

a0005

Trophic Structure

E Preisser, University of Massachusetts at Amherst, Amherst, MA, USA

© 2007 Elsevier B.V. All rights reserved.

Introduction

Control of Trophic Structure

Factors Affecting Control of Trophic Structure

Further Reading

Energy transfer from producers to higher trophic levels

s0005 Introduction

p0005 Trophic structure is defined as the partitioning of biomass between trophic levels (subsets of an ecological community that gather energy and nutrients in similar ways, that is, producers, carnivores). The forces controlling biomass accumulation at each trophic level have been a central concern of ecology dating from the early twentieth-century work of Elton and Lindeman. While interspecific interactions such as omnivory and intraguild predation can make it difficult to assign many organisms to a single trophic level, several broadly defined trophic levels are nonetheless clearly distinguishable. Primary producers, autotrophic organisms (primarily plants and algae) that convert light or chemical energy into biomass, make up the basal trophic level. Primary consumers, generally referred to as herbivores, feed on primary producers. Their consumption of individual producers can range anywhere from a small fraction of the total producer biomass (caterpillars feeding on trees) to the entire organism (fish feeding on algae). Secondary consumers kill and feed on heterotrophic organisms such as herbivores and/or detritivores. Although secondary consumers are referred to generally as predators, this trophic level includes parasites, parasitoids, and pathogens in addition to carnivores. Secondary carnivores, or top predators, are organisms that eat carnivores. The most common examples of this trophic level occur in aquatic systems, where piscivorous fish such as tuna or pike eat smaller fish that feed on zooplankton (which, in turn, feed on phytoplankton). Finally, detritivores derive sustenance from dead organic matter emerging from each of the above trophic levels. While relatively little attention is paid to this trophic level, decomposers process a large fraction of net primary productivity (hereafter 'NPP') and are integral to nutrient cycling and ecosystem-level processes.

s0010 Control of Trophic Structure

p0010 Factors affecting the partitioning of biomass between trophic levels can be divided into two broad categories. The first of these categories, bottom-up control,

emphasizes the role(s) played by nutrient limitation and energetic inputs to producers and the subsequent efficiency of energy transfer between trophic levels in determining the biomass accumulation at each trophic level. The second category, top-down control, emphasizes the importance of predation in producing patterns of biomass accumulation that are often at odds with those predicted by energy inputs alone. While recognizing the differences between these two factors, it is also important to emphasize that both bottom-up and top-down factors represent extremes along a continuum of importance for regulatory control. While ecologists debate the extent to which bottom-up versus top-down control influence trophic structure in particular ecosystems, there is a broad consensus that both need to be considered when considering community dynamics.

Bottom-Up Control

Bottom-up control of trophic structure means that the production of biomass at each trophic level is a function of energy input into the primary producer trophic level. Biomass accumulated by producers then passes to higher trophic levels as a function of the between-level transfer efficiency. The resulting biomass pyramids are generally characterized by abundant producer biomass and sharp reductions in each higher trophic level. An important exception to this pattern occurs in aquatic food webs, where 'inverted biomass pyramids' can occur as a consequence of the extremely short generation time of unicellular producers relative to resident herbivores and predators (see the section titled 'Aquatic versus terrestrial ecosystems').

Energy transfer to producers

Although a large amount of light energy is potentially available to producers, only a small fraction of the total is actually converted to producer biomass. Net photosynthetic efficiency (the percentage of available light energy that becomes biomass) in naturally occurring terrestrial and aquatic communities falls between 0.01 and 3%, with values approaching 10% for intensively managed agricultural systems. The resulting NPP is critically dependent

s0015

p0015

s0020

p0020

2 General Ecology | Trophic Structure

on temperature and affected by water availability in terrestrial systems and nutrient levels in aquatic systems.

s0025 **Energy transfer from producers to higher trophic levels**

p0025 The overall transfer efficiency of energy between trophic levels is a function of three separate processes. The first of these, consumption efficiency, is the percentage of available productivity at a lower trophic level that is eaten by a higher trophic level. Grazers in temperate lakes, for example, remove nearly four times the fraction of primary productivity eaten by terrestrial grazers. The second process, the consumer's assimilation efficiency, determines what fraction of the biomass ingested by the consumer is converted to energy. Finally, the consumer's production efficiency determines the percentage of assimilated energy that yields new biomass. Taking all three processes into account, the overall between-level transfer efficiency ranges from 2 to 24%.

