Herbivory from Individuals to Ecosystems

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Key Words

Abstract

Herbivores not only consume resources, but they are resources for other
consumers. Consequently, they have much potential to mediate effects that
cascade up and down trophic chains in ecosystems. The way those effects
are mediated depends on individual-scale properties of herbivores including
constraints determining resource limitation, herbivore feeding mode, the
adaptive trade-off to balance nutrient intake and predation risk avoidance,
and the need to maintain homeostatic balance of elemental chemistry in the
face of widely varying elemental composition of plant resources. These fac-
tors determine the rates of ecosystem functions such as production, decom-
position and nutrient cycling. This review integrates those factors to build a
conceptual framework for looking at herbivore-mediated effects in ecosys-
tems. The framework systematically resolves how herbivores and carnivores
directly and indirectly interact with plants to shape ecosystem functions.
It can be used to motivate new field experimentation aimed at elucidating
mechanisms of trophic control of ecosystem function.

INTRODUCTION

The year 1960 was a notable point in the history of studies on herbivory. Hairston et al. (1960) introduced a new way of thinking about the dynamics of ecological systems by integrating the trophic-dynamic perspective of ecosystem ecology advanced by Lindeman (1942) with a population ecological perspective advanced by MacArthur (1958). The purpose of the paper by Hairston et al. was to explain why herbivores did not overrun their habitats and overeat their plant resources. That explanation, now known as HSS (Hairston, Smith, Slobodkin) or the Green World Hypothesis (Pimm 1992, Polis 1999) posits that the world is green because predators limit the abundance of herbivores and therefore reduce the degree to which herbivores limit plants.

The HSS paper was important on two grounds. First, it placed herbivory in a multitrophic ecosystem context and thereby formally recognized that herbivores not only consume their own resources but they are in turn resources for other consumers. Second, linking plant-herbivore and herbivore-predator couplets into a trophic chain created a framework for recognizing emergent indirect effects (Polis et al. 2000, Strauss 1991). In the case of HSS, carnivores are expected to have indirect top-down control over the plant trophic level through direct interactions with their herbivore prey.

The ecological community responded by effectively disregarding this core idea of HSS for about two decades. It instead followed an alternative research direction that addressed concepts and issues raised by the detractors of HSS who argued that a more parsimonious explanation for a green world is that not all plant material is edible because of nutritional inadequacy or protection by structural and chemical antiherbivore defenses (Ehrlich & Birch 1967, Murdoch 1966). This focus in turn spawned a long-standing tradition of exploring herbivory largely in the context of two trophic-level plant-herbivore systems that branched in two general directions: antiherbivore defenses (Bryant et al. 1991, Coley et al. 1985, Dearing et al. 2005, Karban & Myers 1989), and nutritional ecology (Mattson 1980, Robbins 1983, White 1975), including adaptive foraging (Belovsky 1997) and its most recent outgrowth, ecological stoichiometry (Sterner & Elser 2002). The underlying premise in all of these studies is that the world is entirely bottom-up controlled such that the supply rate of nutrients to plants is what primarily determines the nature and kind of plant-herbivore interaction (e.g., Coley et al. 1985, Mattson 1980, White 1975). The tradition of considering plant-herbivore interactions in the context of two trophic-level systems largely continues today despite decades-old appeals to consider issues of edibility, defense, and herbivore population control in the context of three trophic levels (Fretwell 1987, Hunter & Price 1992, Huntly 1992, Lawton & McNeil 1979, Leibold 1989, Odum & Biever 1984, Oksanen et al. 1981, Price et al. 1980).

I revisit the idea of examining herbivory in the context of a multitrophic ecosystem, but I do this in two new ways. I continue where HSS left off (DeAngelis 1992, Pastor & Cohen 1997) and extend the idea of indirect top-down control fully to ecosystem functions such as production, decomposition, and elemental cycling. I also move beyond a classic perspective that examines trophic interactions wholly at the population level.

Herbivores, being intermediate players in trophic chains, must balance the trade-off between eating and being eaten (Abrams 1984, Bernays 1998, Lawton & McNeil 1979, Schmitz et al. 2004). Understanding the implications of such trade-off behavior on ecosystems requires a perspective that views herbivores as individuals that flexibly change their behavior to balance fitness gains from foraging with fitness losses from predation among different environments (Abrams 1984, 1995; Agrawal 2001; Lima 1998; Schmitz et al. 2004). Such an individual-based perspective forces some rethinking about the nature of trophic control of ecosystems. This is because top-down and bottom-up control may not arise directly from factors such as changes in predator abundances or resource supplies to plants that are exogenous to herbivore populations, as is currently envisioned by much ecological theory. Rather, counterintuitively, the nature and degree of trophic control may
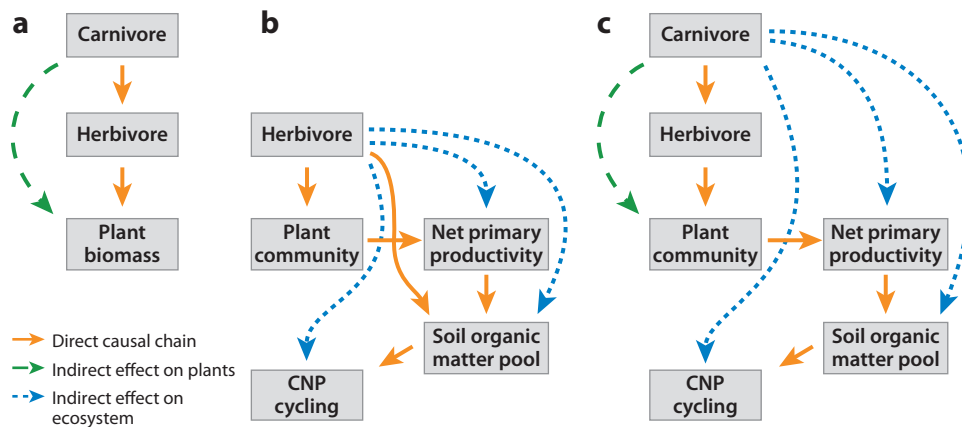
Figure 1

Conceptualization of the way to extend classic HSS theory to ecosystem function. Carnivore indirect effects on plant community composition (*dashed lines*) and on ecosystem functions (*dotted lines*) determined by the direct causal chain (*solid arrows*) running from predators, through herbivores through plant community composition. (*a*) According to classical theory for a three-trophic-level food chain (HSS), predators have indirect effects on the plant trophic level by directly limiting herbivore abundance. (*b*) Classic HSS theory can be extended to understand multitrophic effects on ecosystem function by first recognizing that herbivores directly impact the species composition of the plant community through selective foraging. Ensuing changes in mean leaf tissue chemistry owing to preponderance of uneaten plants will propagate indirect effects on ecosystem properties and functions like net primary productivity (NPP), the quality and quantity of plant matter entering the soil organic matter pool (SOM) to be decomposed and mineralized as nutrients (N mineralization). (*c*) HSS is then completely linked to ecosystem function by recognizing that carnivore indirect effect on ecosystems is mediated through direct effects with herbivores in ways that change the nature of herbivore indirect effects on ecosystems.

be an emergent indirect outcome of the way herbivores balance the foraging-predation trade-off at the individual behavioral level.

