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ARE TROPHIC CASCADES ALL WET? DIFFERENTIATION AND DONOR-CONTROL IN SPECIOSE ECOSYSTEMS¹

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INTRODUCTION

Trophic cascades mean runaway consumption, downward dominance through the food chain. Especially vulnerable are the autotrophs. Standing crop and coverage of the plant community are reduced wholesale when one or a few species of potent herbivores are not suppressed. In archetypical trophic cascades, overwhelming effects propagate down through three trophic levels. Primary carnivores or diseases, by suppressing herbivores, switch the substrate from open and virtually bare to well occupied by plants. The discovery that these potent forces extend through four levels, in some instances (Carpenter and Kitchell 1988, Power 1990b), is surely one of the most important in all of ecology of the last decade; secondary carnivores, by suppressing primary carnivores, unleash herbivores that clear the substrate and greatly decrease standing crop of plants. In true trophic cascades, pervasive top-down influence combines with the always strong bottom-up influence through the food chain to produce acute intertwining between population, community, and ecosystem processes (Carpenter and Kitchell 1988, Oksanen 1990, Power 1992; M. J. Wiley, *personal communication*). True trophic cascades imply keystone species (Paine 1980), taxa with such top-down dominance that their removal causes precipitous change in the system. But all trophic interactions do not cascade, and simple top-down dominance is not the norm of communities or ecosystems. This point is central to the issues of this Special Feature, to Hunter and Price's (1992) proposal that the null hypothesis of food webs should be bottom-up forces, and Power's (1992) search for appropriate models of population dynamics of consumer and consumed.

My premise is that true trophic cascades in the community sense are a relatively unusual sort of food web mechanics. I argue that, over the full range of ecological communities, evidence is that these cascades are restricted to fairly low-diversity places where great influence can issue from one or a few species; the majority of examples of true trophic cascades have algae at the

base and are aquatic. Analogously, Carney (1990) has argued that lenitic cascades are restricted to mesotrophic lakes. The corollary of my assertion is not necessarily that top-down forces are unimportant. Rather, consumption is so differentiated in speciose systems that its overall effects are buffered. Much buffering must come from defensive adaptations of the autotrophs in higher diversity systems, of corals and higher plants, adaptations not well developed by the algae and other lower plants that are involved in trophic cascades. I propose that differentiation and other sorts of refuges for the consumed generate an unbalanced reciprocity in speciose food webs; influences propagating up are not often matched by commensurate reciprocal influences. This unbalanced reciprocity amounts to donor control. In addition, complex side-to-side and reticulate suppression of cascading behavior are common in speciose food webs. Suppressing forces include consumption (predation and herbivory), interspecific competition, spatial and temporal heterogeneity, and habitat grain set in a stochastic matrix. The heterodox food web notions of Polis are pertinent to my reasoning (1991). Most importantly, we know about trophic cascades in streams and lakes because of experiments; there is insufficient experimental evidence for an understanding of speciose food webs in any general sense.

This is to agree with Hunter and Price's (1992) position that variability and heterogeneity (I favor the term "differentiation") of interactions at roughly the same trophic level are key to understanding community relations in ecosystems. The distinction is between the "unified" consumption, which we see in true trophic cascades, consumption lacking the variability emphasized by Hunter and Price, and consumption that does not generalize among the trophically similar species that we see in cascades. This distinction bears upon Power's (1992) focus upon productivity gradients, omnivory, disturbance, and the vexing question of appropriate population dynamic models.

THE VULNERABLE TURF OF SOME ALGAL ECOSYSTEMS

Autotrophs as a group are vulnerable and substrates are cleared of plants by intense herbivory in trophic

¹ For reprints of this Special Feature, see footnote 1, p. 723.

TABLE 1. (A) Potential trophic cascades, systems in which autotrophic standing crop is extremely vulnerable to herbivores, but where carnivore suppression of the herbivores is not apparent. (B) Actual trophic cascades, with both plants vulnerable to herbivores and herbivores vulnerable to suppression by first-level carnivores. In the most spectacular instances, these concatenated vulnerabilities extend to the second-level carnivores, among four trophic levels. Asterisks indicate interesting aspects of the examples.

