

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).

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

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.)

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 ($700 \text{ g m}^{-2} \text{ y}^{-1}$), 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

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):

$$\frac{dN}{dt} = \Phi_N - \theta_N - \Phi_P \quad (1)$$

$$\frac{dP}{dt} = \Phi_P - \theta_P \quad (2)$$

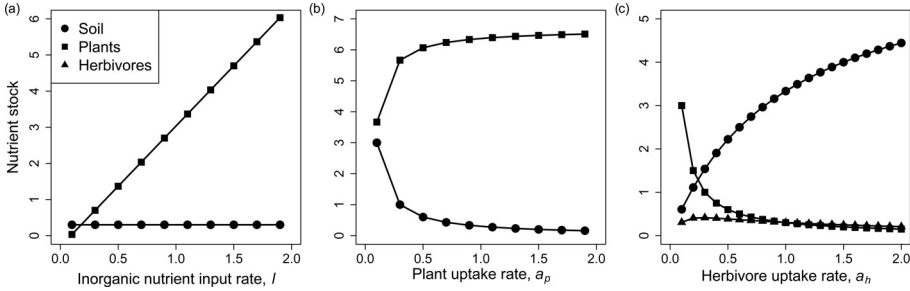


Figure 1.1 Illustration of bottom-up effects of nutrient increases (a), top-down effects of increased plant uptake rate (b), and the cascading effects of increased herbivore uptake rate (c). In a plant–soil ecosystem model, an increase in soil nutrients has a positive bottom-up effect on producer biomass (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:

$$\frac{dP}{dt} = \Phi_P - \theta_P - \frac{\Phi_H}{\varepsilon_H} \quad (3)$$

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

$$\frac{dH}{dt} = \Phi_H - \theta_H \quad (4)$$

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

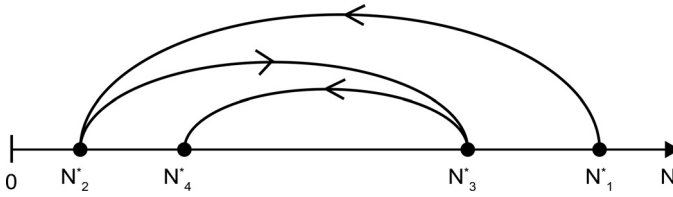


Figure 1.2 Effects of increasing food chain length, n , on the equilibrium amount of soil inorganic nutrient, N_n^* , in an ecosystem with a linear food chain. For example, N_2^* is the soil nutrient stock in a model with two trophic levels (i.e., plant–soil model), N_3^* is the soil nutrient stock for a model with three trophic levels, etc. Modified from Loreau (2010).

of a consumer trophic level (i.e., top-down). Specifically, in ecosystems with linear functional responses, the equilibrium amount of any target trophic level is highest when it lies at the top of the ecosystem, is lowest when it lies just below the top of the ecosystem (i.e., experiences direct top-down regulation), and alternates from low to high and high to low to eventually converge on an intermediate value as more trophic levels are added (Fig. 1.2). These general results suggest that top-down control exerted by top trophic levels cascades down the ecosystem, but becomes progressively weaker as the number of trophic levels above the target trophic level increases or, equivalently, as we move down the food web.

Material cycling for integrating bottom-up and top-down concepts in ecology

As defined with our very simple soil–plant ecosystem model above and classic theory on the topic, the concepts of bottom-up limitation and top-down regulation in ecosystems are very clear. Bottom-up effects are encountered when an increase (decrease) in the resource stock (e.g., via an increase in nutrient supply rate) leads to an increase (decrease) in the biomass of the next higher trophic level, and top-down effects occur when an increase (decrease) in the biomass of the higher trophic levels (e.g., via an increase in uptake rate or a decrease in loss rate) results in a decline (increase) in the biomass of the next lowest trophic level. In more complex ecosystems (i.e., ecosystems with more trophic levels), bottom-up and top-down processes can lead to cascading trophic interactions or indirect effects on non-adjacent trophic levels. Bottom-up, top-down, and cascading trophic interactions arise in models that track energy flux (e.g., Oksanen et al., 1981; Huxel and McCann, 1998; Rip and McCann, 2011) and material flux (e.g., DeAngelis, 1992; Loreau, 1995; Gravel et al., 2010; Leroux and Loreau, 2012) throughout ecosystems. The difference between these two classes of models is that material flux models include an explicit abiotic compartment at the bottom of the food web, whereas energy flux models only include biotic