This review examines the different key ideas and empirical insights related to the role of herbivores in multitrophic ecosystems. The review is used to build a conceptual framework for looking at top-down effects on ecosystems mediated by herbivores. The conceptual framework is developed systematically in three major sections. I begin with the HSS concept of an ecosystem (**Figure 1a**) to address how the nature of herbivore resource limitation determines the emergence of carnivore indirect effects on the plant trophic level. I then bore into the plant-herbivore interface more deeply (**Figure 1b**) by examining herbivore resource selection and its direct and indirect implications for plant community structure and ecosystem functions like production, decomposition, and elemental cycling. Finally, I examine how the nature of carnivore-herbivore interactions determines the way carnivores indirectly affect ecosystem functions (**Figure 1c**).

HERBIVORE RESOURCE LIMITATION AND TOP-DOWN CONTROL

Much current thinking about the relative importance of top-down versus bottom-up control of ecosystems derives from meta-analytic syntheses (e.g., Borer et al. 2005, 2006; Chase et al. 2000). Such approaches make generalizable inferences based on the average trend among ecosystem types or along environmental gradients. In doing this, these approaches downplay variation in the strength of trophic control among systems by treating it as noise about the putative general trend. I argue and show here that the noise should not be overlooked because embedded within it is much

information about mechanisms of trophic control. This noise can represent contingency in the way that herbivores balance the trade-off, and hence the degree to which they mediate direct effects cascading from the top down. Thus, generalizable insights may not come from identifying average trends in the metadata, but rather from developing a predictive understanding of contingency (or heterogeneity sensu Hunter & Price 1992).

I begin by readdressing the whole notion of resource limitation from the perspective of herbivores acting as adaptive consumers that are attempting to maximize the intake of nutrients to meet needs for survival, growth, and reproduction (fitness). Adaptive herbivores effectively deal with an optimization problem that is constrained by their physical and physiological capacities within a given environment (Belovsky 1997). At the very least, all herbivores must maintain thermal homeostasis (Karasov & Martinez del Rio 2007), which sets upper limits on daily feeding time (Belovsky & Slade 1986). Because abiotic conditions can limit resource intake through time constraints, herbivores might become more limited by the ability to gather and ingest resources (relative resource limitation) than simply by total resource availability (absolute resource limitation). That is, herbivores could face a surfeit of edible resource but not consume much of it because of time constraints.

The idea that consumers could face either relative or absolute resource limitation was introduced quite some time ago (Andrewartha & Browning 1961; see also Polis & Strong 1996). It is an explicit assumption of mechanistic theory on population dynamics (Schoener 1973) that has been extended to predict trophic interactions (Schmitz 1992, 1993). I now review the essence of this theory to illustrate how alternative mechanisms of herbivore resource limitation influence plant trophic-level biomass and the strength of top-down control.

To keep things conceptual, trophic interactions and food chain dynamics are described using dynamical systems models that treat plants (P) and herbivores (H) as dynamically varying trophic levels and carnivores (C) as a fixed component of the environment of the plant-herbivore interaction. Such an assumption accords with many experimental systems examining trophic control in ecosystems. Nonetheless, the predictions that emerge using this simplification do not differ from theory that explicitly treats carnivores as a dynamically varying trophic level (cf. Schmitz 1992, 1993).

Plants are assumed to exhibit logistic growth [the qualitative conclusions do not change with other assumptions about plant growth; e.g., Monod-type growth (Tilman 1988; also Schmitz 1992, 1993)] and herbivores are assumed to compete exploitatively for resources. These simplifying assumptions allow a focus on the mechanism of herbivore resource limitation independently of other interactions (e.g., interference competition) within the herbivore trophic level. The generic structure of a model embodying these assumptions is

$$dP/dt = r\,P[1 - (P/K)] - f_H(P)H$$
$$dH/dt = H[\rho\,f_H(P) - m] - f_C(H)C, \qquad\qquad 1.$$

where r is the intrinsic growth rate; K is the carrying capacity of plants; $f_H(P)$ is the per capita herbivore consumption rate of plants (i.e., the herbivore functional response); ρ is the conversion rate of energy into herbivore production; m is the energy cost for maintenance and replacement reproduction, and $f_C(H)$ is the per capita carnivore consumption rate of herbivores. The implications of alternative forms of resource limitation can now be explored by substituting into Equation 1 appropriate mechanistic functions for $f_H(P)$.

If consumers are limited by relative food shortage, then per capita resource consumption depends on daily feeding time and the rate at which food can be harvested. Note that this form of resource limitation is not restricted to consumption per se because herbivores limited by digestive tract volume and digestive passage rate will exhibit similar dynamics (Schoener 1973). One function

describing time-limited resource intake that could apply generally to herbivores (Gross et al. 1993), is the Type-II functional response $f_H(P) = \alpha PT/(\beta + \alpha \tau P)$, where α is the instantaneous cropping rate (biomass $\cdot$ time^{-1}), τ is the handling time for a unit of plant biomass (time $\cdot$ biomass^{-1}), β is the biomass at which cropping rate is 1/2 maximum, and T (time $\cdot$ time^{-1}) scales the instantaneous cropping rate to the herbivore's longer feeding period, e.g., daily feeding time [Abrams (1987) and Penry & Jumars (1987) provide a counterpart to describe resource intake limited by digestive flow]. This form of resource limitation is assumed in classical theory that explicitly formalizes HSS (Oksanen et al. 1981) and has been referred to as a consumer-controlled system (Chase et al. 2000).

