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REVIEW / SYNTHÈSE

Top-down and bottom-up forces in mammalian herbivore – vegetation systems: an essay review

Roy Turkington

Abstract: For almost 50 years ecologists have debated why herbivores generally don't increase in numbers to such levels as to deplete or devastate vegetation. One hypothesis is that herbivore populations are regulated at low densities by predators, and a second hypotheses is that plants are fundamentally poor food for herbivores. This has lead to two main hypotheses about the role of herbivores in structuring vegetation: the "bottom-up" and "top-down" hypotheses. Here I survey the literature, with a focus on field experiments designed to investigate the soil resource – vegetation – mammalian herbivore system, specifically asking five questions about how each trophic level responds to (*i*) resource addition, (*ii*) vegetation removal, (*iii*) herbivore removal or reduction, (*iv*) herbivore addition, and (*v*) the interaction of resource levels and herbivory? I use these to develop 12 testable predictions. I document the major areas of research as they relate to these 12 predictions, and use these to evaluate weaknesses and limitations in field methods. There are surprisingly few terrestrial studies that conduct factorial manipulations of multiple nutrients or herbivores, even though it is clear that these are essential. Specifically, I argue that a manipulative experimental approach is the most valuable way to advance our theory and understanding, and I advocate the continued use of long-term factorial field experiments that simultaneously manipulate soil resources levels and herbivory (preferably at multiple levels), repeated in a range of environments in which individual species or functional groups are monitored.

Key words: bottom-up, field experiments, herbivory, top-down, trophic cascades, vegetation regulation, world is green.

Résumé : Depuis plus de 50 ans, les écologistes se sont demandé pourquoi les herbivores n'augmentent généralement pas leur nombre pour en arriver à des populations susceptibles de ravager la végétation. Une hypothèse propose que les prédateurs assurent une faible densité des populations d'herbivores et la seconde suggère que les plantes constituent fondamentalement une nourriture pauvre pour les herbivores. Ceci a conduit à deux hypothèses principales sur le rôle des herbivores dans la structuration de la végétation, soient les hypothèses « bottom up » (du bas vers le haut) et « top-down » (du haut vers le ba). L'auteur analyse la littérature avec une attention particulière aux expériences sur le terrain, conçues pour étudier le système ressource édaphique – végétation – mammifère herbivore, en posant cinq questions spécifiques; comment chaque échelle trophique réagit à (*i*) l'addition de ressources, (*ii*) l'enlèvement de la végétation, (*iii*) la suppression ou la réduction des herbivores, (*iv*) l'addition d'herbivores, et (*v*) les interactions des échelles des ressources avec l'herbivorie? Sur la base de ces questions, l'auteur a énoncé 12 prédictions vérifiables. Il regroupe les principaux champs de recherche selon leur relation avec 12 prédictions, et les utilise pour évaluer les faiblesses et les limitations des méthodes de terrain. De façon surprenante, il existe peu d'études terrestres conduisant des manipulations factorielles de multiples nutriments ou herbivores, bien qu'il soit évident que celles-ci soient essentielles. Spécifiquement, l'auteur avance que l'approche par manipulation environnementale constitue la façon la plus valable pour étayer sa théorie et sa compréhension et il favorise l'utilisation à long terme d'expériences factorielles sur le terrain qui manipulent simultanément la variation des ressources édaphiques et de l'herbivorie (préférablement à plusieurs échelles), répétées sur un ensemble d'environnements, dans lesquels on assure le suivi des espèces individuelles ou de groupes fonctionnels.

Mots-clés : « bottom-up », expériences aux champs, herbivorie, « top-down », chaînes trophiques, régulation de la végétation, la planète est verte.

[Traduit par la Rédaction]

Introduction

Almost 50 years ago, Hairston et al. (1960) asked a simple, but provocative question about the limiting processes in biological communities, and whether they were more likely to be resource-driven from below, or consumer-driven from above. Although they didn't use the phrase, in essence Hairston et al. (1960) asked "why is the world green?" or "why

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Table 1. Hairston et al. (1960) argued that predators reduce the abundance of herbivores, thus allowing plants to flourish; this is often referred to as "The green world hypothesis" and this has since spawned a number of additional hypotheses.

Hypotheses	Summary
Exploitation Ecosystem Hypothesis (EEH) (Fretwell 1977, 1987; Oksanen et al. 1981)	Low productivity environments can only support low herbivore populations, and plant biomass will be limited by nutrient availability. In moderate environments plants can support herbivore populations but not predator populations and the system will be dominated by the plant–herbivore interaction. In rich systems, plants can support populations of both herbivores and predators, and predators will keep herbivore populations low enough to have little impact on the plant biomass
The world is prickly and tastes bad (Murdoch 1966; Pimm 1991)	Plants are not only green but most of them contain some defensive systems such as spines, thorns, tannins, and alkaloids, thus reducing herbivory upon them
Green desert (Murdoch 1966; White 1978; Moen et al. 1993)	This is a restatement of the world is prickly and tastes bad hypothesis. Here, plants play a direct defensive role in herbivore regulation and prevent herbivores from consuming many parts of green plant material
The world is white, yellow, and green (Oksanen et al. 1981; Pimm 1991)	This is a coloration of the EEH where "white" habitats such as tundra have low productivity, "yellow" habitats such as temperate forests and grasslands have intermediate productivity, and "green" habitats such as tropical forests have high productivity
The cruddy ingredient hypothesis (Hartley and Jones 1997)	This is a subcomponent of the world in prickly and tastes bad hypothesis. The "cruddy" ingredients of plants are poor food and prevent herbivores from readily obtaining nutrients
Large parts of the world are brown or black (Bond 2005)	Contrary to the usual view that terrestrial vegetation is largely determined by climate and soils, Bond argues that if fire is included as a consumer, then the world is "multicoloured": "brown" where mammal grazing controls vegetation; "black" where vegetation is largely controlled by fire; and "green" where vegetation is controlled by climate, rather than by consumers
Brown ground (Allison 2006)	A soil carbon-and-detritivore analogue for the green world hypothesis

don't herbivores increase in numbers to such levels as to deplete or devastate vegetation?" This question spawned a number of additional questions and hypotheses (Table 1) that address whether ecosystems are structured from the top-down, or from the bottom-up, and these have been accompanied by much debate and review (Hunter and Price 1992; Polis 1994, 1999; Kay 1998; Sinclair et al. 2000; Sinclair and Krebs 2001).

