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PART I

Theory

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CHAPTER ONE

Theoretical perspectives on bottom-up and top-down interactions across ecosystems

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Introduction

The study of the determinants of biomass pyramids (i.e., the patterns of biomass of organisms at different trophic levels of an ecosystem) within and across ecosystems is an enduring endeavor in the ecological sciences (Gripenberg and Roslin, 2007; Gruner et al., 2008). This classic ecological problem still fascinates ecologists worldwide and the lively debate on this question is an attestation of the complexity of ecological systems. The ecological literature reveals two main perspectives for predicting biomass pyramids; one perspective emphasizes the role of resources such as inorganic nitrogen (N) and phosphorus (P) or primary producers in determining the biomass of higher trophic levels, and the other perspective emphasizes the role of consumers such as herbivores and predators in determining the biomass of lower trophic levels (Oksanen and Oksanen, 2000; Gruner et al., 2008).

The resource-based hypothesis states that organisms are resource-limited, and therefore resources determine the shape of biomass pyramids (Elton, 1927; Lindeman, 1942; White, 1978; McQueen et al., 1986). Consistent with Elton's (1927) perspective, Lindeman (1942) and others (e.g., White, 1978; McQueen et al., 1986) argued that inorganic nutrients and solar radiation limit plant growth and subsequently the potential transfer of energy and nutrients from lower trophic levels to higher trophic levels in ecosystems. This bottom-up perspective has been expanded to consider the role of plant defense in limiting herbivory (Strong, 1992; Polis and Strong, 1996; also, see Chapter 8 and Chapter 13).

In contrast, the consumer-based hypothesis (i.e., Hairston Smith Slobodkin (HSS) Hypothesis) states that organisms are consumer-regulated, and therefore higher-level consumers determine biomass pyramids (Hairston et al., 1960).

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Oksanen et al. (1981) further developed the consumer-regulated framework by developing the exploitation ecosystem hypothesis (EEH), which suggests that top-down control of ecosystems will vary along environmental gradients. Top-down perspectives gained additional support through Carpenter et al.'s (1985) empirical evidence of trophic cascades, whereby top predators have indirect positive effects on non-adjacent trophic levels. White (1978) referred to the debate on resource- versus consumer-based limitation as populations being "limited from below" or "controlled from above." McQueen et al. (1986) first introduced the terms "bottom-up" and "top-down" to describe White's (1978) use of resource- versus consumer-based limitation. For many years, ecologists have focused on demonstrating the primacy of their favorite hypothesis (White, 1978; McQueen et al., 1986). However, recent empirical results from a wide range of ecosystems, many of which are reviewed in this volume, provide unequivocal evidence that both resources and consumers interact to shape natural populations, communities, and ecosystems (e.g., Hunter and Price, 1992; Brett and Goldman, 1996; Hassell et al., 1998; Polis, 1999; Fath, 2004; Borer et al., 2006; Gruner et al., 2008; Polishchuk et al., 2013; Whalen et al., 2013). Ecological theory (e.g., Hairston et al., 1960; Oksanen et al., 1981) has been at the forefront of integrating our empirical knowledge of the interdependence of resource and consumer impacts on food webs and ecosystems (Table 1.1).

Contemporary ecological theory is now investigating the interrelationship and variability of bottom-up and top-down interactions in ecosystems in space and time. Building on Carpenter et al.'s (1985) foundational work and a plethora of empirical studies demonstrating the role of consumer-mediated recycling on ecosystem functioning, Leroux and Loreau (2009; 2010) and Schmitz et al. (2010) outline the many consumptive and non-consumptive mechanisms by which consumers can indirectly influence primary production and nutrient cycling. The key role consumers play in storing, recycling, and redistributing nutrients in ecosystems (Loreau, 1995; reviewed in Vanni, 2002; Schmitz et al., 2010; also, see Chapter 9) provides a mechanistic link between bottom-up and top-down forces in ecosystems. Specifically, organic nutrients recycled by organisms are mineralized by microorganisms and made available to plants, thus completing the energy cycle (Lindeman, 1942). Organismal material cycling has the potential to synthesize bottom-up and top-down processes, but it must overcome the current confusion surrounding these processes, which is evidenced by the fact that some authors refer to organism-mediated nutrient cycling as a bottom-up process (e.g., Northcote, 1988), while others call it a top-down process (e.g., Glaholt and Vanni, 2005).