trophic levels. We favor the material cycling class of models because these models allow ecologists to explicitly incorporate important ecosystem feedbacks that arise from ecosystem nutrient cycling (Loreau, 2010; Leroux and Loreau, 2010). Ecological interactions must obey the basic laws of thermodynamics, in particular mass-balance constraints, and this puts fundamental constraints on ecosystem dynamics (Loreau and Holt, 2004). An issue that arises but is seldom discussed when trying to investigate the influence of bottom-up and top-down forces in ecosystems is that it is difficult to separate bottom-up and top-down processes in practice (Pace et al., 1999; Leroux and Loreau, 2010). Below we show how adopting a material cycling framework can allow us to understand the interrelationship between bottom-up and top-down forces in ecosystems.

The interdependence of bottom-up and top-down processes arises because plants and consumers can influence ecosystems via many different mechanisms (reviewed in Leroux and Loreau, 2010; Schmitz et al., 2010). Organismal nutrient recycling is one important feedback between plants and consumers and the soil nutrient pool. In a meta-analysis of the fate of primary production in different terrestrial ecosystems, Cebrian (1999) showed that up to 90% of terrestrial plant matter is not consumed by herbivores, but actually enters the dead organic matter pool as litterfall. It is therefore surprising (or concerning) that many food web and ecosystem models do not include this ecologically important feedback. As we show below, nutrient recycling can have very important impacts on ecosystem functioning (DeAngelis, 1992; Loreau, 2010; also, see Chapter 9). In real ecosystems, materials recycled from biotic compartments are first processed by detritivores and decomposers that mineralize nutrients and make them available for plant uptake (Loreau, 1995; reviewed in Moore et al., 2004). For simplicity, we do not include decomposition in our model, as our goal is simply to illustrate the connection between bottom-up and top-down processes via organismal nutrient recycling.

Let us start with the plant–soil model from above and add feedback loops from the plant trophic level back to the soil nutrient pool (Loreau, 2010). The plant feedback loop represents litterfall. To incorporate plant nutrient recycling, we add one parameter to the model: δ_P . This parameter describes the portion of plant nutrients lost from the ecosystem and $1 - \delta_P$ describes the portion of plant nutrients that is returned via senescence to the soil nutrient pool. Adding nutrient recycling to our simple plant–soil ecosystem model yields a modified Eq. 1 (see Eq. 5 below) but the same equation for the plant (Eq. 2) dynamics (Loreau, 2010).

$$\frac{dN}{dt} = \Phi_N - \theta_N - \Phi_P + (1 - \delta_P)\theta_P \quad (5)$$

At equilibrium $N^* = \frac{m_P}{\alpha_P}$ and $P^* = \frac{I - m_N N^*}{\delta_P m_P}$, and the effect of plant recycling on plant nutrient stocks (P^*), primary production (Φ_P), and plant nutrient

recycling flux $((1 - \delta_p)\theta_p)$ can be seen by taking one minus the partial derivative of these ecosystem properties with respect to the fraction of plant nutrient that is lost from the ecosystem, δ_p . A positive effect of plant nutrient recycling on plant stocks (i.e., $1 - \frac{\partial P^*}{\partial \delta_p} > 0$), production (i.e., $1 - \frac{\partial \Phi_P}{\partial \delta_p} > 0$), and recycling flux (i.e., $1 - \frac{\partial \delta_p \theta_p}{\partial \delta_p} > 0$) emerges when the plant and soil trophic levels persist at equilibrium (i.e., the ecosystem is feasible, with feasibility condition $I > \frac{m_N m_P}{\alpha_P}$).

Organism-mediated nutrient recycling has important impacts on the dynamics of ecosystems, but is it a bottom-up or top-down process? In our simple plant–soil ecosystem model, plant nutrient recycling is not a clear bottom-up effect, as it has a positive influence on plant function via an indirect route through nutrients recycled from plants. However, plant nutrient recycling also is not a clear top-down effect in this model, as it does not represent a direct influence of plants on the soil nutrient pool as outlined for models without material recycling above. Recent work that has adopted a materials cycling framework (reviewed in Vanni, 2002; Leroux and Loreau, 2010; Schmitz et al., 2010) questions the usefulness of the bottom-up and top-down terminology. This work suggests that there is a need for caution when discussing bottom-up and top-down effects in ecology because organism-mediated nutrient recycling and other mechanisms (see Leroux and Loreau, 2010; Schmitz et al., 2010) do not fit within the classic definitions of bottom-up limitation or top-down regulation. We advise authors to be specific about the process of interest when using the terms bottom-up and top-down to avoid perpetuating the sometimes incorrect and confusing applications of these terms.