If consumers are limited by absolute resource supply, then per capita consumption depends upon the fixed amount of resources available at a location. In this case, all the edible standing crop is consumed by herbivores and an individual, on average, acquires an amount equal to the total edible biomass divided by the number of individual herbivores within a population or trophic level (Schoener 1973). This mechanism is described by the function $f_H(P) = \varepsilon P/H$, where ε (% $\cdot$ time^{-1}) is the proportion of total plant standing crop biomass that is edible per unit time (Schmitz 1992, 1993) and has been referred to as a resource-controlled system (Chase et al. 2000).

In such models, as well as in experimental systems, the existence of top-down control (i.e., trophic cascades) is resolved by systematically removing higher trophic levels and quantifying the response in the herbivore and plant trophic levels. One can do this in a modeling framework by setting $dP/dt = dH/dt = 0$ and solving for equilibrium densities of plants (P^*) in food chains without herbivores, with herbivores, and with herbivores and carnivores; and herbivores (H^*) in food chains with and without carnivores. The modeling shows that relative and absolute resource limitation of herbivores has different effects on total plant biomass (**Figure 2**). Carnivores should have an indirect influence on plant biomass whenever herbivores face a relative food shortage (**Figure 2**). This is because those herbivores surviving predation cannot compensate and consume a higher per capita share of resources owing to time limitations. Alternatively, carnivores should have no net effect on plants whenever herbivores face absolute food limitation (**Figure 2**). Predation, again, increases the per capita share of plant resources for surviving herbivores, but now the herbivores can compensate and consume that increased share. Thus, relative resource limitation leads to the emergent capacity of predators to control trophic structure; absolute resource limitation leads to a decoupling of top-down effects. This mechanistic insight underscores that it is somewhat inaccurate to distinguish between the two forms of trophic interactions as consumer versus resource controlled dynamics (e.g., Chase et al. 2000). In both cases, herbivore consumers are both limited by and control the abundance of plants by consuming them. Counterintuitively, the existence of top-down control is an emergent property of the way herbivores are limited by resources. Thus, the dichotomy between top-down and bottom-up control of ecosystems is a false one (see also Hunter & Price 1992).

One implication of this theory (Schmitz 1992) is that changing environmental conditions should alter the nature of herbivore resource limitation by altering the interplay between feeding time and resource supply. This could cause abrupt change in the nature of the carnivore indirect effects on ecosystem structure and function. I call this the Mechanism Switching Hypothesis of trophic control. There is direct and indirect empirical evidence for mechanism switching.

Chase (1996) experimentally tested for top-down control in a grassland ecosystem in Montana in which he manipulated the number of trophic levels in experimental food chains comprised of herbs and grasses, a generalist grasshopper species, and hunting spiders. Chase (1996) also manipulated abiotic conditions by shading one set of trophic-level manipulations and keeping a matching set of trophic manipulations as unshaded controls. The shading treatment reduced air temperatures by 4–8°C, which translated into a 53% reduction in grasshopper daily feeding time (349 min d^{-1} in unshaded control conditions versus 188 min d^{-1} in shaded conditions). The
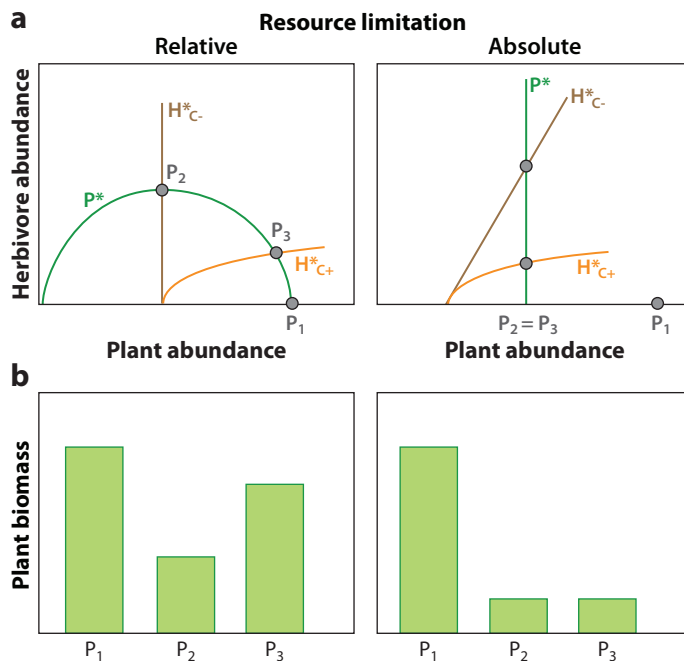
a

Resource limitation

Relative | Absolute

Figure 2

Qualitative predictions generated from mechanistic theory of food chain interactions in which herbivores face relative and absolute resource limitation. (*a*) The zero growth isoclines for plants (P*) and herbivores in the presence of carnivores (H^*_{C+}) and absence of carnivores (H^*_{C-}). Intersections of the plant and herbivore isoclines give plant abundance in plant-only one-trophic-level systems (P_1), two-trophic-level systems comprised of plants and herbivores (P_2), and three-trophic-level systems comprised of plants, herbivores, and carnivores (P_3). (*b*) The equilibrium plant abundances plotted as a function of the number of trophic levels. These graphs predict that relative resource limitation of herbivores should lead to a positive effect of carnivores on plant abundance, relative to a plant-herbivore system, i.e., emergence of top-down control; whereas absolute resource limitation should result in no net effect of carnivores on plants.

shading did not alter plant quality or plant standing crop biomass relative to unshaded conditions (Chase 1996). But in unshaded conditions the pattern of plant biomass among treatments matched predictions for herbivore absolute resource limitation (**Figure 2**); that is, carnivores do not have an indirect effect on plants. Shading and associated reduction in feeding time created conditions that matched predictions for herbivore relative resource limitation (**Figure 2**). The point here is that neither resource abundance nor the nature of the carnivore effect changed between the different environmental conditions. Instead, environmental changes altered how herbivores consumed resources leading to abrupt emergence of indirect top-down control by carnivores.