Additional progress in bottom-up and top-down theory has occurred with the consideration of these processes along distinct energy pathways (e.g., brown versus green webs, Moore et al., 2004; Hulot and Loreau, 2006; Rooney et al., 2006). Indeed, a parsimonious explanation for the stability and dynamics of complex food webs is emerging based on two key ecosystem attributes: the

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Table 1.1 *Chronological summary of the development of classic theories of community regulation; the table provides the citation, a brief summary of the history, general predictions, and original model system for each contribution*

Contribution	History	Prediction	Systems
Lindeman, 1942	Trophic-dynamic ecology	Inorganic nutrients and solar radiation fuel primary productivity, which provides energy for higher trophic levels. Death of higher order organisms provides a source of energy to decomposers, which make organic substances available for producers, thus completing the energy cycle	Lakes
Hairston et al., 1960	HSS or Green World Hypothesis (GWH) – based on ideas formulated in Elton (1927) regarding the structure of food webs	Predators have strong top-down regulation of herbivores, therefore releasing plants from herbivory. Plants are abundant because of this. An increase in plants will be passed on to the predators in a three-level food chain	Terrestrial
Rosenzweig, 1971	Paradox of enrichment	Increasing the resources to a system can be destabilizing and is known as the paradox of enrichment. Rip and McCann (2011) have generalized this concept as the principle of energy flux	Theoretical
Menge and Sutherland, 1976	Menge–Sutherland Hypothesis (MSH) – based on observations that omnivory is abundant in natural food webs	Predators regulate plant abundance not indirectly through consumption of herbivores but directly via omnivory on plants	Rocky intertidal and terrestrial

(*cont*.)

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Table 1.1 *(cont.)*

Contribution	History	Prediction	Systems
Oksanen et al., 1981	Exploitation Ecosystem Hypothesis (EEH) – based on Fretwell (1977) and HSS	Similar to HSS, but incorporates productivity gradient. Stepwise accrual of plants and herbivores along a productivity gradient. At relatively high productivity (700 g m^{-2} y^{-1}), predators are present and regulate herbivores to a relatively constant biomass (converges with predictions from HSS). At low productivity, predators are absent and herbivores regulate plant biomass	Terrestrial, low productivity systems like Tundra and Boreal
Carpenter et al., 1985	Trophic Cascade Hypothesis (TCH) – based on HSS and EEH	Nutrient supply does not explain all the variation in plants. Cascading trophic interactions similar to HSS explain the differences in plants in systems with similar nutrient levels. First demonstration of this for a four-level food web	Lakes
McQueen et al., 1986	Bottom-up:Top-down hypothesis (BU:TD) – extension of EEH	Combines reciprocal effects of predators and resources. Biomass of plants is regulated by resources, and herbivores are regulated by predators, but both effects attenuate along food chains. At high resource levels, an increase in predators will have no effect on plants	Lakes
Arditi and Ginzburg, 1989	Ratio-Dependent Hypothesis (RDH)	The ratio of consumer to resource determines structure and abundance of different trophic levels. All trophic levels increase with an increase in primary production	Terrestrial
Strong, 1992; Polis and Strong, 1996	Diversity-Defense Hypothesis (DDH) – opposite to EEH	Strong cascading interactions are rare. Plants are abundant because of a diversity of defenses against herbivory	Grasslands

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presence of mobile and generalist consumers that can couple energy pathways (e.g., McCann et al., 2005; Rooney et al., 2006; Wollrab et al., 2012) and the length of component food chains (Wollrab et al., 2012). Meta-ecosystem (i.e., a set of ecosystems connected by spatial flows of energy, materials, and organisms across ecosystem boundaries, sensu Loreau et al., 2003) theory provides another promising avenue to investigate variability in the spatial dynamics of resource limitation and consumer regulation (Loreau et al., 2003; Gravel et al., 2010; Massol et al., 2011). For example, Leroux and Loreau (2012) show how top-down regulation in one ecosystem can have indirect effects on the structure and dynamics of adjacent ecosystems (also, see Chapter 6 and Chapter 7).