There are two main hypothesis about the role of herbivores in ecosystems. In the "bottom-up" or resource-control hypothesis, systems are regulated by resource flow from below, and higher trophic levels have no regulating effect on productivity or biomass on the levels below them (Hunter and Price 1992). Conversely the "top-down" or consumer-control hypothesis assumes that top predators are self-regulating, and each level then regulates the trophic level below (Menge and Sutherland 1976), and plants are limited by herbivores, rather than resource levels. Many other models involve variations of the top-down and (or) bottom-up hypotheses (e.g., Oksanen et al. 1981; Carpenter et al. 1985; Fretwell 1987; Oksanen 1990*b*; Sinclair and Krebs 2001). Understanding whether ecosystems are structured from the top-down or the bottom-up is not only of theoretical interest, but has management implications for conservation and wildlife management, especially in National Parks, Nature Reserves, and other protected areas. The relative effects of these forces is becoming increasingly important as humans alter the function and services of ecosystems (Millennium Ecosystem Assessment 2005; Worm et al. 2006) by overharvesting of consumers (Duffy 2003), increasing nutrients over large spatial scales (Vitousek et al. 1997; Smith et al. 1999; Stevens et al. 2004), eutrophication of lakes (Elser et al. 2007), acid pollution of lakes and terrestrial ecosystems, and clear cutting of forests (Sinclair et al. 2000). These anthropogenic influences are lowering species diversity of terrestrial ecosystems globally (Hillebrand et al. 2007) and are changing the strengths of top-down and bottom-up forces in ecosystems worldwide. Therefore, identifying how the relative strengths of these forces differ across different types of ecosystems is increasingly important for understanding how communities are structured, and especially across different spatial (Oksanen et al. 1995; Haynes et al. 2007; Gripenberg and Roslin 2007) and time scales (Olofsson et al. 2007).

Scope of this review

Ecosystem dynamics have been analyzed both by comparative methods and by manipulative experiments (Hunter 2001). These studies have tested models of ecosystem organization that involve variations of top-down and bottom-up hypotheses. The underlying principle in bottom-up hypotheses is that organisms are resource limited in some way (e.g., poor quality soils for plants, and plants of insufficiently high quality for herbivores because plants contain repellent or deterrent chemicals), even if those resources appear superficially to be abundant. With regard to plants, bottom-up hypotheses assume that herbivores have neither a regulating effect nor any influence on productivity or overall biomass on the plants. There are various top-down hypotheses with different implications on vegetation regulation. For example, Hairston et al. (1960) proposed that predators limit herbivores and therefore herbivores have only a small impact on plants. Caughley and Lawton (1981) in turn argued for a reciprocal interaction between herbivores and plants. In addition, the Exploitation Ecosystem Hypothesis (EEH) (Fretwell 1977; Oksanen et al. 1981; Oksanen 1988, 1990*a*, 1990*b*; Oksanen and Oksanen 2000) make different predictions for ecosystems dependent upon productivity levels

(Table 2). There have been a number of theoretical advances (Table 2) in understanding the relative roles of bottom-up and top-down forces and how they compare between aquatic and terrestrial systems (Polis 1999; Chase 2000; Borer et al. 2006; Shurin et al. 2006; Hillebrand et al. 2007; Gruner et al. 2008). Recent analyses by Shurin et al. (2006), Borer et al. (2006), Hillebrand et al. (2007) and Gruner et al. (2008) suggest that the mechanisms that govern top-down and bottom-up effects on plant biomass and diversity are consistent across a wide range of systems.

It is puzzling that mammals, especially large mammals, have not been more central in the trophic control literature, although some studies have shown that small mammals (e.g., Batzli 1975; Batzli et al. 1980; Howe et al. 2006) and "unapparent native herbivores" or "cryptic herbivores" can sometimes have as large an impact on vegetation as large mammals (Brown and Heske 1990; Keesing 2000; Howe et al. 2006; MacDougall and Wilson 2007). To specifically examine the soil – vegetation – mammalian herbivore system requires that we ignore predators, even though predators are likely to have significant indirect effects on plant community structure (e.g., Croll et al. 2005; Maron et al. 2006; Schmitz 2006; Ripple and Beschta 2007). It is also puzzling that so little attention has been paid to the decomposer community (Grime 2002) and the entire soil food web (Wardle et al. 2005); this important topic is gaining increased research attention but is outside the scope of this review (but see Niklaus et al. 2003; Zak et al. 2003; Wardle et al. 2004; Bezemer et al. 2006). My primary focus will be on field experimental investigations on the soil – vegetation – mammalian herbivore system. This is not a thorough review of the literature, but a survey in which I will summarize the major areas of research effort, and use these to identify current weaknesses in our knowledge.

As primary producers, plants provide energy and nutrients to the herbivores on which higher trophic levels depend (Power 1992). Therefore, understanding the factors that limit the quantity and the quality of plants is fundamental. Consequently, much research effort has been focused on the relative roles of resource levels and herbivores in regulating vegetation abundance (e.g., Pastor and Naiman 1992; Power 1992; Turkington et al. 2002). Most of the published literature agrees with the premise that top-down and bottom-up forces act simultaneously, in all sorts of ecosystems. Recent meta-analyses have shown subtle interactions between herbivores and resources in controlling the species diversity of primary producers in aquatic communities (Shurin et al. 2002; Worm et al. 2002; Nowlin et al. 2008) suggesting that these interactions might be important for controlling primary producer abundance across a range of ecosystems, environmental conditions, and types of producers. How far these general principles apply to terrestrial systems is still open to debate (Polis 1999; Chase 2000; Shurin et al. 2006). The current emphasis of the discussion is on deriving empirically based principles about what controls the strength and relative importance of the various forces under varying conditions, i.e., "context-dependent" effects (Burkepile and Hay 2006).

Experiments and predictions

To address the question of the relative importance of top-down and bottom-up forces in any vegetation type, ideally we would like to both increase and decrease the abundance of each trophic level (soil productivity, vegetation, and herbivores) and monitor the response in the remaining levels. We can easily add resources, remove vegetation, and exclude herbivores: increasing herbivore numbers can be done in some cases, but it is very difficult to reduce resource levels and to add vegetation. Regardless, from this we can then ask five questions about how each trophic level responds to (*i*) resource addition, (*ii*) vegetation removal, (*iii*) herbivore removal or reduction, (*iv*) herbivore additions, and (*v*) the interaction of resource levels and herbivory? From these questions we can make predictions about the direction of change in the biomass at each trophic level under different experimental treatments; in many cases, authors also report changes in productivity, species composition, and diversity. In addition, we can monitor responses of trophic levels to natural changes in herbivore density, such as that which occurs during the 8–11 year cycle in snowshoe hare populations (Krebs et al. 1992) in which densities may fluctuate from 5- to 25-fold, or by taking advantage of predator-free conditions created by disturbances (Terborgh et al. 2006), or the removal of carnivores from the Great Plains (Ripple and Beschta 2007). I will now summarize and formalize the predictions of responses to these five experimental treatments (Table 3) and then compare the results of some published studies with the predictions.