Indirect evidence for switching comes from a comparison of food chain manipulations across three sites (Connecticut and Montana in the United States, and Ontario, in Canada) that differed in biotic and abiotic conditions (Schmitz 1993, Schmitz 1994; Schmitz & Suttle 2001). This collection of studies used similar species of grassland plants, grasshoppers, and hunting spider predators. In Montana there was no significant difference in plant biomass between three-trophic-level treatments and two-trophic-level treatments consistent with conditions for herbivore absolute resource limitation (**Figure 2**). However, in both Ontario and Connecticut, carnivores had significant indirect positive effects on plant biomass relative to the two-trophic-level treatment, consistent with predictions for herbivore relative resource limitation (**Figure 2**). That these differences arise from

altered herbivore resource limitation is supported by data on plant biomass, aboveground net primary production (ANPP, g m^{-2} d^{-1}) and daily feeding time (min d^{-1}) (O.J. Schmitz, unpublished data). Total standing crop biomass in mesocosms that excluded herbivores and carnivores was three to four times higher in Ontario and Connecticut than in Montana. These differences arose because ANPP in Montana was 25–30% of that in Ontario and Connecticut. However, growing season temperatures in Ontario and Connecticut range between 17–23°C, whereas in Montana they range between 25–40°C, leading to a 28–36% lower feeding time in Ontario and Connecticut than in Montana. Indeed, grasshopper feeding times at the Montana site [324 $\pm$ 25 (1 SE; n = 10) min d^{-1}] matched Chase's (1996) study for unshaded conditions and the feeding times in Ontario and Connecticut [211 $\pm$ 23 (1 SE; n = 10) and 264 $\pm$ 20 (1 SE; n = 10) min d^{-1}] approached shaded conditions in Chase's (1996) study (O.J. Schmitz, unpublished data). That is, grasshoppers in Ontario and Connecticut faced relative resource limitation; those in Montana faced absolute resource limitation.

Differences in the mechanism of herbivore resource limitation determine whether or not carnivore effects propagate all the way down trophic chains to affect plants. But how does one distinguish between decoupling of top-down control from merely weak top-down control in meta-analyses of studies that do not resolve the mechanism of herbivore resource limitation? Here again theory (**Figure 2**) can provide some guidance.

Direct and indirect effect magnitudes can be calculated using the log ratio [ln(V_{P+}/V_{p-})] where V_{P+} and V_{p-} are community variables (herbivore abundance and plant biomass) in the presence (three-level treatment +) and absence (two-level treatment –) of carnivores (Schmitz et al. 2000), respectively. These effect magnitudes can be plotted in relation to each other on an x-y plane and in relation to a 45° reference line that represents equivalence in strength of direct and indirect effect of carnivores (**Figure 3a**). The log ratio effect magnitude of carnivores on herbivores should always be negative if carnivores are limiting herbivores, regardless of the way herbivores are resource limited (**Figure 2**). But the log ratio of the carnivore indirect effect should differ depending on the mechanism of herbivore resource limitation. It should be zero if herbivores face absolute resource limitation because total plant biomass in two-level and three-level systems should be identical (**Figure 2**). It should be positive if herbivores face relative resource limitation because total plant biomass in two-level systems should be lower than in three-level systems (**Figure 2**). Thus, systems in which top-down effects propagate to plants (herbivore relative resource limitation) should have direct and indirect effect magnitudes that fall within the x-y plane near the 45° line. Systems in which top-down effects do not propagate at all (herbivore absolute resource limitation) should have direct and indirect effect magnitudes that fall along the x-axis. This is exactly the pattern observed between the different experimental studies described above in which the mechanism of resource limitation is known (**Figure 3a**). This analysis underscores that simply estimating the average trend in strength of top-down control using the aggregate data without paying attention to the mechanism of herbivore resource limitation would give misleading insights because there are two very different signatures of trophic control embedded in the metadata.

Effect of Herbivore Feeding Mode

The discussion thus far implicitly assumes that herbivores are strictly consumers of plant tissue, i.e., herbivores are grazers or leaf chewers. Herbivores, however, can be grouped into two broad classes of feeding mode: grazing and sap feeding (Bernays 1998, Murdoch 1966, Odum & Biever 1984). Within these feeding modes there are differences in the degree to which herbivores are specialized or generalized in their use of plant resources (Bernays 1998). These feeding modes can lead to differences in the nature of trophic control of ecosystems. To illustrate this point,

a
b

Plant log ratio (carnivore indirect effect)

◆ Relative resource limitation
◆ Absolute resource limitation

● Specialist leaf-chewing
■ Specialist sap-feeding
▲ Generalist sap-feeding
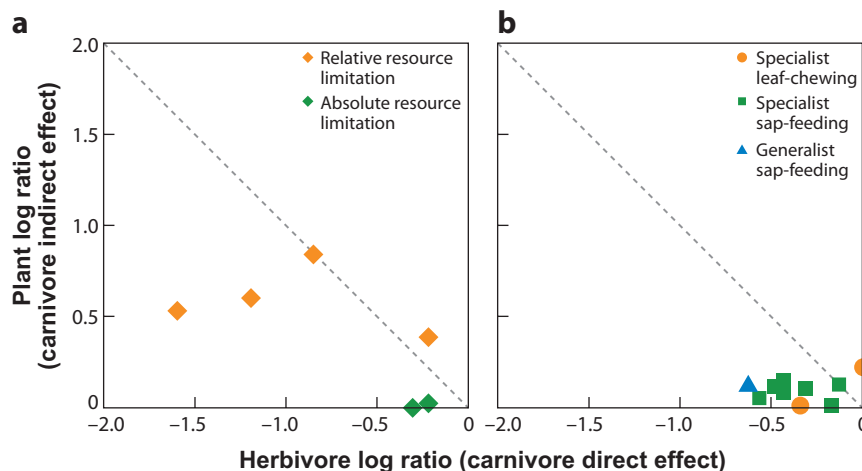
Herbivore log ratio (carnivore direct effect)

Figure 3

Relationship between the magnitude of direct effects of carnivores on herbivores and indirect effect of
carnivores on plant biomass. The 45° line is a reference representing equivalence of direct and indirect effect
magnitude. (*a*) Effect magnitudes for systems in which generalist leaf-chewing insect herbivores face
absolute resource limitation and relative resource limitation. Top-down effects are completely absent when
herbivores are absolute resource limited and propagate when herbivores are relative resource limited.
(*b*) Effect magnitudes for food chain experiments in which a single specialist leaf-chewing, specialist
sap-feeding, or generalist sap-feeding insect herbivore is present. In all cases except for one leaf-chewing
specialist herbivore, top-down effects do not appear to propagate at all. Data in (*a*) are from Schmitz (1993,
1994), Chase (1996), and Schmitz & Suttle (2000). Data in (*b*) are from Messina (1981), Fraser & Grime
(1998), Schmitz (1998), Cardinale et al. (2003) and O.J. Schmitz, unpublished data.