In this chapter, we provide an overview of theoretical models and approaches that address the relative importance, variability, and interdependence of bottom-up and top-down forces in ecosystems and illustrate this theory with empirical examples from both aquatic and terrestrial realms. We begin by defining bottom-up and top-down processes independently; then we show how they can be related through material cycling. We review current work toward understanding spatial and temporal variability in bottom-up and top-down interactions and end with some future directions for bottom-up and top-down theory to pave the way for ecological synthesis on this matter. Ecosystems are complex, encompassing great horizontal (i.e., diversity within a single trophic level, e.g., competitors) and vertical diversity (i.e., diversity of food web interactions; Duffy et al., 2007). The bottom-up versus top-down debate was originally centered around vertical diversity; therefore, we focus on vertical diversity in this chapter, although we explore more complex ecosystems in later sections.

Defining bottom-up and top-down effects in ecosystems

Here, we derive ecosystem models to illustrate the basic definitions of bottom-up and top-down effects in ecosystems. Throughout this chapter, we consider a trophic level to consist of a group of species with shared resources. Since most ecosystems are thought to be limited by N or P (Elser et al., 2007; LeBauer and Treseder, 2008), we derive nutrient-limited ecosystem models. The same approach could be used for energy as long as nutrient recycling is ignored and the energetic content and stoichiometric composition of the various trophic levels are roughly equal. To illustrate bottom-up effects, consider a minimal ecosystem model with inorganic nutrient (*N*) as a basal resource for primary producers (*P*). Both trophic levels follow nutrient mass-balance constraints such that, at equilibrium, nutrient inputs balance nutrient outputs. This model tracks the basic ecosystem processes of consumption and production in each trophic level as follows (Loreau, 2010):

$$\frac{dN}{dt} = \Phi_N - \theta_N - \Phi_P \tag{1}$$

$$\frac{dP}{dt} = \Phi_P - \theta_P \tag{2}$$

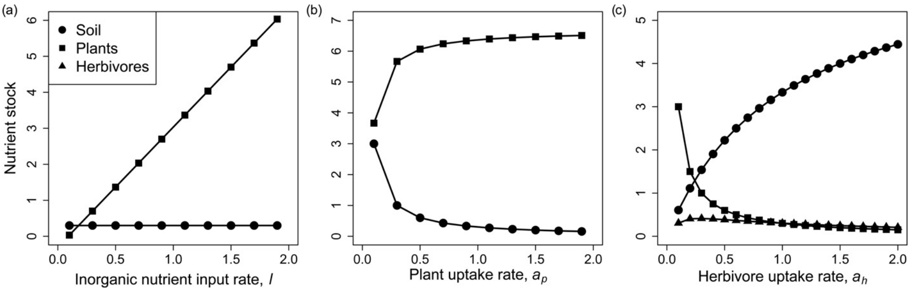

Figure 1.1 Illustration of bottom-up effects of nutrient increases (a), top-down effects of increased plant uptake rate (b), and the cascading effects of increased herbivore uptake rate (c). In a plant–soil ecosystem model, an increase in soil nutrients has a positive bottom-up effect on producer biomass (a) and an increase in producer nutrient uptake rate has a negative, top-down effect on soil nutrient stocks (b). In a herbivore–plant–soil ecosystem model, increasing herbivore nutrient uptake rate leads to negative, direct effects on plant biomass and positive indirect or cascading effects on soil nutrient stocks (c). α_P *and* α_H are the producer uptake rate and herbivore attack rate, respectively. e_H is the herbivore production efficiency, and m_N , m_P , *and* m_H are the mass-specific loss rates of soils, plants, and herbivores, respectively. Our results are not sensitive to particular model parameters, therefore, we selected arbitrary model parameter values of $\alpha_P = \alpha_H = 1$, $e_H = 0.1$, $m_N = m_P = m_H = 0.3$, $I = 2$ for illustration purposes.