Resource addition

Resource addition will lead to an overall increase in the total biomass or standing crop of herbaceous vegetation

Much of our data come from comparative studies rather than experimental manipulations. McNaughton et al. (1989), using data from a wide range of ecosystem types, illustrated that herbivores consume proportionately less biomass in unproductive ecosystems such as tundra and temperate grasslands, and proportionately more in productive ecosystems such as unmanaged tropical grasslands. This relationship is particularly strong when comparisons are made among similar ecosystems. Shaver et al. (2001) reported that 15 years of N and P fertilizer addition to an Alaskan moist tundra increased aboveground biomass and primary production 2.5-fold. Chase et al. (2000) showed that producer and herbivore biomass both increased across a natural precipitation gradient in grasslands. In the grasslands of Argentina the biomass of mammalian herbivores increases with increasing productivity along a gradient of water availability (Oesterheld et al. 1992). Similar results have been reported from African savannas (Coe et al. 1976), the boreal forest understory (Nams et al. 1993; Turkington et al. 1998, 2002), tussock tundra (Chapin et al. 1995; Shaver et al. 1998, 2001), and arctic tundra heath (Grellmann 2002). Baez et al. (2006) reported that cover of plant functional groups was positively related to seasonal precipitation in aridland shrub vegetation. Steinauer and Collins (1995) demonstrated experimentally that plant production was strongly affected by urine addition in ungrazed prairie: an addition of both water and nitrogen. It is widely accepted that the abundance of medium-sized ungulates, particularly wildebeest and buffalo, is determined principally by their food resources (Coe et al. 1976; Sinclair 1979; East 1984; Mduma et al. 1999; Grange

Table 2. An outline of the development of the ideas associated with top-down and bottom-up control of vegetation.

Authors	Theoretical and conceptual advances
Hairston et al. 1960	The original statement of the Hairston, Smith, and Slobodkin (HSS) hypothesis that the world is green because predators, parasites, and disease keep herbivores rare
Murdoch 1966	A critique of HSS
Sinclair 1975	Showed that whole-year plant biomass values can be seriously misleading as a true index of food availability to herbivores, and that the relative importance of top-down and bottom-up forces can change seasonally
Fretwell 1977, 1987	The Exploitation Ecosystem Hypothesis (EEH) generalized the HSS to fewer or more than three trophic levels and proposed that strong consumption leads to an alternation of high and low biomass between successive levels
Oksanen et al. 1981	Developed the EEH model relating the trophic structure of ecosystems to their primary productivity; the effects of herbivores should be greater in relatively unproductive habitats, and with increasing productivity, the impact of herbivores should decrease
Menge and Sutherland 1987	Presented a model of community regulation that incorporated the effects of abiotic disturbance, competition and recruitment density
Hairston 1989	A review of trophic control and the experiments used to study it
Leibold 1989	Presented a model, and confirmed by experiments, that the effects of predators and nutrients on consumers (zooplankton) and resources (phytoplankton) depends on the diet breadth of the consumers
Ecology 1992,**73**(3) (www.esajournals.org/toc/ecol/73/3)	A special feature of four papers on top-down and bottom-up forces. All agree that top-down and bottom-up forces act simultaneously on populations and communities, and focus the question on what controls the relative strength and importance of the various forces under various conditions
Strong 1992	Argued for the importance of heterogeneity within and among trophic levels, and concluded that top-down forces do not cascade in high diversity systems
Brett and Goldman 1996	A meta-analysis that provided unequivocal support for the trophic cascade hypothesis in freshwater food webs
Polis and Strong 1996	Developed models to include the importance and dynamics of detritus, omnivory, resources crossing habitats, life history, nutrients, pathogens, resource defenses, and trophic symbioses. They concluded that donor-controlled and "multichannel" omnivory is a general feature of consumer control and central to food web dynamics
Stiling and Rossi 1997	A study that compared the strength of top-down effects of parasites and bottom-up effects of plants on herbivores demonstrating that bottom-up forces set the stage on which top-down forces may act
Polis 1999	Productivity and biomass distribution is a function of many factors that vary because habitats and time periods differ markedly. Emphasises the need to distinguish between species and community-wide cascades. Polis identified five under-studied areas that are essential to our understanding in these topics
Pace et al. 1999	Reported increasing evidence of trophic cascades in theoretically unlikely systems such as tropical forests and the open ocean, and a deepening understanding of the conditions that promote and inhibit the transmission of predatory effects
Oksanen and Oksanen 2000	Argued why both the Defence Diversity Hypothesis (DDH) and HSS are incomplete. Also reanalyzed the 1981 EEH model with a focus on endotherms, and outlined a research strategy on trophic dynamics
Sinclair et al. 2000, 2001; Krebs et al. 2001	A bold attempt to do a whole-ecosystem (boreal forest) experimental test of trophic level interactions including soils, vegetation, herbivores and predators
Hunter 2001	As well as clarifying terminology, Hunter argued that no single approach can provide an adequate description of the top-down and bottom-up forces that influence terrestrial herbivores, and suggested some possible areas for future research
Menge et al. 2002	Used the comparative-experimental approach to examine the role of geographic location (coastal ecosystems in different hemispheres) and oceanographic conditions (upwelling vs. downwelling) on bottom-up and top-down linkages
Burkepile and Hay 2006	Alterations to food webs and nutrient availability in marine ecosystems produce context-dependent effects that vary across latitudes, primary producers, and the inherent productivity of ecosystems
Schmitz 2006	Predators have large effects on ecosystem properties by changing plant diversity rather than plant biomass
Shurin et al. 2006	Aquatic–terrestrial differences in food webs are consistent across the global range of primary productivity and contrasts between aquatic and terrestrial food webs are driven primarily by the growth rate, size, and nutritional quality of autotrophs
Borer et al. 2006	Showed a consistent pattern across many ecosystem types that top-down effects of predation are transferred through more trophic levels than are bottom-up effects of fertilization

Table 2 (*concluded*).

Authors	Theoretical and conceptual advances
Hillebrand et al. 2007	Showed a general process that system productivity and producer evenness determine the direction and magnitude of top-down and bottom-up control of species diversity
Gripenberg and Roslin 2007	Urge that we switch our focus from whether the relative strength of top-down and bottom-up factors vary in space and time to why there is variation, how much there is, and at what spatial scale it occurs
Nowlin et al. 2008	Argue the need to elucidate the indirect effects and long-term implications of resource pulses in both terrestrial and aquatic ecosystems

and Duncan 2006). Grange and Duncan (2006) demonstrated that the biomass of buffalo, wildebeest, and zebra is lower on low nutrient soils, higher in areas with high soil nutrients, and also increases with rainfall. These studies don't distinguish whether increasing soil nutrients, or soil moisture, produces more abundant, or better quality, plant material or both. In general, these studies indicate a strong bottom-up influence in terrestrial communities where increased soil resources results in greater vegetation biomass.