We can further investigate the indirect effects of organismal nutrient recycling by adding herbivores to the above model and a nutrient recycling feedback loop from the herbivore trophic level back to the soil nutrient pool, $1 - \delta_H$. The herbivore recycling feedback loop represents excretion and death. With the inclusion of this feedback loop, the dynamical equation for the soil nutrient pool is as follows:

$$\frac{dN}{dt} = \Phi_N - \theta_N - \Phi_P + (1 - \delta_p)\theta_p + (1 - \delta_H)\theta_H \quad (6)$$

The equilibrium stocks in this herbivore–plant–soil model are given by $N^* = \frac{\alpha_H H^* + \varepsilon_H m_P}{\varepsilon_H \alpha_P}$, $P^* = \frac{m_H}{\alpha_H}$, $H^* = \frac{\alpha_P (m_P P^* - (1 - \delta_P)m_P P^* - I) + m_N m_P}{\alpha_P m_H (\varepsilon_H (1 - \delta_H) - 1) - \alpha_H m_N}$. The addition of plant and herbivore nutrient recycling feedback loops has a positive effect on soil and herbivore stocks in ecosystems with Lotka–Volterra functional responses (Fig. 1.3). These feedback loops have no effect on the equilibrium plant stock, as the equilibrium plant stock is regulated by the herbivore mass-specific loss rate (m_H) and attack rate (α_H). Based on the above equilibrium, we can distinguish four distinct conditions; no organismal recycling ($\delta_p = \delta_H = 1$), plant-only nutrient recycling ($\delta_H = 1$), herbivore-only nutrient recycling ($\delta_p = 1$), and plant and herbivore nutrient recycling ($\delta_p = \delta_H \neq 1$). Soil and herbivore stocks are highest

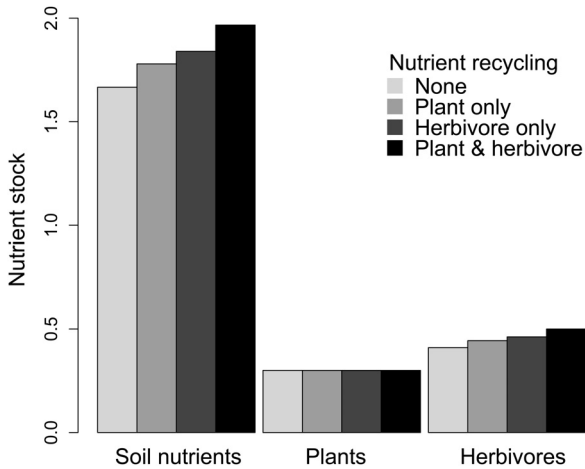


Figure 1.3 Effect of plant and herbivore nutrient recycling on the equilibrium amount of soil, plants, and herbivores in a herbivore–plant–soil ecosystem model. Results are for models with no organismal nutrient recycling $\delta_P = \delta_H = 1$, for models with plant-only nutrient recycling $\delta_P = 0.25$, $\delta_H = 1$, for models with herbivore-only nutrient recycling $\delta_P = 1$, $\delta_H = 0.25$, and for models with both plant and herbivore nutrient recycling $\delta_P = \delta_H = 0.25$. Model parameters are $\alpha_P = \alpha_H = 1$, $e_H = 0.3$, $m = m_P = m_H = 0.3$, $I = 1$.

in models with both plant and herbivore nutrient recycling, followed by models with only herbivore recycling, then models with only plant recycling, and lastly models with no organismal nutrient recycling (Fig. 1.3). Similar positive feedbacks of organismal nutrient cycling can be seen for herbivores on soil and plant resources via grazing optimization, i.e., the enhancement of primary production by herbivores (de Mazancourt et al., 1998). Grazing optimization requires that herbivores improve an ecosystem’s nutrient conservation efficiency enough to compensate for loss of plant biomass to grazing.