where Φ_N and Φ_P are the production of the soil nutrient pool and primary producers, respectively, and θ_N and θ_P are the loss fluxes that include soil inorganic nutrients and plant senescence and mortality, respectively. The ecosystem is open at the basal level through a constant and independent input of inorganic nutrients; i.e., $\Phi_N = I$. We assume, as in classical theory of exploitation interactions (sensu Oksanen et al., 1981), that there is no interference among producer species so that the production of plants can be written as $\Phi_P = f_P(N)P$, where $f_P(N)$ is the functional response of plants. For simplicity, we use Lotka–Volterra functional responses for plants and herbivores throughout this chapter, as our main goal is to use simple models to illustrate bottom-up and top-down processes (see Loreau (2010) for generalized results to other functional responses). The Lotka–Volterra functional response for plants is $f_P(N)P = \alpha_P NP$, where α_P is the producer uptake rate. The loss flux is $\theta_N = m_N N$ from the soil nutrient pool and $\theta_P = m_P P$ from the primary producer pool, where m_N and m_P are the mass-specific loss rates of the soil and plants, respectively. At equilibrium, $N* = \frac{m_P}{\alpha_P}$ and $P* = \frac{I}{m_P} - \frac{m_N}{\alpha_P}$. We can investigate the bottom-up effect of increasing inorganic nutrients on the biomass of primary producers by taking the partial derivative of plant biomass with respect to the inorganic nutrient input rate, I (i.e., $\frac{\partial P^*}{\partial I}$). This partial derivative is positive ($\frac{\partial P^*}{\partial I} = \frac{1}{m_P}$), which demonstrates a positive, bottom-up effect of increasing basal resources on primary producer biomass (Fig. 1.1a). We obtain similar qualitative results for the bottom-up effect of increasing inorganic nutrients on primary production ($\frac{\partial \Phi_P}{\partial I} > 0$). Empirical evidence in support of this simple bottom-up effect of nutrients on plant biomass in aquatic and terrestrial ecosystems abounds (reviewed in Gruner et al., 2008). For example, Gratton and Denno (2003a) observed an increase in *Spartina alterniflora* production for 2–3 years after N fertilizer was added to their salt marsh study area, Rosemond et al. (1993) observed an increase in periphyton biomass and production after N and P additions to their woodland stream in eastern Tennessee, and in a meta-analysis of N and P fertilization experiments, Gruner et al. (2008) found an increase in producer biomass with fertilization in freshwater, marine, and terrestrial ecosystems.

The top-down effects of primary producers on soil inorganic nutrient stocks also can be elucidated through this simple ecosystem model. Top-down effects can occur via an increase in production (i.e., Φ_P) or a decrease in loss flux (i.e., θ_P). Consequently, the direction of top-down effects in this ecosystem can be determined by taking the partial derivative of soil inorganic nutrient stocks with respect to the producer uptake rate, α_P, or producer mass-specific loss rate, m_P. The top-down effect of increasing producer uptake rate has a negative effect on soil nutrient stocks ($\frac{\partial N^*}{\partial \alpha_P} = -\frac{m_P}{\alpha_P^2}$, Fig. 1.1b). Similarly, a decline in producer mass-specific loss rate leads to a negative top-down effect on soil nutrient stocks ($\frac{\partial N^*}{\partial m_P} > 0$). There is considerable empirical evidence in support of top-down effects of organisms on adjacent trophic levels in aquatic and terrestrial ecosystems. For example, Frank et al. (2007) presented evidence of top-down forcing (i.e., negative correlation between predator and prey abundance) in fish of the North Atlantic marine ecosystem and Creel et al. (2007) showed lower elk calf recruitment with the introduction of wolves to Yellowstone National Park.