I gathered effect magnitude data for food chain experiments involving single herbivore species
from a previous meta-analysis of top-down control in terrestrial systems (sap-feeding herbivores
do not exist in aquatic systems) for which feeding mode and degree of specialization was known
(Schmitz et al. 2000). I also calculated additional metrics from those studies postdating Schmitz
et al. (2000) that tested for top-down control with single herbivore species. In all cases, the studies
used had to measure responses in terms of plant biomass (as opposed to plant damage) and had to
be conducted in a field setting, defined as plots or enclosure cages containing naturally growing
vegetation or crops within agricultural fields. These requirements avoid likely biased estimates
of interaction strength owing to poor surrogates for herbivore impacts on the plant trophic level
(i.e., plant damage) and to artificial confinement within laboratory arenas (Schmitz 2007). The
resulting data set, comprising 10 species from four different studies, indicates that sap feeders and
specialist leaf chewers all appear to be limited by absolute resource supply and therefore top-down
control did not propagate from carnivores to plants (**Figure 3*b***).

In addition, data for seven of the 10 herbivore species (sap feeders and specialist leaf chewers)
come from the same Connecticut study system used to examine top-down effects with generalist
grasshoppers (Schmitz 1998, O.J. Schmitz unpublished data). This analysis reinforces the previous
assertions that the nature of trophic control mediated by herbivore species can be quite different for
different herbivore species within the same system (Moon & Stiling 2002), so it is not appropriate
to infer the nature of trophic control of a whole system based on examinations of single herbivore
species within a system (Hunter 2001, Polis 1999).

That said, there may be certain herbivores whose dominant effects on ecosystems determine
overall ecosystem structure and function. For example, in the Connecticut old-field system, the

community-level patterns and top-down effect magnitude within experimental cages that exclude all herbivores but the dominant generalist grasshopper species (Schmitz 1998) matched community-level patterns and effect magnitudes within experimental field plots open to all herbivore species (Schmitz 2003). This insight, combined with the observed weak top-down effects propagating through specialist leaf chewers and specialist and generalist sap feeders in that same system (**Figure 3b**), suggests that the dominant grasshopper has an overriding effect on system structure and functioning. It is impossible to tell whether this result holds generally because studies reporting on carnivore effects propagating down to plants through herbivore species with different feeding modes—singly and collectively within the same system—do not yet exist. Thus, focusing on herbivore foraging mode as a functional trait determining trophic interactions would be one productive way to begin addressing the call to link functional diversity of intermediate trophic levels to ecosystem function (Duffy et al. 2007, Polis & Strong 1996).

The above treatment of trophic interactions offers a coarse-grained look at herbivory because it treats plants in the aggregate owing to the requirement that plant responses in studies of community-level top-down control be measured in terms of total trophic-level biomass (Hunter 2001, Polis 1999, Polis et al. 2000). However, this approach can give a distorted perspective about the nature and importance of higher trophic-level effects on ecosystem functions. Herbivores are quite selective among plant species and plant parts within plant species to meet tight nutritional requirements. Consequently, herbivores can have profound direct and indirect effects on ecosystem functions by changing plant community composition without necessarily having appreciable effects on total plant trophic-level biomass (Huntly 1992, Pastor & Cohen 1997, Ritchie et al. 1998) I next explore the basis for this selectivity and its implications for ecosystem function (**Figure1b**).

HERBIVORE RESOURCE SELECTION AND ECOSYTEM FUNCTION

In order to grow, survive, and reproduce, herbivores must maintain a homeostatic balance of chemical elements within their bodies (Elser et al. 2000, Karasov & Martinez del Rio 2007, Sterner & Elser 2002). But there are wide disparities between the chemical elemental composition of plant resources important to herbivore fitness (specifically carbon (C), nitrogen (N), and phosphorus (P) composition) and the elemental composition of herbivore body tissue (Elser et al. 2000, Sterner & Elser 2002). Plant species and parts are characterized by highly variable C:N:P ratios with a relatively high abundance of low-quality tissues, i.e., tissues with high C:N or C:P ratios (Karasov & Martinez del Rio 2007, Robbins 1983). Yet, herbivores must regulate body elemental composition within narrow and often low C:N or C:P levels to maximize survival, growth, and reproduction (Elser et al. 2000, Fagan et al. 2002). This discrepancy between resource quality and herbivore needs would entail huge fitness penalties if herbivores were not selective and thus did not optimize the balance of nutrients through resource consumption (Belovsky 1984, Raubenheimer & Simpson 1993).

Stoichiometry and Herbivore Resource Use

Herbivores maintain optimal stoichiometric balance in different ways that are related to their feeding modes. Leaf-chewing herbivores consume structural tissues that tend to be high in carbon (comparatively poor quality). They regulate their intake of different plant species and parts to achieve balanced nutritional intake (Belovsky 1997; Raubenheimer & Simpson 1993, 2004) and have evolved morphological and physiological means for processing and selectively retaining limiting elements (Bernays & Chapman 2000; Demment & Van Soest 1985; Yang & Joern 1994a,b; Zanotto et al. 1993, 1997). However, balancing nutritional chemistry requires being selective

in resource choice and therefore moving widely to encounter suitable, high quality plant tissue (Belovsky 1997, Bernays 1998). Sap-feeding insects, which do not ingest structural tissue, tend to rely on endosymbionts that can synthesize essential amino acids from ingested sucrose carbon (Bernays 1998, Febvay et al. 1999, Wilkinson & Ishikawa 2001). Sap-feeding species are comparatively stationary and have high daily feeding rates by moving large amounts of fluids through their bodies (Andersen et al. 1992, Bernays 1998). They may also possess extremely high conversion efficiency for organic compounds and amino acids (Andersen et al. 1989, 1992; Brodbeck et al. 1993, 1995).

The nature of the feeding mode in turn determines how consumers might impact plants. Leaf chewers, through compensatory feeding on different leaf tissue, may be able to use a wider range of plant species quality and thus impact the plant community more broadly and perhaps more heavily than sap-feeding species. Accordingly, the way herbivores with different feeding modes achieve stoichiometric balance may explain the basis for variation in trophic interaction strengths among species within and among ecosystems (Borer et al. 2005, Fagan & Denno 2004, Sterner & Elser 2002). To date, however, this remains a wholly unexplored area in trophic ecology.