The confusion surrounding the classification of organism-mediated nutrient recycling as a bottom-up or top-down process occurs because the classic definitions of bottom-up and top-down forces were applied to a limited number of mechanisms (i.e., nutrient enrichment, predator consumption) that did not consider the complex feedbacks involved in material cycling. Recent integrations of community and ecosystem ecology (e.g., Loreau, 2010; Schmitz, 2010) highlight a large number of mechanisms that can lead to indirect effects in ecosystems, particularly in the context of nutrient-limited ecosystems. The suite of mechanisms includes ones related to organismal consumption such as excretion and egestion (Vanni, 2002; McIntyre et al., 2008), translocation of nutrients (Moore et al., 2007; Abbas et al., 2012), and consumer-resource stoichiometric mismatches (Leroux et al., 2012; Cherif and Loreau, 2013). Other non-consumptive mechanisms like predation risk (Hawlena and Schmitz, 2010) and ecosystem engineering (Jones

et al., 1994) can also lead to indirect effects in ecosystems. These consumptive and non-consumptive mechanisms can lead to complex indirect feedbacks on material cycling in ecosystems, which blur the lines between bottom-up and top-down processes. Adopting a material cycling framework encourages researchers to be clear about the processes of interest and allows us to explicitly track the feedbacks among processes, as well as the dynamical consequences they have in ecosystems.

For example, a material cycling framework has been instrumental in deciphering the keystone role of Pacific salmon (*Oncorhynchus* spp.) in freshwater and riparian ecosystems of the Pacific Northwest. Detailed empirical studies have demonstrated how salmon carcasses and gametes can provide nutrients for plants and consumers in freshwaters and riparian forests (e.g., Holtgrieve et al., 2009; Hocking and Reynolds, 2011; Field and Reynolds, 2011). Also, it has been demonstrated that salmon excretion and bioturbation can influence freshwater nutrient cycling and primary production (Moore et al., 2007; Verspoor et al., 2010). We encourage other empirical ecologists to adopt a material cycling framework as it can shed light on the key processes regulating ecosystems.

Bottom-up and top-down interactions across space and time

Early ecological theory investigated bottom-up and top-down processes in simple or relatively closed ecosystems at equilibrium (e.g., Hairston et al., 1960; Oksanen et al., 1981; Carpenter et al., 1985). Likewise, most empirical work on the importance of bottom-up versus top-down processes is done at very small spatial scales and short time frames (Gripengberg and Roslin, 2007). But with the emergence of landscape and spatial ecology as disciplines, there is mounting evidence for the role of space in shaping the dynamics of ecosystems. Indeed, there exists no natural ecosystem that is completely closed from outside influence, whether it be rainfall (e.g., Anderson et al., 2008), species dispersal (e.g., Cadotte, 2006), or nutrient flux (e.g., Vannote et al., 1980). What is more, most ecosystems are in a constant state of temporal flux driven by seasonality, life history dynamics, and environmental change, and the time scales of many ecological phenomena may be short (Hastings, 2004; 2010). Empirical evidence that the strength of bottom-up and top-down interactions can vary in space and time has helped to end the divisive debate on the dominance of either mechanism and instead shift our attention to explaining variation in the relative strength of each process in space and time (Gripengberg and Roslin, 2007; Leroux and Loreau, 2012; also, see Chapter 11). In this section, we review recent theoretical work on bottom-up and top-down interactions in spatially extended and temporally variable ecosystems.

The spatial flow of energy, materials, and organisms across ecosystem boundaries has the potential to influence the dynamics of donor and recipient ecosystems (Polis et al., 1997; Loreau et al., 2003). For example, consumers in streams

(Nakano et al., 1999; also, see Chapter 6), riparian forests (Murakami and Nakano, 2002), coastal marine zones (Rose and Polis, 1998; also, see Chapter 7), and pelagic ecosystems (Schindler and Scheuerell, 2002) can obtain a significant amount of their energy from food sources originating in neighboring ecosystems. Nowhere are the ecological implications of spatial subsidies more obvious than in the Pacific Northwest where large runs of Pacific salmon (*Oncorhynchus* spp.) provide a seasonal pulse of marine-derived nutrients to freshwater lakes and streams, and riparian forests. This nutrient pulse influences the distribution and abundance of many and diverse organisms, including plants (Hocking and Reynolds, 2011), fish (Flecker et al., 2010), birds (Field and Reynolds, 2011), and bears (Holtgrieve et al., 2009). Whereas Pacific salmon are mostly a nutrient subsidy (but see Moore et al., 2007) as it is their bodies and gametes that provide resources for plants and consumers in freshwaters and riparian forests, other consumers may functionally link distinct ecosystems by actively feeding on resources in multiple ecosystems. For example, bears in the Pacific Northwest may feed on stream and riparian forest resources thereby linking aquatic and terrestrial ecosystems (Helfield and Naiman, 2006). These mobile consumers couple neighboring ecosystems (McCann et al., 2005; Rooney et al., 2006) and have the potential to translocate nutrients among ecosystems (Leroux and Loreau, 2010; 2012). Other examples include roe deer (*Capreolus capreolus*), which translocate significant quantities of N and P between their primary foraging grounds (croplands) and their primary resting grounds (forests) (Abbas et al., 2012), and lake trout (*Salvelinus namaycush*), which feed in both pelagic and benthic habitats and effectively couple these distinct lake ecosystems (Vander Zanden and Vadeboncoeur, 2002). What is evident from empirical research on spatial subsidies and mobile consumers is that flows of energy, material, and organisms can drive bottom-up and top-down processes across ecosystem boundaries.