Bottom-up and top-down interactions are meant to describe direct interactions among adjacent trophic levels. The trophic cascade is a concept for understanding indirect (i.e., non-adjacent) trophic interactions. By adding herbivores to the above ecosystem model, we can demonstrate the indirect, top-down effects of herbivores on soil nutrient stocks via a trophic cascade. Trophic cascades result in alternating abundance, biomass, or production across more than one trophic level in an ecosystem (Carpenter and Kitchell, 1993; Pace et al., 1999). To add herbivores (i.e., H) to this model, we must add an additional loss term to the primary producer trophic level (Eq. 2); herbivore production (Φ_H) scaled by the herbivore production efficiency (ε_H), which represents consumption by herbivores. Eq. 2 then becomes:

$$\frac{dP}{dt} = \Phi_P - \theta_P - \frac{\Phi_H}{\varepsilon_H} \tag{3}$$

The dynamical equation for the herbivore trophic level is as follows:

$$\frac{dH}{dt} = \Phi_H - \theta_H \tag{4}$$

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and the dynamical equation for soil nutrients (Eq. 1) remains unchanged. Similar to primary producers, the production of herbivores can be written as $\Phi_H = f_H(P)H = \alpha_H PH$, where α_H is the herbivore attack rate. The equilibrium stocks of this three-level ecosystem are $N^* = \frac{I}{m_N + \alpha_P P^*}$, $P^* = \frac{m_H}{\alpha_H}$, $H^* = \frac{\varepsilon_H(\alpha_P N^* - m_P)}{\alpha_H}$. Using partial derivatives as above we can show positive, indirect, bottom-up effects of increasing the inorganic soil nutrient input rate on herbivore stocks ($\frac{\partial H^*}{\partial I} = \frac{\alpha_P \varepsilon_H}{\alpha_H m_N + \alpha_P m_H}$), negative direct top-down effects of herbivore consumption on primary producer stocks ($\frac{\partial P^*}{\partial \alpha_H} = -\frac{m_H}{\alpha_H^2}$), and positive, indirect, top-down effects of increasing herbivore consumption on soil nutrient stocks via a trophic cascade ($\frac{\partial N^*}{\partial \alpha_H} = \frac{\alpha_P m_H I}{(\alpha_H m_N + \alpha_P m_H)^2}$, Fig. 1.1c).

Recent meta-analyses have demonstrated that top-down trophic cascades tend to be stronger in aquatic than terrestrial ecosystems (Schmitz et al., 2000; Shurin et al., 2002; Borer et al., 2005). The leading hypotheses to explain variation in the strength of trophic cascades across ecosystems include system differences in producer quality and defense (Borer et al., 2005; Hall et al., 2007; Cebrian et al., 2009), primary productivity (Borer et al., 2005; Shurin and Seabloom, 2005), ecosystem complexity (Strong, 1992; Hillebrand and Cardinale, 2004), behavioral avoidance of predation by herbivores (Persson, 1999; Schmitz et al., 2004), and rates of exogenous inputs (Leroux and Loreau, 2008). Overall, aquatic ecosystems tend to have producers with less structural material, receive higher quantities of external subsidies, and have less reticulated food webs, thus facilitating the propagation of indirect top-down interactions (Shurin et al., 2006).

While trophic cascades most often have been applied to explain indirect top-down effects in ecosystems, at its core, the concept is applicable to both bottom-up and top-down interactions. Broadly defined, trophic cascades simply refer to indirect effects of an ecosystem perturbation (i.e., change in soil nutrients or predation rate) throughout an ecosystem. Indeed, empirical studies have shown indirect effects originating from both bottom-up and top-down processes. For example, Gratton and Denno (2003a) demonstrate bottom-up cascading effects of increased nutrients on herbivorous planthoppers and carnivorous spiders in their mid-Atlantic salt marsh food web, whereas Myers et al. (2007) provide evidence of top-down cascading effects of a decline in great shark abundance on cownose ray and bay scallops in the Northwest Atlantic marine ecosystem.

Loreau (2010) has generalized the results we present here to show the functional consequences of bottom-up and top-down forces on biomass, production, and ecological efficiency of ecosystems with n trophic levels. Consistent with the non-nutrient based model of Oksanen et al. (1981), Loreau (2010) shows that an increase in soil nutrient levels will have positive bottom-up effects on trophic levels that lie at the top of ecosystems or at an even number of levels below it (see table 4.2. in Loreau, 2010). The number of trophic levels in an ecosystem and the position of a trophic level along the food chain will determine the relative effect of an increase in soil nutrient levels (i.e., bottom-up) versus the addition