My explicit focus on stoichiometry as a basis for herbivore resource selection is not an accident. Stoichiometry is a powerful way to unify evolutionary ecology of plant and herbivore strategies with ecosystem function (Coley et al. 1985, Elser et al. 2000, Loreau 2001, Reiners 1986) because it transcends plant traits; herbivore foraging, physiology, and fitness; and elemental cycling. It thereby provides a mechanistic way to trace the direct and indirect effects of consumers on ecosystem functions like decomposition, elemental cycling, and production to help explain contingent outcomes.

Resource Selection and Ecosystem Function

Herbivores can have important affects on ecosystem functioning by modifying the feedbacks between plant species and nutrient cycles (Huntly 1992, Loreau 1995, McNaughton et al. 1988, Pastor & Cohen 1997, Pastor & Naiman 1992, Ritchie et al. 1998). The pathway leading to this modification can be direct (**Figure 1b**) when herbivores excrete chemical elements back to the organic matter pool (Frost & Hunter 2007, Vanni 2002, Wardle 2002). The pathway can also be indirect (**Figure 1b**) when selective foraging alters plant community composition and, hence, the chemical composition of dead plant material entering the organic matter pool (Belovsky & Slade 2000, Hättenschwiler et al. 2005, Huntly 1992, McInnes et al. 1992, Pastor et al. 1993, Ritchie et al. 1998, Wardle 2002). For instance, selectivity to avoid plants with chemical or structural defenses can result in a community dominated by species that produce litter that is very recalcitrant to decomposition (high C:N or C:P ratios).

These different pathways can also determine the rate at which chemical elements are recycled in ecosystems. Fast cycling occurs when herbivores excrete readily decomposable organic matter whose chemical elements can be quickly taken up by plants within a single growing season (Belovsky & Slade 2000, Frost & Hunter 2008, McNaughton et al. 1988). Slow cycling occurs when selectively foraging herbivores alter the tissue chemistry or the plant species composition of litter entering the organic matter to be decomposed and mineralized. (See the sidebar, Fast and Slow Cycling and Top-Down Control.) The effects of such changes become manifest over the course of several seasons (Belovsky & Slade 2000, Frost & Hunter 2008, McNaughton et al. 1988). Within the slow cycle, herbivores might also accelerate or decelerate cycling depending on the nature of their resource choice (Loreau 1995, 2001; Pastor & Cohen 1997; Ritchie et al. 1998).

When herbivores increase tissue-loss rates of nutrient-rich plant species that tolerate herbivory, those plant species may compensate for herbivory with faster nutrient uptake and increased

FAST AND SLOW CYCLING AND TOP-DOWN CONTROL

Shurin et al. (2006) use the idea of fast and slow cycling to explain why one observes weaker top-down control in terrestrial than aquatic systems . They hypothesize that herbivores mediate top-down effects, but systematic differences between aquatic and terrestrial systems arise because of the way nutrients are cycled through the respective systems and because of the physical structure of aquatic and terrestrial vegetation. In essence, highly nutritious (very low C:N, C:P ratios) aquatic vegetation is readily consumed in high quantities. Moreover, waste organic matter tends largely to be excreted and enters the fast cycle in aquatic systems (see also Vanni 2002). In terrestrial systems, selectivity to avoid poor quality vegetation (high C:N or C:P ratios) leaves a high amount of unconsumed organic tissue to enter the slow cycle. Shurin et al. (2006) explore the attendant consequences of these different pathways to trophic structure.

production of high quality tissue (Loreau 1995, Ritchie et al. 1998). This arises because higher nutrient content in leaf tissue can enhance nutrient decomposition, nutrient turnover and, hence, nutrient supply to plants. Herbivores could have a decelerating effect on nutrient cycling by selecting plant species that are nutrient rich, thereby shifting community composition to plants that have nutrient poor tissues whose litter decomposes very slowly (Pastor & Cohen 1997, Ritchie et al. 1998). There is evidence for accelerating and decelerating effects as shown with the following selected examples.

In the Greater Yellowstone ecosystem, experiments with grazing elk (*Cervus elaphus*) compared ecosystem attributes in open plots that allowed grazer access to companion herbivore exclosure plots. Grazer free areas had 35% lower plant species diversity than grazed areas (Augustine & Frank 2001). This led to 22% lower plant tissue N in grazer-free areas than in grazed areas that caused a concomitant 24% rise in tissue C:N ratio (Tracy & Frank 1998), and a 53% reduction in N-mineralization rate (Frank & Groffman 1998). Grazer absence also yielded a fourfold increase in plant standing crop, even though NPP decreased by 24% (Tracy & Frank 1998). Thus, herbivore presence created a highly diverse plant community that was high in nutrient quality, which in turn accelerated the N-mineralization rate relative to areas without herbivores.

On Isle Royale, moose (*Alces alces*) prefer highly palatable (low C:N) deciduous species (Pastor & Cohen 1997). This diet preference can reduce the abundance of deciduous species enabling the proliferation of less palatable (higher C:N) species such as balsam fir (*Abies balsamea*). Comparisons of open plots and moose exclosure plots revealed that tree production was 1.6 times higher within exclosures than outside, leading to a similar trend in tree standing crop (McInnes et al. 1992). In addition, litter N quality within exclosures was 32% higher than in open plots, which, in turn, leads to a 6–11% rise in plant C:N quality (McInnes et al. 1992). This change in chemistry had the potential to decrease the N-mineralization rate by 15–30% (Pastor et al. 1993). Thus, herbivory lowered the diversity of the plant community and enabled the proliferation of species with higher C:N content. This, in turn, lowered N cycling owing to more recalcitrant litter feeding back up to lower tree production and standing crop.

A similar decelerating effect was observed after seven years of insect and mammal herbivore exclusion on a Minnesota prairie (Ritchie et al. 1998). Herbivore exclusion led to 1.75 times more plant biomass, 1.2 times higher litter N levels, and 1.4 times higher available soil N than in plots open to herbivory. These differences were brought about largely by a shift in the species composition of the plant community via selective herbivory on N-fixing legumes (Ritchie et al. 1998).

One may also see interplay between direct inputs through fecal matter (that varies with herbivore density) and selective herbivory such that along a gradient of herbivore density one can get

a 5–20% rise in ecosystem properties such as soil N, litter quantity and quality, and decomposition rate, or up to 10% declines in those properties depending on specific densities of herbivores (Belovsky & Slade 2000).