Theory on spatial subsidies has shown that ecosystems that receive spatial subsidies tend to have stronger top-down cascading trophic interactions (Leroux and Loreau, 2008). However, many subsidies are seasonal, occurring in pulses over short time frames (Baxter et al., 2005; Anderson et al., 2008; Yang et al., 2010). The seasonality inherent in many spatial subsidies (e.g., insect emergence, litterfall, anadromous salmon; Baxter et al., 2005) may stabilize ecosystem dynamics by complementing seasonal local resource deficiencies and by shifting consumer pressure between allochthonous and in situ resources (Takitomo et al., 2002; 2009; Leroux and Loreau, 2012). Similar to subsidies at lower trophic levels, mobile consumers can stabilize coupled ecosystems by generating asynchronous responses of resources to predation, thus spreading out the top-down impacts of predation (Rooney et al., 2006; McCann and Rooney, 2009). Two mechanisms that may explain the role of energy, material, and organism fluxes on cascading trophic interactions across ecosystems are increased energy flux up an ecosystem (Leroux and Loreau, 2008; Rip and McCann, 2011) and species

competition mediated through a shared predator (i.e., apparent competition; *sensu* Holt, 1977).

If energy, material, or organism fluxes occur at lower trophic levels, these subsidies can flow up the ecosystem to support higher production of top consumers (i.e., top-heavy ecosystems), and thus larger indirect cascading effects of consumers in the recipient ecosystem (Leroux and Loreau, 2008). While some theoretical work that includes predator saturation has shown that top-heavy ecosystems can be mathematically unstable (Huxel and McCann, 1998; Rip and McCann, 2011), we argue that top-down trophic cascades are not necessarily a biologically destabilizing process but rather a fundamental component of many natural ecosystems. The availability of an allochthonous resource can lead to apparent competition among local and exogenous resources (Leroux and Loreau, 2010). This form of competition may be strongest if the subsidy is donor-controlled (i.e., consumer density does not affect the amount of resources consumed) and sustained, where a predator feeding on this subsidy may also exert strong top-down regulation of local resources. This indirect competition between the subsidy and local resource is an example of apparent competition. Subsidies, therefore, can result in trophic cascades across ecosystems, where resources in one ecosystem can influence the biomass, abundance, and production of neighboring ecosystems (Leroux and Loreau, 2012). Knight et al. (2005) provide convincing evidence of cross-ecosystem cascades where fish (*Centrarchidae* spp.) prey on aquatic dragonfly larvae, which reduces terrestrial adult dragonfly (*Odonata* spp.) abundance. This reduction in terrestrial adult dragonfly abundance resulted in an increase in terrestrial dragonfly prey (*Hymenoptera* spp., *Diptera* spp., and *Lepidoptera* spp.) and an increase in terrestrial host plant (*Hypericum fasciculatum*) production.

