and are influenced by, variation in the chemistry of autotrophs? The short answer is all of them (see chapters 4 and 5 for detailed coverage). For example, herbivores induce well-known changes in plant chemistry that have subsequent effects on herbivore fitness (Hunter and Schultz 1993, Cronin and Hay 1996b). In turn, the predators, parasites and pathogens of primary consumers can change the densities, distributions, and behaviors of herbivores (Werner et al. 1983, Schmitz 1998), thereby changing patterns of plant consumption and subsequent chemical induction. Omnivores, because they feed at more than one trophic level, may have direct and indirect effects on the chemistry of autotrophs and, in turn, respond to variation in autotroph chemistry (Eubanks and Denno 2000). Mutualisms, because they are based on the exchange of resources, can also be considered as trophic interactions or mutual exploitation (Bronstein 2001). Consequently, many mutualisms can both cause, and respond to, variation in the chemistry of primary producers. For example, mycorrhizal fungi influence the defensive chemistry of terrestrial plants (Vannette and Hunter 2011b), while the effects of recalcitrant phytochemicals on digestion by herbivores may depend critically on nutritional mutualists (Lilburn et al. 2001). Microbial symbionts may even influence the rate and direction of plant succession (Rudgers et al. 2007), with concomitant effects on trophic interactions and ecosystem processes at landscape scales. Finally, there are both direct and indirect mechanisms by which competition for resources can result from trophic interactions, with consequences for autotroph chemistry and the structure of ecological communities (Hunter and Willmer 1989). Chapters 4 and 5 consider in more detail how

feedback processes link trophic interactions with variation in the chemistry of primary producers.

## 1.6 WHICH ECOSYSTEM PROCESSES?

A central focus of ecosystem ecology is the cycling of matter and transfer of energy in biological systems (Coleman 2010). In this book, I focus primarily on links between trophic interactions and nutrient cycling, mediated by variation in autotroph chemistry. In terrestrial systems, primary production generates about 100 gigatons of biomass annually (Gessner et al. 2010), of which about 90 percent enters the detrital pathway without being consumed (Cebrian 2004). The chemistry of that plant tissue is a primary determinant of its decomposition rate (Cornwell et al. 2008) and therefore the rate at which nutrients are recycled in terrestrial ecosystems. There are two important facts to note here. First, the chemistry of tissue that is not consumed by herbivores is nonetheless a legacy of trophic interactions. Natural selection for chemical defense (Thompson 1994) and selective foraging by herbivores (Leibold 1989, Pastor and Naiman 1992) combine to influence the palatability and decomposition rate of plant material, whether it is consumed by herbivores or not (Cornelissen et al. 2004). Second, when plants are consumed by herbivores, their chemistry often changes in ways that influence the decomposition process. This includes induced chemical changes in remaining plant tissues (Findlay et al. 1996) and herbivore-derived inputs such as feces and prematurely abscised leaves (Hunter et al. 2012).

In marine systems, total primary production is about the same as that in the terrestrial environment (Field et al. 1998), although annual rates of consumption of marine plant biomass are about four times higher than those in terrestrial systems (Cebrian 2004). As a result, nutrient turnover rates are higher in marine than in terrestrial systems. In the oceans of the world, an average milliliter of seawater may contain a million bacterial decomposers that mineralize between 35 and 80 percent of annual primary production (Duarte and Cebrian 1996). In turn, marine heterotrophic bacteria are consumed by larger organisms and play key roles in the structure and function of marine food webs (Taylor and Stocker 2012). However, just as in terrestrial systems, rates of organic matter decomposition in oceans and lakes vary with the chemical quality of primary production (chapter 6). For example, only bacteria with the appropriate enzyme systems can decompose certain cyanobacterial toxins (Alamri 2012).

These rates of decomposition and nutrient cycling in terrestrial and aquatic environments are important because nutrient availability feeds back to influence the subsequent chemistry of primary producers (Herms and Mattson 1992,

Anderson et al. 2002) (chapter 7). As a consequence, I focus my attention on how rates of nutrient cycling are influenced by, and in turn influence, the chemical traits of autotrophs. I pay particular attention to rates of decomposition, and to the cycling of nitrogen (N) and phosphorus (P), which are often limiting resources that influence both primary productivity and the chemistry of autotrophs. I will also mention more briefly other ecosystem processes, such as productivity, when their expression is linked to both trophic interactions and variation in autotroph chemistry on the phytochemical landscape.

## 1.7 WEBS OF GREEN AND BROWN

We are perhaps most familiar with the mechanisms by which trophic interactions change the chemical traits of living autotrophs in the “green food web.” For example, within communities of living primary producers, chemical induction (Schultz and Baldwin 1982, Hay 1996), selective foraging (Kirk and Gilbert 1992, Pastor and Naiman 1992), and feces deposition by herbivores (Frost and Hunter 2007) all act to change the chemistry of aquatic and terrestrial autotrophs. In turn, these autotrophs produce organic residues that enter the detrital pathway where true decomposers, those species of bacteria, archaea, and fungi that convert organic molecules into inorganic forms, subsequently act upon them, mediating the recycling of nutrients within ecosystems. Most of this book focuses on chemical mediation of interactions in the green food web.

However, complex trophic interactions within the “brown food web” also influence the chemistry of autotroph residues and the dynamics of nutrient recycling. Bacterivorous and fungivorous organisms, detritivores, and a suite of enemies influence the distribution, activity, and abundance of true decomposers (Coleman et al. 2004, Hunting et al. 2012). Moreover, the chemical nature of decomposing autotroph residues is not static, but changes markedly over time, depending on decomposer activity. Recent work has established that the chemical trajectory of decomposing plant material is influenced by trophic interactions within the brown food web (Wickings et al. 2012) such that even higher-order predators can modify the chemistry of decomposing plant material (Hunter et al. 2003a). The key point here is that figure 1.1 can apply just as readily to brown food webs as to green food webs.

Additionally, because brown and green food webs are inextricably linked together (Bardgett and Wardle 2010, Hines and Gessner 2012), figure 1.1 can serve as a template for understanding interactions between them. For example, the trait-mediated indirect effects that link trophic interactions in green food webs with nutrient cycling can then “cascade through” to influence trophic interactions

in linked brown food webs (and vice versa) (chapter 8). Such trait-mediated cascades (Liere and Larsen 2010) represent coupled systems of trait-mediated indirect effects (Utsumi et al. 2010) and are common features of natural systems (Pardee and Philpott 2011). In short, variation in the chemistry of primary producers provides a nexus through which trait-mediated cascades can link together trophic interactions in green and brown food webs and the cycling of nutrients (Reynolds et al. 2003).

In chapter 2, I develop in more detail the concept of the phytochemical landscape, which seeks to describe spatial and temporal variation in the chemistry of primary producers. In subsequent chapters, I describe how this spatial and temporal variation in phytochemistry is both a cause and a consequence of trophic interactions and nutrient dynamics, and acts as a fundamental pathway that links them together.