However, the application of fertilizer does not always lead to increases in biomass and a number of studies from Boreal areas show that biomass remains relatively constant after N fertilization (Mäkipää 1994; Nordin et al. 1998; Skrindo and Økland 2002).

Resource addition will lead to a greater nutrient content of vegetation

Fertilization has many effects on plants and it is difficult to separate the effects of changes in plant quality from changes in plant quantity because plants usually grow faster when fertilized. For example, nitrogen fertilization usually increases foliar nitrogen levels (Glyphis and Puttick 1989; Melnychuk and Krebs 2005), decreases fibre and lignin content, and hence toughness, but it also tends to decrease concentrations of some secondary metabolites, particularly phenolics and tannins (Bryant et al. 1987; Hartley et al. 1995; Hartley and Jones 1997). In low productivity habitats such as the "sour veldt" grasslands of South Africa, and in semi-arid environments, plants have a lower protein content and higher concentrations of chemical defences against herbivores. The higher nutrient "sweet veldt" grasslands support a higher diversity and production of herbivores than do the less fertile "sour veldt" grasslands. Most studies support the prediction but an exception is found in Dutch heathlands where increasing nutrient availability lead to a decrease in nitrogen concentration and an increase in phosphorus concentration in the aboveground biomass of *Molinia caerulea* (Aerts and de Caluwe 1989).

Resource addition will cause a change in vegetation composition as faster-growing species increase in areas where resources have been applied

Many studies from a range of plant communities support this prediction and have shown that changes in fertility, primarily nitrogen, alter species composition (Tilman 1987; Bobbink 1991; Chapin et al. 1995; Shaver et al. 1998, 2001; Lepš 1999; Grellmann 2002; Rajaniemi 2002; Turkington et al. 2002). A classic series of experiments by, e.g., Jones (1933), showed this effect in managed grasslands. Stevens et al. (2004) showed that long-term, chronic nitrogen deposition in acid grasslands in Great Britain significantly reduced plant species richness. Dutch heathlands, once dominated by the evergreen shrubs *Erica tetralix* and *Calluna vulgaris*, have been replaced by the perennial grass *M. caerulea*, mostly owing to an increase of nutrient availability (Aerts and Berendse 1988, 1989; Aerts and de Caluwe 1989). Understory changes are common after nitrogen application to boreal forests (Gerhardt and Kellner 1986; Dirkse and van Dobben 1989); lichens and bryophytes typically decline (Kellner 1993), and grasses increase (Shaver and Chapin 1986; Tamm 1991; Mäkipää 1995). In general, in the boreal forest understory, long-term fertilization causes a shift from a well-mixed community of grasses, prostrate woody species, and herbaceous dicots to a community dominated by tall, erect grasses and herbaceous dicots. The low-growing species probably suffered the consequences of light limitation caused by by taller neighbours. The decline in some species may be due to a direct effect of added fertilizer. Arii and Turkington (2002) showed that even modest applications of fertilizer to populations of *Anemone parviflora*, in the absence of any neighbours, resulted in their decline. Short-term responses measured over the first few years are typically poor indicators of longer term changes in community composition such as in grasslands (Lawes, et al. 1882; Brenchley and Warrington 1958; Tilman 1988), old fields (Inouye and Tilman 1995; Rajaniemi 2002), Alaskan tundra (Shaver et al. 2001), and boreal forest (Nygaard and Ødegaard 1999; Turkington et al. 2002).

Vegetation removal

When vegetation is removedthere will be an increase in soil resource levels

This is one of the more difficult predictions to document because results are complicated by the removal treatment itself. For example, when vegetation is "removed" either the dead and decaying root systems are left behind, or there is serious disturbance to the system. In addition, removal of vegetation by clipping will have profoundly different consequences than if a systemic herbicide is used: the former leaves a living root system with the potential for regrowth, the latter produces a dead root system with all sorts of consequences for soil structure, physics and chemistry, microbial activity, and leaching. Nevertheless, a short-term rise in nitrate levels after vegetation removal has been reported many times, e.g., the Hubbard Brook Ecosystem Study (Bormann and Likens 1967; Likens et al. 1967). When neighbours were removed from an Alaskan tundra, inorganic soil nutrient availability increased with NH^+_4 availability, increasing less than either NO_3^- or PO_4^- (Bret-Harte et al. 2004). Removal of all vascular plants has been reported to increase NH_4^+ availability in soil solution over the winter

Table 3. Summary of major types of experimental treatments used to test bottom-up and top-down effects, and some predicted responses by the vegetation.

Experimental treatment and predicted responses by vegetation
Resource addition
An overall increase in the total biomass or standing crop of herbaceous vegetation
A greater nutrient content of the vegetation
A change in vegetation composition as faster-growing species increase in areas where resources have been applied
Vegetation removal
When vegetation is removed from a plot there will be an increase in soil resource levels
Herbivore removal or reduction
Vegetation standing crop will increase, usually accompanied by changes in vegetation composition
No change in vegetation standing crop
Plant secondary compound content will decrease
Soil resource levels will decrease because the larger protected and ungrazed plants will extract more resources from the soil
Herbivore addition
An overall decrease in the total biomass or standing crop of herbaceous vegetation
Manipulate both resource and herbivory levels
Interact to control vegetation with outcomes consistent with EEH
Addition of resources will lead to an increase in plant productivity but biomass may remain unchanged
Addition of resources may lead to an increase in grazing intensity

(Grogan and Jonasson 2003). The studies by Sinclair et al. (2000, 2001) in a boreal forest understory and J. McLaren (personal communication) in a dry grassland in the southern Yukon, also confirm the prediction showing that nitrate nitrogen levels were significantly higher in plots from which the vegetation had been removed.

However, measurements have often been made in a management context and generally the findings refute the prediction. Most likely this is because the emphases of management research are typically longer-term consequences rather than immediate measures. Several changes occur in topical forest soils following loss of biomass that may ultimately lead to nutrient losses from the soil. Canopy removal can lead to drying of soils and a reduction in microbial activity and decomposition. Decreased plant nutrient and water uptake lead to greater nutrient concentrations in the soil and soil solution, enhancing the potential for losses due to leaching and erosion (Uhl and Jordan 1984; Matson et al. 1987).

Herbivore removal or reduction

When herbivores are excluded or reduced, vegetation standing crop will increase

The literature on exclosure-based studies in forests in northwest Europe has been reviewed by Hester et al. (2000), and grassland exclosure studies covering a wide range of productivity levels has been reviewed by Milchunas and Lauenroth (1993). Fences have been erected in many habitat types to exclude everything from moose, musk ox, wildebeest, buffalo, zebra, and reindeer, to snowshoe hares, rabbits, voles, lemming, and other rodents. Almost invariably (but see following section) there is an increase in standing crop biomass and this is invariably accompanied by changes in species composition and diversity. Such results have been reported from a wide range of community types (Table 4) and these results indicate that mammalian herbivores are able to limit the biomass of diverse plant communities. An intriguing result from a grassland in southeast England showed that herbivore exclusion decreased net aboveground primary production in the short term, but increased it in the long term (Olofsson et al. 2007).