p0030 System-wide patterns of consumer–resource transfer efficiency are also affected by ecological stoichiometry, the ‘match’ between the nutrient needs of consumers and the nutrient supply of their resources. Transfer efficiencies are highest when consumers feed on resources whose nutrient ratios are similar to their own, and decrease sharply when they feed on resources with dissimilar ratios. Consumer–resource nutrient ratios in aquatic systems are more closely matched than in terrestrial systems, and in predator–herbivore versus herbivore–producer interactions. These facts have been invoked to explain why low transfer efficiencies are generally associated with herbivore–producer interactions and occur in terrestrial systems, while higher transfer efficiencies are characteristic of predator–prey interactions and occur in aquatic systems.

s0030 **Patterns of biomass accumulation**

p0035 As NPP and/or transfer efficiency increases, bottom-up control predicts an increasing number of trophic levels as well as an increase in biomass at each trophic level. As producer biomass changes over time, the effect ‘trickles up’ to produce correlated changes in each of the higher trophic levels (Figure 1, left panel).

AU2

s0035 **Top-Down Control**

p0040 Top-down control means that predation by higher trophic levels affect the accumulation of biomass at lower trophic levels. Top-down control does not negate the importance of energy input into the basal trophic level; however, it suggests that biomass accumulation at any one trophic level depends on the intensity of predation from the above trophic level.

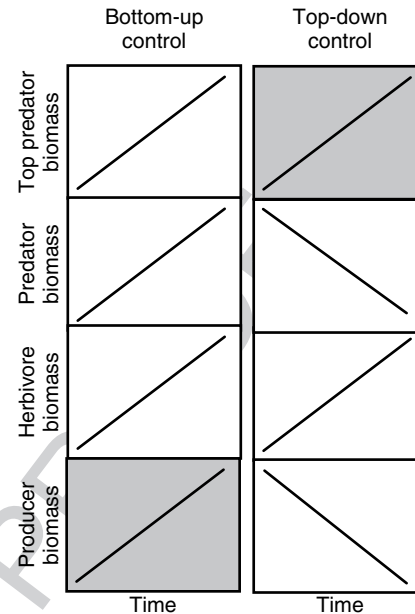


Figure 1 Left panel: Bottom-up control of a food chain. As producer biomass (gray box) increases over time, all other trophic levels show correlated increases in biomass. Right panel: Top-down control of a food chain. As top predator biomass (gray box) increases over time, biomass in the trophic levels below either increase (herbivores) or decrease (predators and producers) in response.

f0005

The ‘green world’ hypothesis

The concept of top-down control first gained widespread attention as a result of the ‘green world’ hypothesis developed by Hairston, Smith, and Slobodkin (hereafter ‘HSS’) in 1960. In brief, HSS posited that the relative rarity of natural disasters and obvious abundance of plant life implied that the producer trophic level was generally limited by competition for light, nutrients, space, and other resources. HSS further reasoned that the ‘green world’ around us is *prima facie* evidence that herbivores do not limit plant abundance; if they did, herbivores would be far more common and plants far less. Given that herbivores seem surrounded by more food than they can eat, it seems unlikely that resource competition limits them; HSS argued that predators are responsible for suppressing herbivore abundance below the level at which they can regulate plant biomass. Predators, in turn, are often territorial and wide-ranging in their search for food; this implies that they are self-limited by competition for their herbivore prey. Finally, the fact that we are not surrounded by masses of decaying matter suggests that decomposers quickly and effectively exploit virtually all of their food resources; as a result, this trophic level is likely self-limited as well. While numerous researchers have subsequently identified potential flaws, limitations, and inconsistencies in the HSS hypothesis, its simplicity, clarity, and intuitive logic catalyzed research into the potentially far-reaching consequences of trophic interactions.