These examples suggest that herbivores can influence the nature of their own resource limitation through feedbacks brought about by resource selection. Selectivity alters the quality and abundance of organic matter entering the soil organic matter pool to be decomposed, mineralized, and then taken up by plants for production. This pathway of effect may, in turn, feed back to alter the interplay between resource production (supply) and daily feeding time and, hence, whether or not herbivores face absolute or relative resource limitation. This leads to the hypothesis that herbivores may indirectly engineer a Green World by creating conditions that favor the cascade of top-down carnivore effects to plants and ecosystem functions—an emergent property of resource limitation.

This possibility means that studies (and syntheses derived from them) that add fertilizer in experiments testing for the relative importance of top-down versus bottom-up control of ecological systems can give altogether misleading insights if fertilizer is added without consideration of its stoichiometric properties and the attendant changes it will cause to both the nature of herbivore resource limitation and resource selectivity by herbivores.

HERBIVORE-MEDIATED CARNIVORE INDIRECT EFFECTS ON ECOSYSTEMS

The fact that herbivores could engineer conditions leading to a Green World begs the question: Can top carnivores indeed have effects on ecosystem functions like decomposition, nutrient cycling, and productivity that are mediated by herbivores (**Figure 1c**)? Theoretically they can for several reasons. First, herbivores change their foraging behavior in response to predation risk (Lima 1998, Schmitz et al. 2004). Such foraging shifts stand to alter resource selectivity in order to balance fitness gains from foraging with fitness losses from predation. This selectivity should change the quality and composition of plant litter that enters the organic matter pool. Second, levels of litter quality and ensuing levels of elemental cycling can be affected by herbivore density in addition to resource selectivity (Belovky & Slade 2000, Persson et al. 2005). Third, carnivores can limit herbivore density.

Even though predators could conceivably have top-down effects on ecosystems, whether or not they generally do remains uncertain. Indeed, it is largely uncharted territory both theoretically and empirically. The theory that does exist (Thébault & Loreau 2003) is based on the assumption that carnivores indirectly influence ecosystems (soil nutrient pool, productivity) by reducing the abundance of herbivores that feed on a diverse plant community. Thus, carnivore indirect effects on ecosystems are assumed to be propagated through changes in plant diversity caused by altered herbivore abundance.

Carnivore Indirect Effects on Plant Diversity

In a classic study, Lubchenco (1978) showed that green crabs (*Carcinus maenas*) have a strong positive indirect effect on fucoid algal species diversity and abundance. This effect was thought to be brought about by green crab limitation of herbivorous *Littorina* snail abundance, which in turn released algae from pressure by selective feeding herbivores. This effect could also be driven by predator avoidance behavior of snails. Trussell et al. (2002) experimentally prevented predation by placing crabs in small perforated tubs within plots containing *Littorina* and fucoid algae but

presenting snails with crab cues. The snails reduced their foraging effort in response to risk. The net community-level effect was qualitatively similar to that observed in Lubchenco's study.

In a rocky intertidal system, experimental exclusion of bird [glaucous winged gulls (*Larus glaucescens*), black oystercatchers (*Haematopus backmani*) and northwestern crows (*Corvus caurinus*)] predation on sea urchins (*Strongylocentrotus purpuratus*) over two years resulted in a sixfold decrease in plant species richness (Wootton 1995) and orders of magnitude decrease in plant species evenness. This effect arose primarily because in the absence of birds, urchin herbivores reached such high densities that they could devastate the macroalgal community and leave behind only poor quality, inedible algal species (Wootton 1995).

Lakes are considered the archetype ecosystem for seeing cascading top-down effects of carnivores on plant abundance. But the nature and strength of that top-down effect can vary with lake size and depth and be manifest at the plant community level without having appreciable effects on total plant biomass. In one study system in particular (Tessier & Woodruff 2002), total phytoplankton abundance was unaffected by trophic structure, even though carnivorous fish were able to reduce the abundance of zooplankton herbivores dramatically. Carnivores appeared to cause herbivore-mediated changes in the composition and quality of the species comprising the phytoplankton community. Zooplankton herbivores preferentially fed on high-quality phytoplankton species, leaving behind a less diverse community of inedible species that underwent compensatory increase in biomass (Tessier & Woodruff 2002). Carnivores lowered zooplankton abundance, which, in turn, released edible phytoplankton from herbivore control producing a highly diverse phytoplankton community (Tessier & Woodruff 2002).

In an old-field ecosystem, *Melanoplus femurrubrum* grasshoppers prefer to feed on the grass *Poa pratensis* in the absence of predators enabling a competitive dominant plant *Solidago rugosa* to overwhelm the plant community (Schmitz 2003). Predation risk causes grasshoppers to switch from feeding on grass to seeking refuge in and foraging on the less nutritious *Solidago rugosa* without appreciable changes to total herbivore density (Schmitz 2003). This, in turn, releases other herb species from competitive domination thereby enhancing plant species diversity (evenness).

In a laboratory mesocosm experiment designed to emulate an estuarine system, Duffy et al. (2005) assembled food chains comprised of different combinations of blue crab (*Callinectes sapidus*) predators; amphipod (*Cymadusa compta*, *Ampithoe longimana*, *Gammarus mucronatus*) and isopod (*Erichsonella attenuata*, *Idotea baltica*) herbivores; and eelgrass (*Zostera marina*), macroalgal, and epiphytic plants. In this system, grazers preferred macroalgae and epiphytes to eelgrass. In food chains with a single grazer species, crabs on average caused a 1.4-fold increase in plant species evenness by suppressing herbivore consumption of macroalgae and epiphytes. The effect appeared to be a consequence of herbivores shifting their habitat use in response to predation risk (Duffy et al. 2005).

There are other notable examples in which predators appear to enhance the diversity of plants (Bruno & O'Connor 2005, Terborgh et al. 2001, Sergio et al. 2005). However, the chain of causality is not as clear as in the above examples because there are multiple species of herbivores within treatment groups.

When the mechanisms determining carnivore indirect effects on plants are elucidated in experimental studies, it appears that those effects arise from two kinds of carnivore direct effects on herbivores. Carnivores can alter herbivore density by capturing and consuming them. Alternatively, predation cues can cause herbivores to modify foraging activity to reduce predation risk. The former leads to a density-mediated indirect effect of carnivores on plants. The latter leads to behavior-[trait] mediated indirect effects. Are there predictable features of carnivores that lead to one or the other kind of indirect effect on plants?