When herbivores are excluded or reduced, there will be no change in vegetation standing crop

Olofsson et al. (2002) showed that after 11 years of experimental treatment, aboveground plant biomass was significantly higher inside exclosures than in the open plots in a low productivity site, but that excluding herbivores had no substantial effect on standing crop in a tall herb meadow (also see Moen and Oksanen 1998). Baez et al. (2006) conducted long-term rodent exclosure experiments in low-productivity aridland ecosystems and concluded that rodents exerted no control on these plant communities. Likewise, John and Turkington (1995), and Turkington et al. (2001, 2002) found no consistent significant differences between the herbaceous vegetation inside and outside of exclosures, and no response has yet been detected at the most recent survey in 2008 after 22 years. Jefferies et al. (1994) conclude that there is relatively little evidence from northern ecosystems that herbivores influence plant species assemblages in the different communities in the long-term, but may have considerable influence on vegetation composition of communities in the short-term at the local scale. These findings are consistent with the Ecosystem Exploitation Hypothesis (EEH) (Fretwell 1977, 1987; Oksanen et al. 1981)

Table 4. Exclosure-based studies have been implemented in a wide range of community types.

Community type	References
African savanna	Sinclair 1975; McNaughton 1985; Belsky 1992; Goheen et al. 2004
Arctic tundra heath	Oksanen and Moen 1994; Grellmann 2002
Arctic-alpine tundra	Batzli 1975; Batzli et al. 1980; Mulder 1999; Olofsson et al. 2002
Arid lands	Brown and Heske 1990; Gibbens et al. 1993; Guo et al. 1995; Meserve et al. 2003
Forest edges	Manson et al. 2001
Mountain pastures	Hill et al. 1992
Mountain snowbed	Virtanen 2000
Subantarctic islands	Leader-Williams et al. 1987
Tallgrass prairie	Keesing 2000; Howe et al. 2006
Temperate grasslands	Bishop and Davy 1984; Milchunas and Lauenroth 1993; Chase et al. 2000; Peters 2007
Woodlands	McInnes et al. 1992

that in very poor environments, plant productivity will be too low to support sizable herbivore populations, so their removal will have little impact.

When herbivores are excluded or reduced, plant secondary compound content will decrease

Many have argued that the world is green because most plants are inedible, and full of indigestible components such as cellulose and lignin (Polis 1999) so the impact of herbivores is secondary compared with bottom-up nutrient limitations. However, the occurrence of secondary chemical defences in the first place may be due to strong top-down forces, thus highlighting a common theme that top-down and bottom-up forces interact in complex ways. It is now well documented that herbivory can increase secondary compound levels in plants (Tallamy and Raupp 1991; Karban and Baldwin 1997), but I am not aware of any studies where secondary compounds have been directly measured inside and outside of exclosures. Studies of antiherbivore defences of plants have proposed a variety of relationships between resource availability and plant defense that are relevant to models of herbivore regulation (Koricheva et al. 1998; Dyer et al. 2004). Sinclair and Smith (1984) and Sinclair et al. (1988) showed that phenolic compounds respond to browsing during the snowshoe hare cycle. Sharam and Turkington (2005) reported a significant daily cycle of sparteine concentration in leaves of the arctic lupine, with maximum concentrations during the night and minimum in the afternoon. This may be a temporally optimal response to higher levels of herbivory that occur at night. A closely related lupine species, *Lupinus polyphyllus*, can induce greater concentrations of several quinolizidic alkaloids, including sparteine, when damaged by herbivory (Wink 1983).

When herbivores are excluded or reduced, soil resource levels will decrease because the larger ungrazed plants will extract more resources from the soil

Herbivores often have both direct and indirect effects (Steinauer and Collins 1995), and positive and negative effects on soil nutrient mineralization rates and on plant nutrient availability (Frank and Groffman 1998; Ritchie et al. 1998), and consequently, the exclosure of herbivores can have complex and unpredictable outcomes. Urine and fecal depositions generally have a positive influence on the nutrient turnover rate. Stark and Grellmann (2002) excluded reindeer, and both rodents and reindeer, from nutrient-poor arctic tundra heath. In the exclosures, microbial respiration, microbial C, and extractable organic N were significantly increased, but soil NH_4 and NO_3 contents were not affected. It has also been reported that reindeer grazing decreases microbial respiration and microbial biomass C in boreal forests (Väre et al. 1996; Stark et al. 2000), whereas soil microbial C has not been affected by reindeer grazing in several arctic-alpine tundra heaths studied (Stark et al. 2000). Mohr and Topp (2005) excluded red deer from oak forests in central Europe and reported an increase in C_{org}, N_t, Ca^{2+}, and PO_4^{3-} on some sites. Thus, because of the complex interactions between herbivores, plants, soil processes, and microorganisms it is impossible to make consistent predictions.

It is appropriate that the decomposer community be briefly considered in this context. There are strong feedbacks and interactions between soil fertility, plant species, litter quality, and the decomposer community (Niklaus et al. 2003; Zak et al. 2003; Wardle et al. 2004; Bezemer et al. 2006) and this area is wide open for profitable research. In low-productivity systems we expect a large accumulation of low-quality litter and a comparatively small decomposer community (Grime 2002). This has global implications for carbon sequestration, as such systems are thought to be important carbon sinks due to the long-term accumulation of this "low quality" (i.e., high C:N ratios) litter (Christian and Wilson 1999). With increasing soil resource levels we predict larger and more dynamic decomposer communities. Below-ground processes themselves can be regulated by top-down grazing by microbivores like collembola and diplopods, and bottom-up factors such as N and P (Milton and Kaspari 2007).