Habitat and autotrophs	Herbivores	First carnivore or disease	Second-level carnivore	Reference
A. Potential trophic cascades				
Rocky seashores, epilithic algae	invertebrates and fish			Lubchenco and Gaines 1981, Fig. 2; Carney 1990, Fig. 1
* Sediment and algae are removed by the herbivore, a littorine snail, which was recently introduced to North America. Herbivore causes great habitat changes; rocky shores come to replace mud and <i>Spartina alterniflora</i> .				Bertness 1984
Arctic moss banks	lemmings	?		Oksanen 1983
B. Actual trophic cascades				
Tropical and temperate streams	catfish, minnows	birds, bass		Power 1984, 1990a, Power et al. 1985
* Sediment also cleared away by the herbivorous catfish				
Temperate trout streams, epilithic algae	caddisfly larvae	microsporidian disease of caddisflies		M. J. Wiley, <i>personal communication</i>
* New disease, unstable; local extinctions and recolonizations				
Ocean margin, giant kelp (questionable example)	sea urchins	sea otters		Dayton 1985, Elner and Vadas 1990
Temperate streams, filamentous algae	midge larvae	fish fry insect predators	large steelhead, roach	Power 1990b
Temperate lakes, phytoplankton	zooplankton	planktivorous fish	piscivorous fish	Carpenter et al. 1987, Carpenter and Kitchell 1987
* High temporal and spatial variance in interspecific effects, deriving from complexities of behavior and life history.				

cascades (Table 1). True trophic cascades are systems built upon two levels of Paine's (1980) keystone species. In Table 1, before the list of examples of true trophic cascades, are listed "Potential trophic cascades." This category includes algae and herbivores of some streams and mesotrophic lakes, where autotrophs as a group and their substrate are vulnerable to keystone herbivores (Lubchenco and Gaines 1981, Carney 1990). The one terrestrial system in this category is the arctic moss-based food ladder, with lemmings as consumer (Oksanen 1983). When lacking primary carnivores sufficiently dense or effective to suppress the potent herbivores, only the bottom two-thirds of the vertical architecture necessary for a trophic cascade is present in potential trophic cascades. If there were a potent carnivore to suppress the herbivore, these systems could be caught up in a trophic cascade.

The list of "Actual trophic cascades" appears in Table 1. These are found in some tropical and temperate

streams, trout streams, temperate lakes, and kelp forests, perhaps. An almost bare substrate or clear water, greatly reduced in standing crop of primary producers, is the result of normal herbivory in these systems. As a matter of course, normal increases in grazer density drastically reduce epilithic algae or phytoplankton where archetypical trophic cascades occur. A fairly complete literature has developed illustrating keystone herbivory in streams (Lamberti and Resh 1983, McAuliffe 1984, Hart 1987, Hill and Knight 1987, Feminella et al. 1989).

Kelp forests *sometimes* appear to be at least potential trophic cascades, with sea urchins, and in some cases amphipods, mowing down these large algae and clearing the substrate. The population dynamics of these long-lived herbivores are enigmatic, however. The roles of the carnivores: sea otters, lobsters, and fish, are poorly understood in the eastern Pacific (Estes et al. 1978, Dayton 1985, J. A. Estes, *personal communication*)

and controversial for the western North Atlantic (Elner and Vadas 1990). There is a distinct possibility that this is a donor-controlled system, without effective carnivore suppression of the herbivore. Episodic settlement of the urchin herbivores, rather than lost suppression by carnivores, may account for the periodic runaway grazing. Healthy skepticism of simple dominant top-down forces is due even in these relatively depauperate food webs.