s0040

p0045

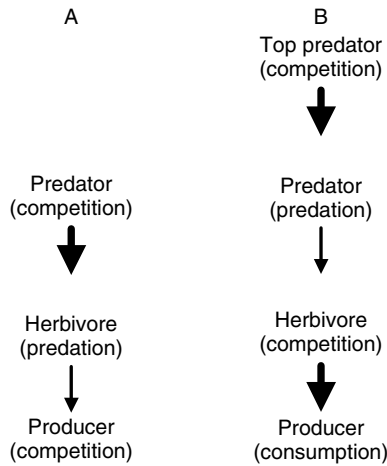


Figure 2 Top-down control of a food chain. In a three-level food chain (part A), predators are limited by competition for resources (thick arrow), herbivores are limited by predation and so cannot limit producers (thin arrow), which are thus limited by competition. In a four-level food chain (part B) the pattern is reversed, with predators and producers limited by resource competition and top predators and herbivores limited by resource competition.

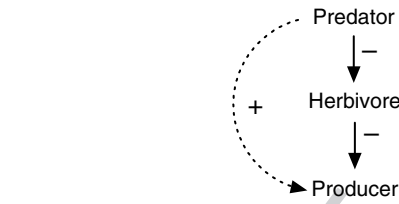


Figure 3 A trophic cascade. Predators suppress herbivores ('-' arrow), which suppress producers ('-' arrow). By suppressing herbivore biomass, predators indirectly benefit plants ('+' dotted arrow).

in terrestrial systems has been the subject of vigorous debate. Current research seems to indicate that while predators suppress herbivores in both aquatic and terrestrial systems, indirect predator effects on producer biomass occur predominantly in aquatic systems. In terrestrial systems, predator addition often decreases herbivore damage to producers but has less of an impact on overall producer biomass.

Importance of Bottom-Up Versus Top-Down Control

Biomass production at all trophic levels is ultimately dependent on the quantity and quality of resources comprising the basal trophic level. Experimental manipulations have generally found that biomass at all trophic levels increases with increased NPP. The ecosystem-level importance of bottom-up control is further underlined by the fact that global patterns of NPP correspond generally to predictions generated by models using only data on abiotic factors such as light, temperature, and water availability. There are also many systems, however, where top-down control clearly acts as a regulatory force; when unchecked by natural enemies, herbivores are capable of population outbreaks that can devastate producer biomass. In agricultural systems, the biological control of crop pests is predicated on the ability of natural enemies to suppress herbivore abundance, reduce producer damage, and increase overall yield. Given that bottom-up control is essential to determining biomass production, the critical issue becomes understanding the conditions and systems in which top-down processes are also important.

Factors Affecting Control of Trophic Structure

A variety of factors affect the magnitude of top-down versus bottom-up control over trophic structure. While these factors can be a function of among- versus within-level trophic interactions, they can also emerge from the

Patterns of biomass accumulation

The hypothesis of top-down control predicts that trophic-level biomass is a function of the trophic interaction most influencing that level. The highest trophic level is always self-limited by competition, making the next-lowest trophic level limited by predation, which in turn allows the trophic level below it to again be limited by competition. In a three-level system, this means that predators and producers are limited by competition (thin top-down arrow) while herbivores are limited by predation (thick top-down arrow) (Figure 2, part A); in a four-level system, the top predators and herbivores are limited by competition while the predators and producers are limited by predation/herbivory (Figure 2, part B). Control exerted via the top trophic level also produces patterns of biomass accumulation distinct from those seen in bottom-up control (Figure 1, right panel). In comparison to Figure 1, an increase in top predator biomass leads to decreased predator biomass, thereby releasing herbivore populations which subsequently depress producer biomass.

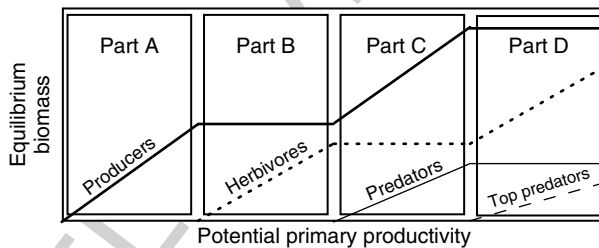
Trophic cascades

The archetypal form of top-down control involves trophic cascades, where predators indirectly benefit producers by suppressing herbivores (Figure 3). Such top-down control can be important in freshwater, marine, terrestrial, and belowground systems; in temperate lakes, it can produce visually spectacular differences in producer biomass. While trophic cascades are demonstrably important in many aquatic food webs, their importance

linkage between ecological communities and the surrounding environment.