Herbivore addition

An increase in herbivores will cause an overall decrease in the total biomass or standing crop of herbaceous vegetation

In 1944, 29 reindeer were introduced to St. Matthew Island (in the Bering Sea), which had a poorly developed land fauna. By 1963 there were 6000 reindeer; lichens had been completely eliminated as a significant component of the winter diet, and the reindeer population crashed during the following winter (Klein 1968). This is a classic and dramatic example, but there are innumerable examples of herbivores having significant impacts on vegetation (Huntly 1991; Hartley and Jones 1997; Mulder 1999). Nevertheless, outside of agriculture, there have been few experimental ma-

nipulations of herbivore densities. Three approaches have been used. First, observational studies have been done during the naturally occurring high densities of cyclic populations of snowshoe hares (Krebs et al. 1992) and voles and lemmings (Grellmann 2002), or by sporadic outbreaks of grazers such as snow geese (Jefferies et al. 1994). These have shown significantly increased impacts by the herbivores on the vegetation, and in the case of snow geese almost complete destruction of the vegetation. Second, using a combination of food additions and predator exclusion Krebs et al. (1992) and Hodges et al. (2001) increased population densities of snowshoe hares by more than six-fold to more than 600 hares·km^{-2}. Again, there was a significantly increased impacts of herbivory on the vegetation. Third, where predators have been reduced or eliminated, typically there is an increase in herbivore numbers that have a negative impact on the vegetation. For example, in the absence of wolves, beaver, white-tailed deer, and other ungulates become abundant and consequently severely deplete vegetation (McShea et al. 1997; Ripple and Larsen 2000; Pedersen and Wallis 2004; Beschta 2005). It is quite likely that Great Plain ecosystems were being profoundly altered by increasing levels of herbivory following the removal of large carnivores (Ripple and Beschta 2007). Likewise, the creation of predator-free islands in Venezuela caused an increase in leaf-cutter ants and howler monkeys, resulting in increased mortality and lower recruitment of seedlings and sapling cohorts (Terborgh et al. 2006). The eradication of feral cats from the subantarctic Macquarie Island lead to an explosion of rabbit populations which had major and wide-scale impacts on the vegetation (Bergstrom et al. 2009).

Interactions of resources and herbivores

Resource availability and herbivory interact to control vegetation

The predictions from this hypothesis are again dependent upon the productivity of the habitats according to the EEH (Fretwell 1977, 1987; Oksanen et al. 1981) and many of these issues have already been considered in earlier sections. The EEH has been partially verified by Chase et al. (2000) who reported that the strength of top-down forces in plant community composition of grasslands increases with net primary production. This suggests that net primary production is a strong regulator of trophic interactions but that the relative importance of top-down control on plant community structure and dynamics will be weakest in arid ecosystems where net primary production is chronically low (Leibold et al. 1997; Chase et al. 2000).

Addition of resources will lead to an increase in plant productivity but biomass may remain unchanged

The productivity of a system can be increased by fertilization, but the standing crop remains unchanged if the additional biomass produced is consumed by herbivores. This would seem to be an obvious question to address, yet there are few examples in the literature. Dlott and Turkington (2000) showed that fertilization resulted in increased survival and growth of transplants inside exclosures, but a decreased survival outside where the additional growth was consumed by herbivores. John and Turkington (1997) reported a similar result for some species eaten by snowshoe hares in the boreal forest understory.

Addition of resources may lead to an increase in grazing intensity

Data on the relative performance of fertilized versus unfertilized plants is sparse and conflicting. Onuf et al. (1977) and Glyphis and Puttick (1989) showed that fertilized plants suffered greater losses to herbivory, while Hartvigsen et al. (1995) argued that plants responded to fertilization with increased growth only in the absence of herbivores. Steinauer and Collins (1995) reported significant interaction effects of urine deposition and grazing on species richness, evenness, diversity, total cover of grasses, cover of several individual species, and on overall grassland community composition.

Limitations and difficulties

The development of a coherent ecological theory is subject to many difficulties, one of which is the lack of consensus about which factors will be important in which systems. This is partially due to the difficulty of designing experiments to disentangle these factors in complex natural ecosystems. The natural complexity of most communities limits us in three ways. First, multifactorial field experiments are often difficult, yet trophic interactions are by nature multifactorial, combining at a minimum, productivity by the plants and herbivory. Second, it is not possible to study every component of the system and then assemble all of the component parts into a working model. Third, ideally we should study the entire ecosystem as a unit, but for most terrestrial systems this poses logistical, experimental, statistical and funding nightmares. One such ambitious attempt to understand an entire ecosystem is the Kluane Boreal Forest Ecosystem Project (KBFEP; www.aina.ucalgary.ca/scripts/minisa.dll/144/proe/klrsprok/se+kluane+boreal*?COMMANDSEARCH) undertaken by Sinclair et al. (2000) and Krebs et al. (2001) in which they expended 157 person years of effort, between 1986–1996, to understand the dynamics of a Boreal forest ecosystem using manipulative field experiments. Other such ambitious attempts to conduct such studies are The Nutrient Network (NutNet; web.science.oregonstate.edu/~seabloom/nutnet) spearheaded by Eric Seabloom at Oregon State University, and the series of long-term, whole-ecosystem experiments began in 1982 at Toolik Lake, Alaska lead by John Hobbie and Gus Shaver (e.g., Shaver 2001; ecosystems.mbl.edu/ARC).

There are also a number of important conceptual issues that need to be considered in the design of field experiments, and yet their inclusion can stretch the logistic practicability of some experiments. This leaves us vulnerable to criticism that our field experiments are too abstract or too simple, and our hypotheses make trivial predictions. Others have noted that the level of replication and the spatial and temporal scales of manipulation required for appropriate tests are impractical in most systems (Englund and Cooper 2003). Many of these apparently insurmountable issues are not a signal to abandon our pursuit, but rather a signal that we might re-evaluate the questions we are asking and refocus our attention on different components of the overall question. Even such restricted tests can contribute to our understanding of ecological systems. Following are some of

the factors that must be considered when designing field experiments to explicitly test components of top-down and bottom-up regulation of vegetation.

Indirect effects

By focusing on the plants and on only three trophic levels, soils (resources), plants, and their vertebrate herbivores, we are necessarily limiting our tests to direct interactions where there is a physical relationship between the species such as herbivores eating plants, or plants absorbing resources. However, indirect interactions are also a reality in most ecosystems (Croll et al. 2005; Maron et al. 2006; Schmitz 2006), and here the impact of an organism is one trophic level, or more, removed. For example, in a meta-analysis Schmitz et al. (2000) showed that in 45 out of 60 studies, there were significant effects of carnivore removal on some plant variables. Other indirect interactions involve exploitation competition, apparent competition (Holt 1977), and indirect mutualism (Wootton 1994). Even though in terrestrial systems, indirect effects attenuate quite rapidly (Sinclair et al. 2000; Krebs et al. 2001; Shurin et al. 2002), Schmitz (2006) has demonstrated that weak trophic cascades do not necessarily lead to weak indirect effects of predators on plants; long-term manipulations of predators lead to changes in plant community structure through the alteration of plant dominance, and hence plant species evenness.

Response variables

Operationally, in the field we typically detect the effects of changes in one trophic level on another level by whether the biomass or productivity of one changes when the other is moderately perturbed from stable conditions but before a new equilibrium is established. On occasion, other plant variables such as reproductive output or concentration of secondary compounds are measured. Schmitz et al. (2000) and Schmitz (2006) showed that conclusions about the strength of top-down effects of carnivores varied with the plant-response variable measured, and Dlott and Turkington (2000) showed that it varied with the life history stage of the plant. Carnivores, in general, have stronger effects when the response is measured as plant damage rather than as plant biomass or plant reproductive output. Therefore, conclusions about the strength of top-down effects could be dependent on the plant-response variable measured.

