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## CHAPTER 1



# Trophic Cascades: What They Are, How They Work, and Why They Matter

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Humans have been waging war against predators since the dawn of history. Lion slayers were heroes of Greek mythology. Shepherds bred large, aggressive dogs to fend off wolves and bears in the Pyrenees, Carpathians, and elsewhere. Gamekeepers were hired by the great estates of Britain to eradicate foxes, goshawks, and badgers. In the United States, an agency of the federal government, the Biological Survey (later the U.S. Department of the Interior), hired hundreds of predator control agents to shoot, trap, and poison wolves, cougars, coyotes, eagles, and a host of lesser predators. Bounties and culls have been used in Alaska and Canada to control seals and sea lions in the name of fishery management. An almost endless list of such measures could be compiled.

Humans have been so effective at decimating or entirely eliminating predators over most of the land and sea that the effects of these persecutions are becoming apparent to the ordinary citizen. There is hardly a resident of suburban America today whose efforts to grow flowers or vegetables isn't thwarted by ubiquitous deer. Ask any gardener why there are so many deer, and the answer is a consistent refrain: "Because they don't have any predators." The line of reasoning from cause to effect is simple and linear. It is precisely what Hairston, Smith, and Slobodkin (HSS 1960) posited nearly 50 years ago.

Recognition on the part of official agencies that predators play important roles in nature has been belated but is now spreading in the United States, Canada, Europe, and the industrialized countries generally, where legal structures

protect wildlife and managers intervene to mitigate human–wildlife conflicts. In these countries, the tide of opinion is changing. Whereas predators were actively persecuted a generation ago, they are now being restored. Examples from the United States include reintroduction of the gray wolf in Wyoming, Mexican wolf in Arizona and New Mexico, red wolf in North Carolina, lynx in Colorado, black-footed ferret in Wyoming, South Dakota, and Chihuahua, Mexico, and sea otters in southeast Alaska, Washington, and southern California. And after an absence of more than 100 years, jaguars are returning to the borderlands between the United States and Mexico.

Why should we celebrate this development and encourage its expansion to additional places and predators in other parts of the world? The answer is a complicated one, blending philosophical, aesthetic, practical, and scientific reasoning. In this book we shall be concerned primarily with the scientific reasons for sustaining predators while recognizing that more philosophical approaches are also valid.

Predators are important because they occupy the top rung of the trophic ladder and from that position regulate the food web below them. Top vertebrate predators are large bodied and can move over large areas, thus coupling the dynamics of seemingly distinct communities and ecosystems. Recently, the ability of predators to move flexibly between communities, responding opportunistically to shifts in prey abundance, has been suggested to be an important governor of food web stability (McCann et al. 2005; Holt 2009). Eliminating predators destabilizes ecosystems, setting off chain reactions that eventually cascade down the trophic ladder to the lowest rung. In 1980, Robert Paine coined the term *trophic cascade* to describe this process. The altered state that develops after the loss of apex predators is invariably simpler than the initial state, supporting less biodiversity. Thus, predators hold an important key to retaining the high levels of biodiversity we associate with primordial nature.

Three-level cascades are the simplest and most familiar case (e.g., wolf–deer–vegetation). Wolves eat deer and thereby indirectly benefit vegetation, depending on their efficiency in maintaining deer numbers at low levels. If wolves are efficient deer predators, deer populations remain low and the vegetation experiences only light herbivory; if they are inefficient, deer populations are higher and herbivory is heavier. This efficiency is analogous to Paine's (1980) interaction strength. However, unlike the case of Paine's *Pisaster*, it is generally not possible to use rigorous, controlled experiments to determine the impact of a large predator such as a wolf because such demonstrations require wolf removal and subsequent assessment of the demographic response of deer. Responses of deer and their allies to the local extirpation of wolves or other top

predators have typically lagged by decades, during which time other factors, such as plant succession, hunting, land use changes, and other human activities, can intervene to complicate the picture (McShea et al. 1997).