The most spectacular true trophic cascades are four-tiered. In one temperate stream, large steelhead and roach suppress fish fry and insect predators, allowing herbivorous midge larvae to increase to suppress filamentous algae (Power 1990b). Four-tiered cascades in lakes fall from piscivorous fish that suppress planktivorous fish, allowing zooplankton to increase enough to suppress phytoplankton, thus clarifying the water; both top-down and bottom-up forces are intense in these four-tiered cascades (Carpenter et al. 1987). The top-down forces are unified and homogeneous in these spatially discrete and isolated systems.

A fascinating variation on the theme, so new as to be unpublished, concerns a microsporidian disease, *Cougourdella* sp., of the nymphs of the herbivorous caddisfly *Glossosoma nigrum*, which is the dominant grazer in Michigan cold-water streams (M. Wiley and S. L. Kohler, *personal communication*). Previous to the advent of the disease in these streams, both biogeographic comparisons and manipulations had shown periphyton biomass to vary linearly with density of the caddisfly (McAuliffe 1984, Kohler 1992). Soon after appearing, prevalence of the disease increased to >90% of *G. nigrum* nymphs in several streams, with density decreasing from a mean of >2000 nymphs/m² to virtually zero. Algal biomass increased by as much as an order of magnitude after the collapse of the diseased caddisfly populations. Interspecific competition is intense among herbivorous insect nymphs in these streams. Species formerly suppressed by the dominant caddisfly increased greatly as the disease built up. However, the herbivores released from competition are not able to graze the substrate clean, and this trophic cascade may depend upon a particular herbivore species. The disease and its host appear to be unstable, with wide density oscillations of the pathogen. This is consistent with the predilection of Carpenter et al. (1987) for nonequilibrium models of trophic cascades.

In these cases, herbivores unsuppressed are able to open a large fraction of the substratum and reduce standing crop of autotrophs, usually by an order of magnitude or more. In all, primary carnivores (or a disease of the herbivores!) can suppress the herbivores to allay their effect. Thus, both the herbivores and the carnivores function as keystones. Intense unified influences of primary carnivores cascade down through her-

bivores and then through autotrophs to have tremendous community-wide influence.

BUT NOT EVEN ALL ALGAL ECOSYSTEMS CASCADE

The large majority of trophic cascades have algae at the base, and most are in isolated, discrete freshwater habitats, streams and mesotrophic lakes. With no indication of either keystone herbivores or keystone carnivores, most temperate rocky seashores are characterized by large standing stocks of algae in the form of seaweeds (Hay and Steinberg 1992). On tropical shores of oceans, though intense herbivory can regularly maintain patches of open substrate, algal-based food webs of oceans are not as volatile as those in discrete freshwater habitats. The same is true for coral reefs, which are not changed fundamentally by the removal or addition of any single consumer species (Lessios 1988). There is much omnivory, substitutability of species, and compensation among species for the functions of others (Menge and Lubchenco 1981, Menge and Farrell 1989). In shallow, marine, hard-bottom habitats, physical prey refuges together with dispersal generate great spatial heterogeneity (Menge and Olson 1990, Hixon and Menge 1991). This imposes differentiation in space and time among trophically similar species. Spatial and temporal heterogeneity and tangles in trophic architecture prevent intense consumption from becoming runaway consumption; these are not trophic cascades.

The propagation of unified and potent herbivory through the entire autotrophic community in true trophic cascades is not a result of unique herbivores. The mollusks, crustacea, fish, insects, and voles in Table 1 are a broad taxonomic selection from herbivores in general. Likewise, the densities of consumers in potential and true trophic cascades are not higher or more volatile than in other ecosystems without these intense influences. Outbreaks of the densest herbivores in terrestrial ecosystems, insects, often reach levels as high or higher than those in true trophic cascades without clearing the substrate (Barbosa and Schultz 1987).