Short-term vs. long-term responses

Operationally we typically measure immediate or short-term responses to manipulations. However, manipulation of any trophic level will often lead to transient dynamics (Tilman 1988) and short-term responses are generally poor indicators of longer term changes in the ecosystem (Olofsson et al. 2007). In the Park Grass experiments at Rothamsted, changes were still occurring after 90 years (Tilman 1988; Silvertown et al. 2006). Therefore, the magnitudes of initial responses may not be a reliable indicator of the relative strength of bottom-up and top-down forces at equilibrium and an appropriate timescale for assessing trophic cascades at the plant community level may extend well beyond that of typical field studies and a reasonable test would need to extend over multiple plant generations (Holt 2000).

Productivity levels

Fretwell (1977, 1987), Oksanen et al. (1981), Oksanen (1988*a*, 1990*a*, 1990*b*) and Oksanen and Oksanen (2000) proposed an hypothesis in which the influence of herbivores on vegetation depends upon productivity. In unproductive habitats, plant cover is too low or unpalatable to support large populations of herbivores: both plants and herbivores will be limited from the bottom-up. In intermediate habitats, there are insufficient herbivores to support viable populations of predators therefore herbivore numbers increase and have important top-down regulating effects on vegetation quantity and quality. However, in productive habitats both Fretwell and the Oksanens (see above in this section) argue that herbivores become sufficiently abundant to support a predator population which imposes top-down control of the herbivores. This effectively suppresses herbivore numbers and protects the palatable vegetation from being depleted. The suggestion then, is that productivity can shift the balance between bottom-up and top-down forces by altering the lengths of food chains. However, Crawley (1997) argues that although the probability of attack may be lower for plants in unproductive habitats, the consequences are more serious (Coley et al. 1985). Likewise, while plants in productive habitats are more likely to be grazed, they are better able to compensate. The EEH (Fretwell 1977, 1987; Oksanen et al. 1981) has been tested at a local scale using invertebrates (Fraser and Grime 1998, 1999; Carson and Root 1999) but is begging to be critically tested in a range of habitats over a wide spatial scale with vertebrate herbivores.

Community-level and species-level responses

Polis (1999), Polis et al. (2000), and Grime (2002) have made parallel arguments concerning a recognition of the level at which influences occur. Polis pointed out the necessity of making a distinction between community-level and species-level cascades, while Grime proposed measuring responses by functional type. Chase et al. (2000) also make a strong case for monitoring species composition rather than only a total community effect. At the community level, herbivores as a whole control the abundance of the plants as a whole. But in a species-level cascade, increases in a particular herbivore give rise to decreases in particular plants (or functional groups), without this affecting the whole community. This arises because selectivity differs among animal species. For example, in the Serengeti savannas, some grazers such as wildebeest follow the pulse of grass growth that occurs after rains and they consume most plants that they encounter (Sinclair 1975; McNaughton 1985). Other grazers, such as zebra and gazelle, are more selective choosing leaves of relatively high nitrogen and low fiber content, especially in the dry season (McNaughton 1985). In this case, the wildebeest are more likely to induce a community response, and the more specialist grazers induce a species response. The accumulating evidence seems to support a pattern of obvious community-level cascades in simpler communities such as pelagic communities of lakes and in benthic communities of streams and rocky shore and, but with much more limited cascades in more diverse terrestrial

communities (Sinclair et al. 2000; Krebs et al. 2001). An acceptance of the distinction between community- versus species-level cascades will help clarify many of our predictions.

Seasonality

Almost all environments vary seasonally and plants alter their allocation to defense on a seasonal basis, with allocation to growth during favourable conditions. This makes plants an unpredictable resource for herbivores with considerable fluctuations in the resources available to herbivores. In Serengeti grasslands, Sinclair (1975) showed that in the nongrowing season the excess of food in the growing season is no longer available to herbivores because it has changed both structurally and chemically. This means that whole-year plant biomass values can be seriously misleading as a true index of food availability to herbivores, and of course that the relative importance of top-down and bottom-up forces changes seasonally. Bottom-up processes occur because of limitation during seasonal shortages i.e., what looks like an abundance of food, implying top-down control, may not be because the primary control is the brief period of shortage, not the total or average over the year. In the boreal forest understory, snowshoe hare populations are limited by a shortage of winter food, consequently it is likely that hare population numbers in the summer are held at a level below that at which they may have an effect on the summer vegetation (Turkington et al. 1998, 2002). On arctic tundra heath, grazing by reindeer mainly occurs during their seasonal migrations outside the growing season, and by overwintering voles and lemmings Grellmann (2002). The temporary shortage of food could be a feature common to most terrestrial vegetation – vertebrate herbivore systems.

Spatial environmental variation

At the large scale this is the EEH (Fretwell 1977, 1987; Oksanen et al. 1981) as we compare the relative strengths of top-down and bottom-up forces in productive and unproductive environments. However, productivity and other stresses also change over local gradients at almost every spatial scale, but it is unclear at which point these gradients become irrelevant to the vegetation. The effects of single abiotic stresses on plant growth, defences, and herbivores have received considerable attention, but we know very little about the effects of multiple stresses, despite the fact that plants live in a complex and continuously changing world (Hartley and Jones 1997). Ideally we would need to test spatially explicit change in top-down and bottom-up forces along a landscape gradient where there is known variation in the resource levels of the soils, and the abundance of herbivores (see Oksanen et al. 1995; Haynes et al. 2007). Indeed, Gripenberg and Roslin (2007) have argued that because of spatial variation, we should switch our focus from whether the relative strength of top-down and bottom-up factors vary in space and time to why there is variation, how much there is, and at what spatial scale it occurs.

Disturbances

Fires, storms, and drought are also likely to alter the relative strength of top-down and bottom-up forces because they create gradients of differential impacts on plants and herbivores across landscapes (Denno et al. 2005). The interaction between fire and herbivory as shapers of vegetation has received remarkably little attention. However, Collins et al. (1998) showed that a loss of species diversity owing to frequent burning was reversed by bison, a keystone herbivore in North American grasslands. Bond (2005) argued that very large areas of the world are consumer controlled and he especially focuses on large mammals as biotic consumers and fire as an abiotic consumer. Fire has many analogies to herbivory, and fire-dependent vegetation is so widespread, that it seems long overdue to include fire in debates on the extent of top-down control of vegetation (Bond 2005), and perhaps include them in our experimental designs.