The effects of allochthonous resources on top-down regulation across ecosystems can be illustrated by adding an allochthonous plant resource, A , available to the herbivores in our herbivore–plant–soil ecosystem model. An empirical example of such a case is presented in the roe deer example discussed above (Abbas et al., 2012). Also, we add a parameter, π , which describes the herbivore's preference for the local plant. We do not include organismal nutrient recycling in this model, as we wish to focus on the effects of allochthonous resources on top-down regulation. The revised dynamical equation for herbivores with access to local and allochthonous resources is:

$$\frac{dH}{dt} = \pi \Phi_H + (1 - \pi) \Phi_A - \theta_H \quad (7)$$

where $\Phi_A = f_A(A)H = \alpha_A AH$, and α_A is the herbivore uptake rate for allochthonous resources. Eq. 7 paired with Eq. 1 and 3 leads to the following equilibrium: $N^* = \frac{I}{m_N + \alpha_P P^*}$, $P^* = \frac{m_H - (1 - \pi)\alpha_A A}{\pi\alpha_H}$, $H^* = \frac{\varepsilon_H(\alpha_P N^* - m_P)}{\alpha_H}$. An increase in the stock of allochthonous plants available to herbivores leads to an increase in the soil nutrient pools (i.e., $\frac{\partial N^*}{\partial A} > 0$, Fig. 1.4) and herbivore stocks (i.e., $\frac{\partial H^*}{\partial A} > 0$, Fig. 1.4),

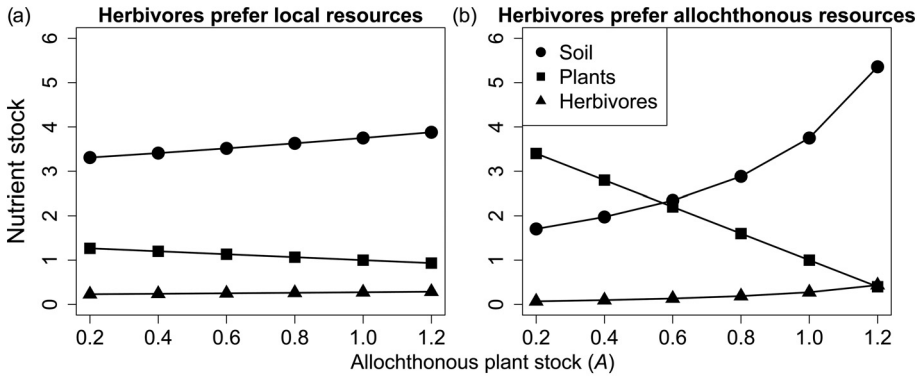


Figure 1.4 Effect of increasing allochthonous plant stock on herbivore, local plant, and soil nutrient stocks. The results are shown for (a) herbivores that prefer local resources ($\pi = 0.75$) and (b) herbivores that prefer allochthonous resources ($\pi = 0.25$). All other model parameters are $\alpha_P = \alpha_H = 0.4$, $e_H = e_A = 0.1$, $m = m_P = m_H = 0.4$, $I = 3$.

and a decline in plant stocks (i.e., $\frac{\partial P^*}{\partial A} < 0$, Fig. 1.4). These qualitative direct and indirect effects of allochthonous resources hold irrespective of the herbivore's preference for local or allochthonous resources (Fig. 1.4). The magnitude of the negative effect of increasing allochthonous resources on plant stocks, however, is larger when herbivores prefer allochthonous resources (Fig. 1.4).

The concept of meta-ecosystems (sensu Loreau et al., 2003) is a useful framework for understanding the dynamics of spatially extended ecosystems within a material cycling framework (Massol et al., 2011), and thus for understanding linkages between bottom-up and top-down interactions. Meta-ecosystem theory is particularly useful in the context of understanding bottom-up and top-down processes in space because source-sink dynamics emerge from meta-ecosystem models as a result of nutrient mass-balance constraints. For example, a flux of inorganic nutrients from an ecosystem with elevated nutrient biomass (i.e., source) to a local ecosystem with low-nutrient biomass (i.e., sink) has the potential to create conditions for switching the source-sink dynamics of this coupled ecosystem (Gravel et al., 2010; Loreau et al., 2013). What is more, if ecosystems are connected via material flows and consumers demonstrate a behavioral response to these resource flows, strong top-down forces in the recipient ecosystem may correspond to weaker top-down forces in its connected ecosystem (Leroux and Loreau, 2012). This occurs because most of the material flowing in this meta-ecosystem will be flowing in the recipient ecosystem. Resolving the cross-ecosystem effects of energy, material, and organism subsidies remains a challenge for both theoretical and empirical ecologists.