s0065 Productivity

p0070 The bottom-up effects of increased productivity of the basal trophic level may be capable of influencing the strength of top-down control in a system and the patterns of biomass accumulation at subsequent trophic levels. The relationship between productivity and top-down control was first developed by Oksanen, Fretwell, and other as the ‘ecosystem exploitation hypothesis’ (hereafter ‘EEH’). EEH suggests that as potential primary productivity (hereafter ‘PPP’) increases, the equilibrium biomass at each trophic level in a food chain either increases linearly or shows no response (**Figure 4**). At very low levels of PPP, there is insufficient producer biomass to support herbivores; as a result, producers are limited by resource competition and their abundance increases linearly as PPP increases (**Figure 4**, part A). As PPP continues to increase, however, herbivores can enter the system and divert the increased production of producer biomass into herbivore flesh. Part B of **Figure 4** shows the result: higher PPP yields an increase in herbivore biomass while producer biomass remains unchanged. This continues until herbivore biomass is sufficiently abundant to support predators (**Figure 4**, part C). The introduction of predators to the system diverts increased herbivore biomass into predator biomass, freeing producer biomass from herbivore control and allowing it to increase with PPP. When a fourth trophic level enters the system at high PPP, it diverts predator biomass and allows herbivore biomass to increase at the expense of further increases in producer biomass (**Figure 4**, part D).



f0020 **Figure 4** The ecosystem exploitation hypothesis for trophic-level biomass accumulation as a function of potential primary productivity. *Part A*: As productivity increases, producer biomass increases. *Part B*: When producer abundance is sufficiently high to support a second trophic level, consumers enter the system and turn excess producer biomass into herbivore biomass. *Part C*: When herbivore abundance is sufficiently high to support a third trophic level, predators enter the system and turn excess herbivore biomass into predator biomass. This releases producers from herbivore control and allows producer biomass to increase. *Part D*: As in part C, but with a fourth trophic level (top predators) entering the system.

AU3

Aquatic Versus Terrestrial Ecosystems

s0070

Ecologists have long speculated that differences between aquatic and terrestrial ecosystems might affect trophic structure. Early researchers suggested that factors like producer size (predominantly small and short generation times in aquatic systems, predominantly large and long generation times in terrestrial systems) might explain the inverted biomass pyramids found in aquatic systems. Limiting nutrients like nitrogen and phosphorus are relatively more abundant in aquatic food webs; other terrestrial–aquatic differences include the fact that aquatic herbivores consume a larger fraction of available producer biomass, their herbivore–producer transfer efficiencies are higher, and aquatic herbivores are more abundant than their terrestrial counterparts.

p0075

Differences in food chain length

s0075

One hypothesis for the relative abundance of herbivores and scarcity of producers in aquatic versus terrestrial systems involves inherent between-system differences in the number of ‘effective’ trophic levels (i.e., levels that contribute substantially to top-down control of trophic structure). This argument suggests that terrestrial systems possess three trophic levels (**Figure 2**, part A) while aquatic systems possess four. Four-level aquatic systems occur via the addition of top predators, for example, piscivorous fish that eat planktivorous fish. In such an example, planktivorous fish are thus predation-limited and cannot control increases in herbivorous zooplankton that suppress phytoplankton biomass (**Figure 2**, part B). As a result, terrestrial systems have relatively few herbivores and appear ‘green,’ while many (but not all) aquatic systems have abundant herbivores and relatively little in the way of producer biomass.

p0080

Differences in herbivore–producer linkage strength

s0080

While research supports the contention that aquatic producers experience greater grazing intensity than their terrestrial counterparts, there is less evidence that the apparent abundance of terrestrial producer biomass is due to predator suppression of herbivores. Studies manipulating top predator communities in aquatic versus terrestrial systems demonstrate that the resulting trophic cascades greatly affect producer biomass in aquatic systems. In contrast, the effect of predator addition on terrestrial producers is seen most strongly in reduced producer damage and less in increased producer biomass. Abundant research has shown, however, that manipulating the abundance of top and intermediate predators can strongly affect the biomass of both aquatic and terrestrial herbivores; this implies that system-specific variation in the top-down effect of herbivores on producers may be