General treatments of algae-herbivore interactions that apply to these issues can be found in Lubchenco and Gaines (1981): redrawn here as Fig. 1A, and in Carney (1990), redrawn as Fig. 1B. These figures relate abundance of algae with their invulnerability to and defenses against herbivores. As herbivore effectiveness increases, edible algae are suppressed, thus releasing from competitive suppression the inedible or defended algal taxa in Fig. 1A. I have added the downward arrows indicating the effects of herbivory and interspecific plant competition. Trophic cascades occur when the plant community is composed entirely of plant-herbivore species combinations in the "Edible" cate-

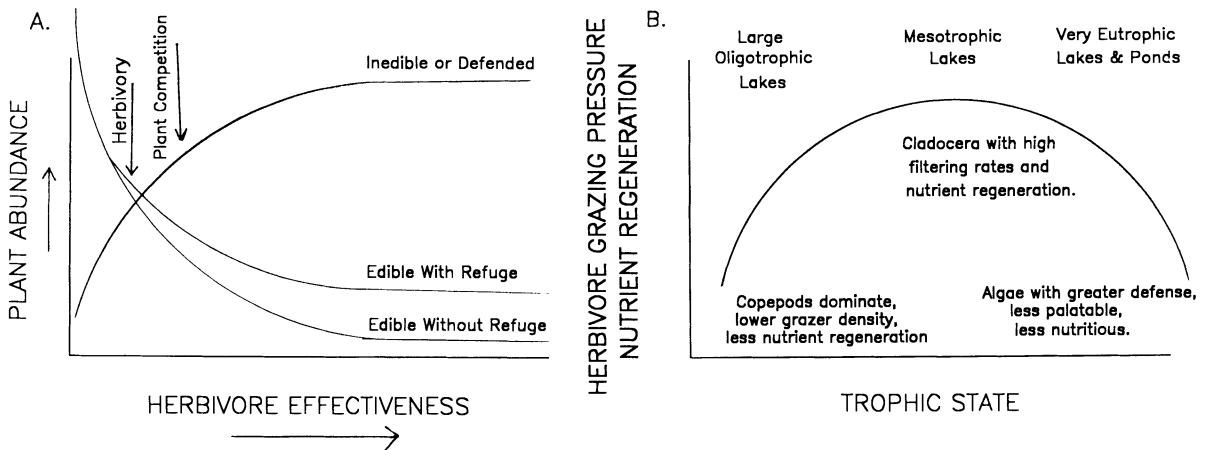


FIG. 1. (A) The replacement of edible or undefended algae with inedible taxa as herbivore effectiveness increases. This figure presumes that edible algae are superior competitors. The presence of refugia for some edible taxa can elevate baseline abundance in the presence of a highly effective herbivore population. (Redrawn from Lubchenco and Gaines 1982: Fig. 2.) (B) Herbivore grazing intensity, nutrient regeneration, and trophic state of the lake. (Redrawn from Carney 1990.)

gory (Fig. 1A); consumption is unified. In Fig. 1B, cascades occur in mesotrophic lakes, but not in oligotrophic lakes, with suppressed herbivore populations and slow nutrient regeneration, nor in eutrophic systems with well-defended or less nutritious algae. Inedible, defended, and less nutritious algae are the stuff of Hunter and Price's "variability" and my "differentiation" of trophically similar interactions. In most systems, plant coverage is not drastically reduced by normal changes in herbivore abundance, unlike the situation in trophic cascades. Generally, those few plant taxa that are greatly decreased in abundance by normal increases in their herbivores are quickly replaced by other plants that are not so affected. Ditto on coral reefs (Hay 1985). This buffers against runaway consumption.

Microalgae, phytoplankton, and epilithic forms can be more vulnerable to herbivory than other categories of plants. Taxa characteristic of oligotrophic and mesotrophic lakes appear to have few effective defenses. Very small relative to their herbivores, they are eaten whole. Seeds or seedlings of higher plants may be eaten whole by terrestrial herbivores, but in very few instances are larger life stages of either higher plants or corals consumed *en gros*. In defoliating epidemics of insects, only a subset of plant tissues is consumed. Though harmed, many large terrestrial plants can survive an episode of even heavy herbivory. The greater degree of morphological differentiation of higher plants should make a large contribution to the greater range of protections relative to small and simple algae.