Classic theories of bottom-up, top-down, and trophic cascades make predictions for long-term or equilibrium dynamics (e.g., Rosenzweig, 1971; Oksanen

et al., 1981). This is often done for convenience, as the mathematical tools for analyzing equilibrium conditions are better resolved than for analyzing non-equilibrium conditions. Most empirical studies, however, track short-term responses of ecosystems to perturbations (Gripengberg and Roslin, 2007; Marczak et al., 2007). There is a need to expand our knowledge of trophic dynamics to non-equilibrium conditions, particularly in light of rapid environmental change (Hastings, 2010; also, see Chapter 14). As discussed above, many spatial subsidies occur as pulses (Holt, 2008; Leroux and Loreau, 2012) due to seasonality (e.g., floods/droughts), life history traits (e.g., anadromy), or other abiotic factors (e.g., rainfall), therefore the effects of space and time on bottom-up and top-down forces in ecosystems are not independent. Resource pulses can be frequent, such as marine wrack from wave action linking oceans to islands (Polis and Hurd, 1995), or infrequent, such as the mass emergence of cicadas every 13–17 years linking belowground and aboveground temperate forest ecosystems (Yang, 2004). The temporally variable driving forces of ecosystems can lead to variation in the extent of bottom-up and top-down regulation over time (Gratton and Denno, 2003b; Denno et al., 2005; Kerimoglu et al., 2013; Whalen et al., 2013). For example, epiphytic algae production in a seagrass ecosystem in the York River, Virginia, USA showed temporal variation in response to mesograzers abundance. Specifically, epiphytic algae production increased in response to nutrient addition in the fall when mesograzers abundance was low, but algae were regulated by mesograzers in the summer when mesograzers were abundant (Whalen et al., 2013). Temporal variations in bottom-up and top-down regulation can even occur in the absence of variable external driving forces as a result of the spatial dynamics of nutrient flows within meta-ecosystems, which generate asynchronous fluctuations of trophic levels in connected patches (Marleau et al., 2010). The transient or short-term response of ecosystems to resource pulses may improve our understanding of the interrelationship between bottom-up and top-down processes. Theory is beginning to investigate temporal variation in the strength of bottom-up and top-down processes (Holt, 2008; Hastings, 2012; Leroux and Loreau, 2012), but more work needs to be done. Given that most empirical studies are conducted on short time frames, the development and application of mathematical methods for analyzing the short-term dynamics of ecosystems will be necessary for bridging the divide between theory and empirical research on bottom-up and top-down processes in ecology. The mathematical concepts of reactivity, maximum amplification, and timing of maximum amplification hold promise for analyzing and understanding the transient dynamics of ecosystems (Neubert and Caswell, 1997; Neubert et al., 2009).

Conclusions

The theory of resource versus consumer limitation of organisms has evolved from the consideration of very simple ecosystems to more complex and realistic

cases that incorporate spatial and temporal variability of natural ecosystems. Guided by empirical research, which has presented a plethora of evidence showing that both bottom-up and top-down forces occur in most ecosystems, theory is now leading the way in our investigation of mechanisms to explain variation in trophic regulation. A better understanding of the relative roles and determinants of variation in bottom-up versus top-down regulation is critical as trophic-dynamic theory is the foundation for many real-world applications in natural resource and wildlife management. For example, the addition or removal of consumers is often used to control overabundant wildlife. Piscivorous fish are frequently added to lakes to indirectly control algal abundance (Findlay et al., 2005), and wolves have been added to Yellowstone National Park with indirect effects on aspen regeneration via predation on elk (Ripple and Beschta, 2005). Further understanding of bottom-up and top-down dynamics will improve our applications of these principles to natural resource management. Below we briefly outline five key areas for future directions for the development of theory on bottom-up, top-down, and cascading trophic interactions.

First, bottom-up, top-down, and in particular, cascading trophic interactions result in a diverse suite of indirect effects in ecosystems. There are a large number of consumptive and non-consumptive mechanisms (see Leroux and Loreau, 2010; Schmitz et al., 2010) that can lead to indirect effects in ecosystems, and theory can be useful in understanding the relative importance of these mechanisms in describing ecosystem dynamics. Such a mechanistic framework is necessary to improve our predictions of bottom-up, top-down, and cascading trophic dynamics in light of environmental change. For example, a meta-analysis of marine systems demonstrated that predator removal experiments show weak top-down effects of predators on marine phytoplankton (Shurin et al., 2002). Stibor et al. (2004), however, showed that top-down effects of jellyfish predation in their marine system are contingent upon the size of algae, with positive top-down effects occurring when large algae are initially abundant, negative effects when small algae are initially abundant, and no effect when algae are combined. This detailed study by Stibor et al. (2004) provides empirical evidence for the need for a better mechanistic understanding of the general patterns of top-down and bottom-up regulation. Consequently, understanding the structure of species interactions in this food web may help to interpret the resulting trophic dynamics, with implications for ecosystem functioning.