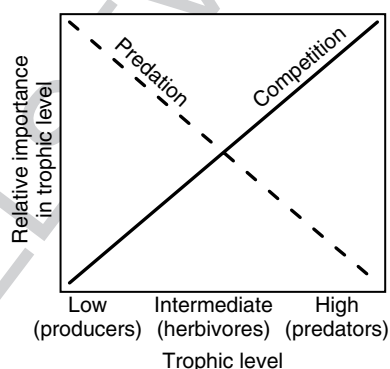
p0085

responsible for the observed differences between aquatic and terrestrial systems.

p0090 There are several suggestions for why aquatic versus terrestrial herbivores might have a greater impact on their resources. Phytoplankton, the primary producers in many aquatic systems, need to remain buoyant and absorb limiting nutrients across their cell walls; these requirements constrain them from reaching large sizes and may, in turn, preclude large investments in structural compounds while selecting for faster generation times. Terrestrial producers, in contrast, compete for light by investing in structural compounds that allow them to outgrow their neighbors. System-specific forces should thus select for small size (and rapid generation times) in aquatic producers and large size (and slower generation times) in terrestrial producers. These varying selective pressures may also mean that long-lived terrestrial producers are more apparent to herbivores and invest more heavily in defensive compounds that reduce the impact of herbivory. Ecological modeling has also shown that herbivore control over producer biomass is greatest when herbivores are larger than their resources; this is often the case in aquatic systems but rarely true in terrestrial food webs.

s0085 Trophic Position

p0095 The Menge–Sutherland hypothesis suggests how the trophic level of organisms within a food web may itself influence the factors that control biomass accumulation. In systems with multiple predator and prey species, herbivorous organisms are often preyed upon by many predators. In such systems, predation thus may play a more important role than resource competition in controlling the biomass accumulated by low-trophic-level organisms (Figure 5). Although organisms at higher



f0025 **Figure 5** The Menge–Sutherland hypothesis for within-community dynamics describing the relative importance of competition versus predation in structuring basal (producers) versus higher trophic levels. Low trophic levels tend to be structured by predation, while higher trophic levels are increasingly structured by competition for resources.

trophic levels are preyed upon by few (if any) predators, they compete fiercely with other members of their trophic level for relatively scarce prey resources. As a result, resource competition should be more influential than predation in determining high-trophic-level biomass. This hypothesis was developed in the context of marine inertial systems, and support for its general applicability has been mixed. A review of experimental literature found that predator effects were strongest on the lowest trophic levels in a food web, supporting the above argument; however, there is less evidence for the corollary that herbivore–herbivore competition is generally weak.

Heterogeneity Within Trophic Levels

Categorizing organisms within a community into discrete trophic levels can conceal a wide range of ecologically relevant differences between and among species. There are several ways in which the species-specific traits of organisms within a trophic level can affect biomass accumulation.

Antiherbivore defenses

An early challenge to HSS came from the argument that the apparent abundance of ‘green’ in terrestrial systems ignores the fact that terrestrial plants possess an array of chemical and physical defenses against herbivory. As such defenses become more effective, an increasing fraction of terrestrial plant biomass becomes effectively invulnerable to herbivory. In the midst of a ‘green world,’ herbivores may thus in fact be forced to compete for access to a limited pool of edible resources. The array of plant defenses found in nature suggests that they are at least somewhat effective in suppressing herbivory; a counter-argument points to the fact that even the best-defended plants have at least one herbivore species capable of devastating it in the absence of predators. Moreover, even if plant defenses reduce the overall impact of herbivory, digestibility-reducing compounds like tannins may force herbivores to develop more slowly and remain vulnerable to predators for a longer period of time, while herbivore-induced plant volatiles may attract predators to feeding herbivores. In both of these scenarios, plant defenses may actually serve to increase the efficacy of top-down control.