TABLE 2. Distinctions between ecosystems dominated by trophic cascades and more speciose ecosystems without runaway consumption.

Feature	True trophic cascades	High-diversity systems
Substrate cleared by normal herbivory?	yes	no
Single or few "keystone" herbivore species?	yes	no
Single or few "keystone" carnivores hold sway over system?	yes	no
Consumption	runaway; consumption "unified"	buffered; consumption "differentiated"
Species number	relatively low	moderate to high number of species
Habitat	aquatic; discrete, isolated in space	terrestrial and aquatic; continuous with adjacent habitats
Autotrophs	lower plants, mainly algae	the gamut of plants
Trophic architecture	trophic ladder; levels fairly distinct	trophic web, levels indistinct; omnivory and looping
Trophic function	balanced reciprocity between levels	unbalanced reciprocity; donor control
Spatial heterogeneity and environmental grain	fairly homogeneous fine-grained	heterogeneous coarse-grained

TROPHIC TRICKLES: RETICULATE WEBS IN HIGH-DIVERSITY ECOSYSTEMS

The terrestrial world would be very different were producers as uniformly vulnerable to consumers as in trophic cascades, were autotrophs grazed away, and were a single or few carnivore species to hold sway over the food web in the normal course of events. The same applies to coral reefs and the lion's share of other webs. Substrates kept bare by herbivores are uncanny to terrestrial ecologists. On land and in speciose aquatic systems, another producer is virtually always ready to stand in for one grazed away. *H. sapiens*, with associated domestic and weedy organisms, appears to be the only terrestrial herbivore able to maintain land bereft of plants (Woodwell 1991).

Trophic trickles rather than cascades are a more appropriate metaphor for communities on land and in more diverse aquatic systems. Contrast the image of a torrent raging over an austere glacial landscape with that of dissected brooks and creeks in a heavily vegetated watershed. Both conduct great volumes of water, but while in the former, flow is unified, in the latter it is well split, finely differentiated, and thus greatly buffered. Although consumption can be intense in high-diversity systems, it does not normally run away as it does in trophic cascades (Table 2).

In speciose ecosystems, when consumption does run away to mimic the base of a trophic cascade, the situation is an aberration imposed by man (e.g., fenced elephants destroying the vegetation of their reserve; Botkin 1990), or transitory and the result of disturbance (e.g., coral clearing by the crown of thorns starfish; Glynn 1985).

The extraordinary case of destructive foraging by Lesser Snow Geese upon graminoids on the shores of Hudson Bay is one of a very few examples of a keystone herbivore and trophic cascade-like behavior for webs based upon higher plants; very few species are involved. Low-diversity lawns of *Carex* and *Puccinellia* are grubbed to oblivion by very high densities of breeding geese, which can destroy the plant community and erode to bare mud the substrate over a period of 5–15 yr (Jefferies 1988). During the past few decades, great increases in densities of geese, perhaps caused by agricultural changes on the wintering grounds to the south, have led to large areas of Hudson Bay shoreline being stripped clean of vegetation by these birds (Kerbes et al. 1990). Such destructive runaway consumption cannot persist.

Grazing by the giant tortoise on the most distant island on earth, Aldabra, is one of only two natural terrestrial cases even in the same league with the commonplace algal clearing of true trophic cascades in streams and mesotrophic lakes (vole grazing on mosses

in the arctic is the other natural terrestrial case; Oksanen 1983). High densities of these tortoises crop the turf down to <5 mm over extensive swards (Merton et al. 1976, Hunter 1992). Species of trees, shrubs, and grasses normally kept out regenerate quickly in sections of the sward where experimental fences exclude these massive beasts (Gibson et al. 1983).