Pathogens and parasitism

Pathogens and parasites are ubiquitous (Burdon and Leather 1990, Kohler and Wiley 1992) and yet, because they are not considered a "trophic level," and it is virtually impossible to measure, or even estimate, the biomass of disease organism, they are difficult to incorporate into field tests (Polis and Strong 1996; Stiling and Rossi 1997). And yet, perhaps the only community-level cascade documented for a terrestrial system involved the rhinderpest outbreak in Serengeti (Sinclair 1979). Rhinderpest, caused by a member of the genus *Morbillivirus*, devastated ungulate populations with a consequent increase in vegetation biomass.

Conclusions

Debate and investigation into the relative importance of top-down versus bottom-up forces in structuring vegetation has been going on for nearly 50 years, and many authors have contributed significantly towards a predictive theory of food-web impacts on plant communities (Table 2). The experimental evaluation of the relative strength of top-down and bottom-up forces in terrestrial systems with mammalian herbivores is still largely lacking (but increasing) compared with aquatic systems where there have been many tests simultaneously manipulating both resource and consumer levels in enclosures, small ponds, and whole lakes. I will conclude by describing the types of approaches that have been used, or should be used in our continued investigation of the relative importance of top-down and bottom-up control of terrestrial vegetation.

Long-term and large-scale studies

One of the greatest obstacles facing field ecologists is the immense spatial and temporal variation that exists in nature. The level of replication and the spatial and temporal scales of manipulation required for appropriate tests are impractical in most systems (Englund and Cooper 2003; Van de Koppel et al. 2005). For most communities we can only guess what spatial scale is large enough but NutNet (web.science.oregonstate.edu/~seabloom/nutnet) provides a good starting point where they use grassland systems spread throughout the world that are at least visually quite homogeneous; the hypotheses described in this paper should be tested in a variety of different biomes. In addition, it would be ideal to test changes in top-down and bottom-up forces along a gradient where there is known variation in the resource levels of the soils, and the abundance of herbivores.

Multifactorial studies

A multifactorial approach specifically incorporating soil resource levels and herbivory is perhaps the strongest test, and is essential, to advance our understanding of the determinants of community structure. While there are many examples of two-factor field experiments in the literature, there are few fully factorial terrestrial field experiments with more than two factors (see Karban 1989; Graham and Turkington 2000) yet these are essential. There are surprisingly few terrestrial studies that conduct factorial manipulations of multiple nutrients or herbivores, even though it is clear that these are also essential (Elser et al. 2007; Harpole and Tilman 2007).

Multi-trophic level studies

Large-scale manipulation experiments carried out in lakes and marine intertidal systems have contributed significantly to food-web theory and population and community dynamics in aquatic systems. However, comparable studies in terrestrial systems are much more complex and much less common, and our theoretical understanding lags behind that of our aquatic colleagues. The KBFEP (Sinclair et al. 2000; Krebs et al. 2001) was an ambitious attempt to understand the dynamics of an entire forest ecosystem and included detailed studies of the top terrestrial and avian predators, many of the herbivores, trees and herbaceous plants, and soils. This multitrophic level investigation generated great insight into the dynamics of the ecosystem, and contributed significantly to advancement of theory, but can it be replicated in say an arid ecosystem, or a grassland? Most ecologists would agree that while these types of studies are immensely valuable, nevertheless they pose real logistical and funding difficulties. They may initially be best attempted using microcosms as done by Fraser and Grime (1998), especially if the decomposer and soil food web communities are to be considered.

Community-level and species-level studies

Whole-community effects are important and interesting, yet they mask many effects that happen at the species level. At the community level, the herbivores as a whole control the abundance of the plants as a whole, but to me that is not the most interesting question. The much more interesting question is how increases in a particular herbivore give rise to decreases in particular plant species or functional groups, and how these responses might vary by life history stage. Combining all of the plants and calling them "vegetation" obscures the obvious and interesting differences among the species such as their ability to compete, their vulnerability to grazing, their ability to recover from grazing, and how all of this influences species diversity (Worm et al. 2002).

Simple and complex systems

The accumulating evidence seems to support a pattern of obvious community-level cascades in simpler communities such as pelagic communities of lakes and in benthic communities of streams and rocky shore, but with much more limited cascades in more diverse terrestrial communities. Development of a robust theory will also require tests in systems with a range of complexity. The relative effects of top-down and bottom-up effects are likely to vary depending upon species diversity. I reiterate a point made by Schmitz et al. (2000) and Schmitz (2006) that understanding of trophic interactions, and specifically the relationship between species diversity and trophic control, could be greatly improved if future studies offer more details about the species composition, life history stage, modes of interaction, and the degree of interconnectedness among the study species. And given the limited evidence for whole-community effects in terrestrial systems perhaps it is time to focus on responses by individual species or on functional groups.

Microcosm and mesocosm studies

Even the simplest terrestrial ecosystems may contain hundreds of species and we can learn a lot from using simple more manipulatable systems such as mesocosms, or constructing simple experimental plant communities. But such methods are not without their critics (see the "Special Feature" of seven papers edited by Daehler and Strong 1996), and Carpenter (1996) argues that when microcosm studies are done without the context of appropriately scaled field studies, they become irrelevant and diversionary. However, microcosm studies have been profitably used by Fraser and Grime (1998, 1999) to test the effects of herbivorous insects on grasslands having different levels of productivity. Such controlled conditions permit researchers to generate experimental results and predictions considerably faster than is possible in the field. This approach may be particularly effective when studying soil processes (Verhoef 1996). In our context, the bigger difficulty is to construct simple artificial systems that can include mammalian herbivores.

Manipulative experimental studies

Developing a coherent theory of these competing hypotheses requires input from a variety of disciplines and methodologies. Chase et al. (2000) make an interesting observation that experimental manipulations of herbivores in grasslands often support the top-down view of important consumer effects, but natural patterns of standing crops and productivity typically support the resource-control view of concurrent increases of all trophic levels with productivity. Community structure and dynamics have been productively studied by comparative descriptive methods, and also by perturbation studies. Perturbation studies may take two forms. First, as described earlier, we may monitor responses of trophic levels to natural changes in herbivore density, or by taking advantage of new opportunities such as the creation of predator-free conditions. However, I feel strongly that to understand feedback processes and interactions between trophic levels, it is necessary to disturb the system with controlled experimental manipulations. The responses to these manipulations will identify which species and trophic links are important. I believe that a manipulative experimental approach is the most valuable way to advance our theory and understanding. In this context I advocate greater focus on long-term factorial field experiments that simultaneously manipulate soil resources levels and herbivory, repeated in a range of environments, and monitoring individual species or functional groups. Only then will we begin to understand the relative importance of top-down and bottom-up forces in structuring vegetation. And a deeper understanding will emerge when we integrate data from many different disci-

plines and studies at various spatial and temporal scales. Overall, the elucidation of clear patterns in the importance of top-down or bottom-up impacts on vegetation remains a challenge for the future, and no doubt, there are many exciting experiments still to be done.

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