Heterogeneity in resource edibility

Several models address how interspecific variation in edibility within the basal trophic level might affect trophic structure. These models assume a tradeoff between defense (reduced edibility) and growth, with fast-growing species investing little in defense while slower-growing species are heavily defended and relatively invulnerable to consumption. In low-productivity

s0090

p0100

s0095

p0105

s0100

p0110

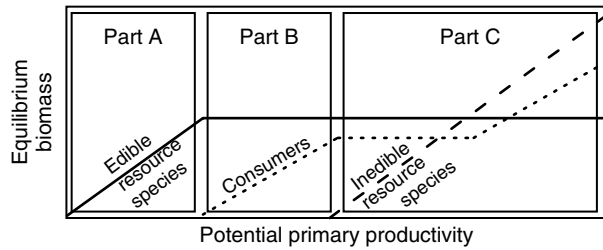


Figure 6 The edible–inedible resource model showing the trophic-level effect of tradeoffs between species that are either fast-growing and edible or slow-growing but invulnerable to consumption. *Part A*: At low productivities, edible resource species outcompete inedible species and increase their biomass linearly with productivity. *Part B*: When edible resource abundance is sufficiently high to support a second trophic level, consumers enter the system and turn excess resource biomass into consumer biomass. *Part C*: When consumer biomass is sufficiently abundant to allow the entry of a third trophic level, predators enter (line not shown in figure) and turn excess consumer biomass into predator biomass. This allows inedible resource species to enter the system and increase linearly with productivity while edible species' biomass remains unchanged.

environments with few consumers, species excelling in resource acquisition will predominate. As productivity and consumer abundance increases, however, the high-growth species will suffer disproportionately from consumption and the slow-growing but highly-defended species will become increasingly abundant.

s0105 **Edible–inedible resource model**

p0115 The edible–inedible resource model (**Figure 6**) posits EEH-type control over trophic biomass and predicts that low-productivity environments are initially inhabited only by rapidly growing edible producer species that competitively exclude inedible producers (**Figure 6**, part A). Its predictions parallel those of EEH for the addition of a second trophic level (**Figure 6**, part B). It diverges from EEH with the addition of a third trophic level that keeps herbivores from regulating producer biomass; in the edible–inedible resource model, the subsequent absence of herbivore control allows inedible producer species to invade the environment (**Figure 6**, part C). Since inedible producers cannot be controlled by predation; further increases in PPP yields an increasingly large inedible fraction of total producer biomass.

s0110 **Keystone predation model**

p0120 A modification of the edible–inedible prey model, Liebold's keystone-predation model (**Figure 7**) views resources as varying continuously rather than categorically in their degree of edibility; it predicts a series of species replacements of less- by more-defended resource species as consumer abundance increases. While it generates some of the same predictions as the edible–inedible resource model, it differs in that both consumer and

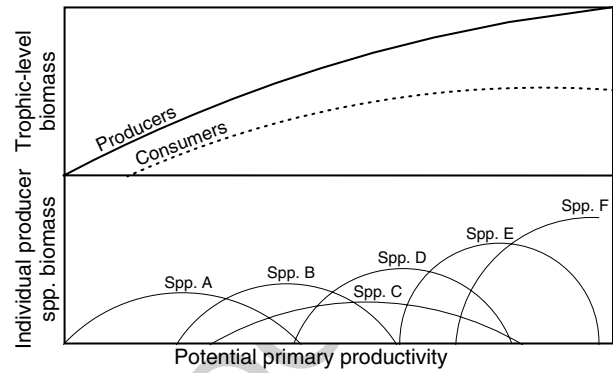


Figure 7 The keystone predation model showing the trophic-level effect of species replacements by resource species that vary continuously in their growth rate and edibility. At low productivities, communities tend to be dominated by edible resource species with high growth rates. As productivity increases, communities come to be increasingly dominated by mostly inedible resource species with low growth rates. Bottom-up control thus increases as a function of productivity.

resource biomass increase at a decreasing rate as PPP increases (**Figure 7**, top panel). This is due to top-down control decreasing as better- and better-defended resource species come to dominate at high PPP (**Figure 7**, bottom panel). While no resource species is completely invulnerable, consumers gain less and less biomass from preying upon marginally edible species and the system becomes increasingly bottom-up controlled.

Antipredator behavior

Most ecologists have traditionally seen the effect of predators on their prey in terms of the number of prey consumed by predators. A mounting array of evidence suggests that prey are far from helpless victims, however, and that they employ a wide array of defensive strategies. The costs of these strategies can include reduced energy income, lower mating success, or increased vulnerability to other predators. Predators can thus reduce prey density both through direct consumption as well as through the costs arising from antipredator strategies. The 'nonlethal' consequences of altered and/or reduced prey foraging in the presence of predators can profoundly affect the biomass of prey resources. For prey capable of antipredator behavior, predator-induced trophic cascades affecting the prey's resources may thus occur despite minimal prey mortality.