Predators of the tortoises have not reached Aldabra, and I suggest that this gives us a clue to potent historical forces from the top down that are ignored in analysis of contemporary speciose food webs. Neither natural predators of adult giant tortoises, like large cats and canids, nor those of tortoise eggs and young, like snakes, lizards, and rodents, occur on distant islands where giant tortoises have evolved. One questions whether this system would last long in biotic contact with the rich mainland fauna. Rather than creating a whole trophic cascade, complete with predators, introduction of carnivores typical of continental terra firma would probably cause the extinction of the giant tortoises. These keystone herbivores and their potential trophic cascades are long gone from all but isolated areas; they have been eliminated by potent predators! Top-down forces do play their role in speciose systems.

At the same time, the case of the Aldabran giant tortoise gives hints of historical developments at the opposite end of the food web, in plants, that probably also thwart and hinder the runaway consumption characteristic of trophic cascades. I would argue that were Aldabra to receive much of the rich mainland flora, colonists would be likely to include impalatable plants, so defended, protected, or just so different, that the tortoises could not graze them down. Competition from these plants would then spell the demise of the sward and of these aberrantly effective herbivores. In this fascinatingly strange circumstance on Aldabra, we see clues of how both top-down and bottom-up forces may preclude trophic cascades from speciose terrestrial food webs.

This is not to suggest that heavy herbivory is limited to trophic cascades in aquatic systems. On the shallow fore-edge of coral reefs, grazing rates are the greatest known. Herbivorous fish can consume a very large fraction of total algal production, taking as many as 40 000 to 156 000 bites \cdot m⁻² \cdot day⁻¹ in patches (Hay and Steinberg 1992). Only the encrusting coralline algae are fairly resistant to the grazing. But intense consumption is checkerboarded and does not run away over the entire reef. Coarse-grained and diffuse in space and time, herbivory, though intense, does not clear the substrate. There is no indication that one or a few carnivores hold back an herbivore blight. Although carnivorous fish as a many-species group can greatly affect reef communities, their removal en masse from reefs close to dense human populations does not lead to the

extirpation of coral by herbivorous fish (M. Hay, *personal communication*). High variance in both grazing and algal growth, ingrained patchiness, is the story on coral reefs. This is in distinct contrast to the homogeneous picture that we see in systems with trophic cascades, in which fine-grained consumption dominates. The consumers themselves generate at least some of this crucial heterogeneity on coral reefs. Coral-eating fish, by a combination of reduced herbivory and increased growth rates within defended territories owing to fertilization effects, are responsible for much of the patchiness (Hay 1991).

Nor would I argue that higher plants are not suppressed, to a degree, by herbivory. Biological control of weeds and defoliating outbreaks of herbivores attest to the great decreases in density, biomass, and standing crop that can sometimes occur. At the spectacular end of examples, the geographical range and standing crop of the introduced St. John's-wort or Klamath weed, *Hypericum perforatum*, were reduced by several orders of magnitude (from "solid" coverage of many of the 8×10^5 ha of its range in 1940 to "a casual roadside weed" in 1952; Holloway 1958) in California by the introduced beetle *Chrysolina quadrigeminata*. But unlike trophic cascades, other plants immediately replaced the eradicated St. John's-wort, with total plant coverage averaging 99.8% in the year after its most precipitous decline (Huffaker and Kennett 1959). *C. quadrigeminata* ignores the long list of other plant species that replaced Klamath weed, just as terrestrial insects in general either ignore or are deterred by most plant species in their environments. Herbivory is rarely if ever unified in terrestrial ecosystems.

Also, it needs little emphasis that contemporary top-down forces, those actually operating today in high-diversity systems, can be influential (Karr et al. 1992). I would argue, however, that top-down forces are by and large much more differentiated, reticulate, and intertwined with other suppressive forces in high-diversity systems than in trophic cascades. Rarely ever cascading, top-down forces in terrestrial systems peter out between levels. Extremely infrequently does a single consumer, herbivore or carnivore, tip the scales of a terrestrial food web. An example of an unusually clear top-down influence is that of the bell miner bird in Australia, which aggressively defends territories of lerp insects (Homoptera, Psyllidae) (Loyn et al. 1983). The bird "farms" the carbohydrate lerp tests, which grow over the dorsum of these herbivores. Experimental removal of bell miners leads to outbreaks of lerp insects, then to colonization by bird species excluded by the bell miners. The colonizers over-exploit the lerps, which soon virtually disappear. The top-down effects of these carnivores terminate effectively with the lerp herbivores; no cascade.