Second, ecological stoichiometry has the potential to shed light on the mechanisms for variation and interdependence in bottom-up and top-down processes in ecosystems. Stoichiometric models allow for explicitly tracking material cycling and for investigating the role of resource quality and consumer-resource quality mismatches on ecosystem functioning (Sterner and Elser, 2002). In addition, stoichiometric theory may help us identify bottlenecks for a switch between bottom-up and top-down processes in complex ecosystems. Ecological

stoichiometry theory is still mostly applied to relatively simple ecosystems, but several studies are shedding light on the implications of stoichiometric constraints in more complex cases (e.g., Grover, 2003; Leroux et al., 2012; Cherif and Loreau, 2013). For example, Leroux et al. (2012) show that consumptive and non-consumptive effects of consumers (i.e., top-down effects) can have direct impacts on the stoichiometry of their prey and indirect impacts on soil nutrient composition. This stoichiometrically explicit approach to studying organism-mediated nutrient recycling shows the interdependence between bottom-up and top-down processes in ecosystems.

Third, as discussed in the previous section, the strength of bottom-up and top-down regulation can vary in space. Spatial subsidies and mobile consumers can influence regulation of coupled ecosystems and the meta-ecosystem framework may be useful for guiding progress on this matter (Loreau et al., 2003; Massol et al., 2011). In addition to spatial subsidies and mobile consumers, species with complex life histories may influence bottom-up and top-down regulation across ecosystems. Schreiber and Rudolf (2008) derive a stage-structured model with juveniles and adults occupying different habitats to show how a change in the abundance of one stage can lead to abrupt shifts in abundances across ecosystems. Similarly, McCoy et al. (2009) show how organisms with complex life histories can generate strong trophic linkages across ecosystem boundaries in what they term “predator shadows.” Theory has an important role to play in deciphering the bottom-up and top-down dynamics of spatially connected ecosystems.

Fourth, there is ample empirical evidence of oscillating or temporally variable trophic control (e.g., Daskalov et al., 2007; Litzow and Ciannelli, 2007; Kerimoglu et al., 2013); therefore we must move beyond demonstrating patterns of trophic regulation to explaining variation in these patterns. As highlighted above, the meta-ecosystem framework (Loreau et al., 2003; Massol et al., 2011) and theory for temporally variable processes (Neubert and Caswell, 1997; Holt, 2008; Neubert et al., 2009; Hastings, 2012; Leroux and Loreau, 2012) will be useful for deciphering the mechanisms for variable trophic control and their implications for ecosystem functioning. In light of seasonality and rapid environmental change, the transient response of communities to perturbations (i.e., addition or removal of organisms, nutrients, etc.) may be just as important to the long-term average response (Hastings, 2004).

Finally, theory has an important role in generating and developing novel hypotheses, clarifying mechanisms, and providing testable predictions. But we must ensure continual feedback between theory and data to improve our understanding of bottom-up, top-down, and cascading trophic interactions in ecosystems. One way to facilitate this interaction is for theoreticians to use bottom-up and top-down metrics that can be easily measured in empirical settings. For example, response ratios are commonly used in experimental studies and

increasingly they are being used in theory (e.g., Shurin and Seabloom, 2005; Leroux and Loreau, 2008; 2010). In addition, both theory and empirical researchers need to better communicate the processes they are studying when referring to bottom-up and top-down effects to facilitate the integration of theory and data.

We are at a critical juncture in the ecological study of biomass pyramids, where the body of empirical and theoretical research has enabled us to move beyond describing patterns of bottom-up limitation and top-down regulation within and across ecosystems to explaining and understanding spatial and temporal variations in the patterns of trophic control. Progress along these lines may be hampered by the inconsistent and often confusing application of the terms “bottom-up” and “top-down.” We urge ecologists to be explicit about the processes they are studying as opposed to proliferating the general use of the bottom-up and top-down terms. We particularly believe that rapid progress in our understanding of trophic dynamics can occur by considering the multiple mechanisms of trophic interactions within a material cycling framework. The mathematical methods and tools now exist for studying spatially expansive ecosystems and temporal variability in trophic interactions. The integration of ecological theory with empirical studies will improve our predictions of trophic dynamics under global change.

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