Generalist versus specialist predators

Species identity at the secondary consumer trophic level may also influence trophic structure. Effective top-down control in diverse ecological communities requires that predators consume a wide variety of prey species. As a consequence, generalist predators feeding on an array of species may be most effective at controlling trophic-level

biomass accumulation. In contrast, specialist predators affect only a restricted subset of all prey. Any reduction in the biomass of prey targeted by specialist predators may simply release nontargeted species from competition and allow them to increase in abundance; in such a situation, even high densities of specialist predators should produce little change in overall trophic-level biomass. Differences in trophic structure due to predator identity should be most apparent when contrasting communities dominated by large generalist predators (strong top-down control) with communities characterized by small specialist predators (strong bottom-up control).

s0125 **Omnivory and intraguild predation**

p0135 Intraguild predators (organisms capable of eating their competitors) and omnivores (organisms that eat both autotrophs and primary producers) pose a major challenge to simple views of trophic structure; even their trophic classification is questionable. While omnivory and intraguild predation have traditionally been considered rare, there is an emerging consensus that both feeding modes occur in (and sometimes dominate) many food webs.

p0140 Abundant omnivory and intraguild predation in an ecological community can alter the strength of top-down control. Both feeding modes may act to reduce the strength of top-down control; this occurs because (1) the top-down effect of feeding is diluted across multiple trophic levels; (2) eating other predators may decrease the total predator impact on lower trophic levels; and (3) changes in abundance and feeding rates affect different trophic levels similarly. For example, increased abundance of an omnivorous crayfish should decrease the abundance of both snails (herbivores) and algae (producers). By feeding on the basal trophic level during periods when animal prey are scarce, however, omnivores may sustain high population densities capable of suppressing any future increases in prey biomass. Omnivory in such systems may thus actually serve to increase the strength of top-down control.

s0130 **Species/trophic diversity**

p0145 There are several arguments for how high ‘diversity’ (a combined function of the number of trophic levels, species per level, and within-trophic-level foraging strategies) in food webs should alter the relative importance of competition versus predation in controlling trophic-level biomass. One argument suggests that low-diversity communities will tend to have fewer trophic levels, with the vast majority of species occupying the lower trophic levels; in such systems, the relative lack of predator pressure will mean that biomass accumulation will be determined primarily by resource competition (Figure 8). As food web diversity increases, both the number and importance of higher trophic levels increase.

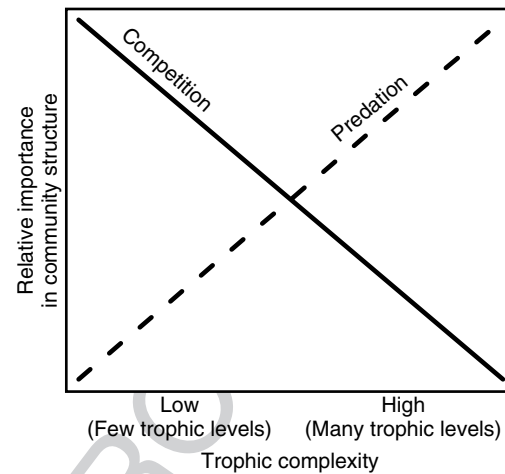


Figure 8 The Menge–Sutherland hypothesis for between-community dynamics describing the relative importance of competition versus predation in structuring communities of low versus high complexity. Low-complexity communities tend to have few trophic levels and be structured primarily by competition, while high-complexity communities tend to have many trophic levels and are structured primarily by predation.

f0040

This leads to an increased number of predator–prey interactions, and a corresponding rise in the relative importance of predation in structuring the community. As a result, more-diverse communities are structured primarily by predation, while competition plays a predominant role in less-diverse food webs. Contrary to this, an array of empirical work seems to show that less-diverse communities (‘food chains’) are more likely to show strong top-down control, while more-diverse communities (‘food webs’) tend to diffuse top-down control and be more affected by bottom-up factors.