In some natural terrestrial systems, a single large herbivore species can sometimes send fairly distinct signals downward to the plants, which can change the composition of the vegetation and/or affect nutrients, soil, or other chemical processes (Naiman 1988). Moose in high densities have great influence upon vegetation and soil (Pastor et al. 1988), as do beaver (Naiman et al. 1988), bison (Detling 1988), and even badgers (Platt 1975), prairie dogs (Whicker and Detling 1988), and pocket gophers (Huntley and Inouye 1988). In one of the most interesting recent cases, small patches of high desert can be changed to a sort of tall-grass prairie by fencing out small rodents (e.g., Brown and Heske 1990). Ecological entomologists have long appreciated the diverse manifestations of herbivore influence on plant diversity, abundance, growth, and chemistry (Hunter 1992). The point is that neither effects upon energy flow nor shifts in vegetation do a trophic cascade make; influence of the strongest terrestrial grazers pales in comparison to the wrenching influence upon ecological processes of herbivores in true trophic cascades. An additional issue with cases of heavy grazing on land is the degree to which single or a few species of carnivores hold simple sway over population density of the herbivore, as in true trophic cascades. I believe the evidence for this is equivocal.

TROPHIC LADDERS VS. TROPHIC WEBS

The architecture depicted in true trophic cascades (Table 1) is reminiscent of a ladder, with distinct trophic levels: autotrophs, herbivores, primary carnivores, and secondary carnivores (Table 2). Building upon the vigorous arguments of Polis (1991), the trophic architecture of high-diversity ecosystems, in contrast to that of trophic cascades, is more like a complex web than a ladder. Trophic webs have a high fraction of omnivores and resource generalists, which defy discrete trophic levels. They have looping, the lack of compartmentalization, many arthropod species, long chains of interacting species, high connectivity, and a rarity of top predators. I suggest that this trophic tangle predisposes damping and subdivision of consumer influence in high-diversity systems. Polis (1991: 145) argues that in at least one speciose ecosystem, in the Coachella Valley desert, this trophic tangle precludes cascades. Diets of different consumers are so differentiated as to send influence different ways—up, across, and down the trophic web. Consumption cannot tumble down in a ladder-like unified fashion. From the bottom up, however, changes in productivity, availability, or the quality of food can have effects that are not so buffered; this corresponds with Hunter and Price's affinity for greater realized upward than downward effects in food webs. Thus, in ecological time close to any "equilibria" for speciose food webs, donor control

should be prominent. This amounts to an unbalanced reciprocity between consumer and consumed. Donor control is an important challenge to dynamic modelling addressed by Power (1992) in this Special Feature.

Spatial and temporal heterogeneity are not a prominent part of true trophic cascades, which are processes operating homogeneously in space among trophically similar species. Substantial patchiness, coarse grain, and trophic differentiation in space and time also probably thwart cascades. Stochasticity plays a role in this spatial and temporal differentiation for African ungulates (McNaughton 1985), for coral reef fishes (Warner and Chesson 1985), and for rain forest tree communities (Hubbell and Foster 1986).

To me, the old intuition should be trusted that complexity and diversity are part and parcel of stability. The corollary is that the runaway consumption of true trophic cascades represents a form of biological instability. Many trophic cascades are not ultimately unstable, however, because quenching their characteristic runaway consumption leads to recovery of the consumed species; the consumed have ultimate refuges even in cascades. Finally, it is reasonable to expect a continuum between trophic cascade-like behavior of ecosystems and well-buffered behavior. At the high-diversity extreme, the consumed at any trophic node have low population or community-wide vulnerability to consumers. At the low-diversity end, where trophic cascades have been found, vulnerability at all levels is fairly high.

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