Carnivore Indirect Effects on Ecosystem Function

Carnivore indirect effects appear to be related to an important predator functional trait—hunting mode—independent of predator taxonomic identity (Schmitz 2005). Sit-and-wait ambush predators cause largely behavioral responses in their prey because prey species respond strongly to persistent, point-source cues of predator presence. Widely roaming, actively hunting predators may reduce prey density, but they exert highly variable predation risk cues and are thus unlikely to cause chronic behavioral responses in their prey. These hunting-mode-dependent herbivore responses could lead to different cascading effects on plant species composition that should further cascade to affect ecosystem function (Schmitz 2006).

Evidence for carnivore hunting-mode-dependent effects on ecosystem function comes from experimentation in an old-field ecosystem comprised of three functional groups of plants (the grass *Poa pratensis*, the herb *Solidago rugosa*, and other herbs), the generalist grasshopper *Melanopuls femurrubrum*, and the sit-and-wait spider *Pisaurina mira* and active hunting spider *Phidippus rimator* (Schmitz 2008). The study showed that, from initially indistinguishable conditions between sit-and-wait and active hunting treatments, there are directional differences in ecosystem properties and functions after two years. Actively hunting predators caused a reduction in plant species diversity by changing plant dominance (evenness). This, in turn, enhanced ANPP and N mineralization. Sit-and-wait predators had slight positive effects on plant species evenness but reduced ANPP and N mineralization. The differences were brought about by predator hunting-mode-dependent effects on plant community composition. Biomass of the competitive dominant plant *S. rugosa* was 1.7 times higher in active predator treatments than in sit-and-wait predator treatments, and biomass of less competitive herbs in active predator treatments was half that in sit-and-wait predator treatments. The shifting composition of *S. rugosa* and other herb species caused plant species evenness to be 14% lower in the active hunting predator treatments than in the sit-and-wait predator treatments. The mechanism driving these differences in plant composition is a trade-off choice grasshoppers must make between feeding on grasses and seeking refuge in and feeding on the competitive dominant plant *S. rugosa* when facing predators. Grasshoppers tend not to exhibit chronic foraging shifts in response to widely roaming active hunters like *P. rimator* that present weak and variable cues, whereas they do exhibit chronic foraging shifts when facing sit-and-wait *P. mira* that provides persistent cues. These hunting-mode-dependent grasshopper responses, in turn, determine the nature of the indirect control spiders exert over the competitive dominant plant *S. rugosa* (Schmitz 2008).

By indirectly controlling plant community composition there was a 1.6 times higher level of net primary productivity in actively hunting predator treatments than in sit-and-wait predator treatments (Schmitz 2008). Plant matter decomposition rate was not different between treatments but N-mineralization rate in active hunting predator treatments was 33% higher than in sit-and-wait predator treatments because litter quality (C:N content) was 14% higher in active hunting treatments than in sit-and-wait treatments (Schmitz 2008).

Carnivores indirectly accelerated or decelerated N cycling by changing the nature of herbivore impacts on a highly competitive plant. Essentially, *S. rugosa* took up N quickly and translated it into plant production (Schmitz 2006). Predators indirectly altered the tissue N concentration entering the organic matter pool by changing the way herbivores impacted *S. rugosa*. Active predators released *S. rugosa* from control by herbivores. Sit-and-wait predators not only caused *S. rugosa* to be suppressed but they caused herbivores to select the higher quality N-rich parts of the plant.

In this system, carnivores had very weak effect magnitudes on total plant biomass (Schmitz 2006). This is because of modestly strong but antagonistic responses of the competitive dominant plant and other herbs described above. Even so, the effect of carnivores on ecosystem properties

and functions was up to three times stronger than on plant biomass (Schmitz 2006). Thus, the existence of weak carnivore effects on total plant biomass does not imply that carnivores will have weak effects on ecosystem function.

These findings may, however, be limited to leaf-chewing herbivores that alter their resource or habitat selection to evade predators. These effects may not arise for comparatively sedentary sap-feeding species that have evolved traits that make them cryptic to predators or that engage in symbiotic relations with species that protect them against predation (Bernays 1998). This may further explain why top-down carnivore effects are less likely to propagate to plants via sap feeders than via leaf chewers (**Figure 3**). It is also uncertain whether or not the effects of predator hunting mode on ecosytem function apply generally across ecosystem types or if the effects described for these single-predator experimental treatments will be maintained in more realistic systems that are typically comprised of multiple predator species and highly reticulate systems that are comprised of a diversity of herbivore species. The ideas presented here offer testable predictions that can guide research by focusing on carnivore hunting mode and herbivore feeding mode as functional traits determining the nature and strength of top-down effects on ecosystems.

CONCLUSION

Much needs to be done to evaluate the conceptual framework presented here. In particular, the current emphasis on meta-analytic syntheses to understand the nature of top-down control of ecosystems can only take us so far because of the limitations of the empirical data to reveal mechanisms. If we want to gain a predictive, mechanistic understanding of contingency, then we must undertake new kinds of experiments that, in the spirit of HSS, deliberately integrate classic ideas of ecosystem ecology (nutrient cycles and fluxes, productivity) with classic ideas in population ecology (trophic interactions, biodiversity) and with contemporary ideas on the evolutionary ecology of adaptive foraging strategies of individual consumers.

SUMMARY POINTS

1. Top-down versus bottom-up control may be an emergent property of the way herbivores are limited by their resources.

2. Herbivores may indirectly engineer a Green World by determining whether top-down carnivore effects can cascade to influence plants and ecosystem functions—an emergent property of resource limitation.

3. Carnivore indirect effects can cascade to affect ecosystem functions such as decomposition and elemental cycling by changing the way herbivores select plant resources.

4. The nature and strength of top-down carnivore effects on ecosystem functions depends on interplay between herbivore feeding mode (e.g., leaf chewing, sap-feeding) and predator hunting mode (e.g., active, sit-and-wait).

FUTURE ISSUES

1. Can herbivore feeding mode, resource use, and stoichiometric balance explain the basis for variation in trophic interaction strengths among species within and among ecosystems?

2. Can herbivores be grouped by feeding mode when attempting to derive a predictive understanding of the link between functional diversity and ecosystem function?

3. Can predator hunting mode generally determine the nature of trophic control of ecosystems?

4. How do predators with different hunting modes combine to influence ecosystem function in multiple predator systems?

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics*
articles may be found at http://ecolsys.annualreviews.org/errata.shtml