Ecological models of even simple food webs incorporating linked food chains and multiple species per trophic level show that such changes may alter the bottom-up importance of increased productivity. Bottom-up effects on predator biomass in a simple food chain can be reduced by predator–predator competition, well-defended herbivores, or herbivores with shared predators and resources. As models grow more complex, outcomes ranging from strong top-down to strong bottom-up effects, and a range of intermediate conditions, are possible.

p0150

Temporal/Spatial Heterogeneity

s0135

Variation in both space and time can also affect the accumulation of biomass at different trophic levels. In the broadest sense, spatial and temporal variation in light, temperature, nutrients, and water availability sets the upper limit for ecosystem-level NPP. Systems characterized by wide seasonal variation often feature similarly wide swings in the strength of competitive

p0155

interactions. Even when less-seasonal systems are included, temporal variation in competitive interactions appear to be the rule rather than the exception; as a result, food webs in a variety of systems may shift between top-down and bottom-up control over time.

s0140 **Stressful environments**

p0160 Trophic structure in harsh environments may be controlled by a different suite of factors than those operating in less-stressed systems. Models developed in the context of marine intertidal systems suggest that the effect of abiotic stress on trophic structure should occur because predators are, on average, more mobile than their prey. In relatively benign environments, predators should find it easy to search for and consume prey; higher trophic levels should be fully represented in such environments and be predominantly structured by predator–prey interactions. As abiotic stress increases, however, mobile predators can flee harsh environments while their sessile prey must remain. As a consequence, the importance of predator–prey interactions decreases sharply and competition, not predation, primarily determines trophic-level biomass accumulation.

s0145 **Refuge habitats**

p0165 Refuge habitats, areas where prey are free from the threat of predation, were at one time thought to play a major role in determining trophic structure. Since predators can only consume the fraction of prey that have lost in competition for refuge access, bottom-up control will dominate in refuge-rich areas. While such refuge-rich habitats are now generally considered to be the exception rather than the rule, they may explain systems where the changes in predator abundance have little overall impact on prey biomass.

See also: 00004; 00039; 00287; 00308; 00454; 00468; 00473; 00479; 00497; 00743; 00642; 00676; 00666; 00647; 00811; 00682

Further Reading

- Abrams P (1993) Effects of increased productivity on the abundance of trophic levels. *American Naturalist* 141: 351–371. [b0005](#)
- Carpenter S and Kitchell J (eds.) (1993) *The Trophic Cascade in Lakes*. Cambridge: Cambridge University Press. [b0010](#)
- Hairston N, Jr. and Hairston N (1997) Does foodweb complexity eliminate trophic level dynamics? *American Naturalist* 149: 1001–1007. [b0015](#)
- Hairston N, Smith F, and Slobodkin L (1960) Community structure, population control, and competition. *American Naturalist* 94: 421–425. [b0020](#)
- Hunter M and Price P (1992) Playing chutes and ladders: Bottom-up and top-down forces in natural communities. *Ecology* 73: 724–732. [b0025](#)
- Jiang L and Morin P (2005) Predator diet breadth influences the relative importance of bottom-up and top-down control of prey biomass and diversity. *American Naturalist* 165: 350–363. [b0030](#)
- Leibold M (1996) A graphical model of keystone predators in foodwebs: Trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* 147: 784–812. [b0035](#)
- Leibold M, Chase J, Shurin J, and Downing A (1997) Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* 28: 467–494. [b0040](#)
- Menge B and Sutherland J (1976) Species diversity gradients: Synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* 110: 351–369. [b0045](#)
- Morin P (1999) *Community Ecology*. Oxford: Blackwell Science. [b0050](#)
- Oksanen L, Fretwell S, Arruda J, and Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118: 240–261. [b0055](#)
- Polis G (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86: 3–15. [b0060](#)
- Polis G and Strong D (1996) Foodweb complexity and community dynamics. *American Naturalist* 147: 813–846. [b0065](#)
- Schmitz O, Krivan V, and Ovadia O (2004) Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecology Letters* 7: 153–163. [b0070](#)
- Shurin J, Gruner D, and Hillebrand H (2006) All wet or dried up? Real differences between aquatic and terrestrial foodwebs. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 273: 1–9. [b0075](#)