The simple example of the wolf–deer–vegetation interaction introduces some key features of trophic cascades. First, predators harvest prey with a certain efficiency that can vary with the topography, vegetation, density, and evasive behavior of the prey and perhaps other factors such as other species of prey and predators (Berger 2008). Thus, the strength of the top–down interaction is not a simple property of predator and prey alone, but it depends on the context in which the interaction takes place. Second, we note that the wolf population interacts only with deer; it is at the top of the pyramid and regulated from the bottom up via the deer population that supports it. However, the deer population is in the middle of a bidirectional flow of resources. It depends on forage (a bottom–up process) and is preyed on by wolves (a top–down process). The density of the deer population thus depends on the balance of these two counter-current forces. Finally, the vegetation is also regulated both by bottom–up (water, sunlight, nutrients) and by top–down (herbivory) processes. In essence, this simple bidirectional interaction scheme is what Hairston, Smith, and Slobodkin proposed in 1960 in their famous “green world” hypothesis.

A common misimpression is that there is an either–or dichotomy between systems driven from the bottom up and those driven from the top down. Bottom–up and top–down processes are not in any way exclusive; they are complementary countercurrent flows, inextricably bound together. Bottom–up processes are fundamental and inescapable, driving photosynthesis and being supported by it. If photosynthesis increases, as along a climatic gradient for example, the responses are quantitative: more productivity, more herbivores, more predators being supported by those herbivores, and occasionally an increase in food chain length (Crête 1999). Only at the very lowest productivity levels, such as near the limits of vegetation in deserts or the high Arctic, does one find ecosystems with fewer than the three standard levels (Oksanen et al. 1981).

With the exception of microbial ecosystems supported by chemoautotrophs, photosynthetic productivity determines the availability of resources to higher levels, either directly (via chains starting with herbivory) or indirectly via detritivores (e.g., the deep sea, caves). How primary productivity is allocated among higher levels is determined not only by the efficiency of material and energy flux upward through the food chain but also from the top down through the trophic cascade. In the absence of herbivores or predators, the entire annual net productivity of a patch of vegetation must pass into the detrital food web. If herbivores are present, some of the productivity will accrue to

them and less will recycle through detritus. If predators are added, the flow of resources will ascend one level further, and less may accrue to herbivores because their numbers are kept in check by the predators (although they will probably turn over faster). Thus, bottom-up processes determine the flow of resources into the system, whereas top-down processes influence how the resources are distributed among trophic levels.

Another issue that has led to confusion is whether trophic cascades are inherently static or dynamic. In fact, a trophic cascade is always dynamic, but the dynamism is not always manifest. When a trophic system is at a stable point (i.e., equilibrium), its component levels remain fairly constant. However, the appearance of stasis is illusory, suggesting the absence of any dynamic process. But under the surface, the interactions between levels are not static but rather highly dynamic. Predators are eating prey, prey are eating plants, plants are growing, and so on. A lot is happening, but the various interacting forces and flows are in balance, so the underlying dynamism is not apparent. Call it cryptic dynamism. The stable, equilibrated condition is quite properly called a trophic cascade because the term refers to the whole interacting system, not just to one or another of the states it can assume.

A final point that warrants clarification in these preliminary comments concerns the role of keystone species in trophic cascades. Paine's (1966) founding example of the starfish *Pisaster* has left an indelible mark on the literature. *Pisaster* is an unequivocal keystone species, defined by Mary Power and colleagues (1996) as one having effects on other elements of an ecosystem that are large relative to its numbers or biomass. The wolves of Yellowstone are another keystone species. Dramatic responses can be obtained by perturbing a keystone species, but are keystone species necessary as mediators of strong trophic cascades? The *Pisaster* example, and some other equally dramatic ones, has led some authors to conclude that keystone species are necessary ingredients of strong trophic cascades (Polis et al. 2000). We shall see definitively that this is not the case. Keystone species are notable because they concentrate much of the interaction strength of an entire trophic level in a single species, but across nature more generally, keystone species possessing such concentrated interaction strength are probably the exception rather than the rule.

Because of controversy over why the world is green, there has been a focus in much of the trophic cascade literature on indirect carnivore impacts on plants (or space occupiers in marine systems), via shifts in herbivore abundance and activity. The concept of a trophic cascade actually has a much broader scope than just indirect mutualisms between predators and plants; the basal species might be space occupiers in marine systems or detritivores and decomposers in



soil food webs, for instance. There can also be trophic cascades between species, all of which are predators (e.g., in the Bahamas, lizard cuckoos may eat *Anolis* lizards or force them into hiding and so reduce predation on spiders). But the main heat in the literature on trophic cascades seems to arise from efforts to understand patterns in plant communities.

The basic question posed by HSS (and, they believed, answered by them) is this: To understand plant ecology (e.g., distributions of life forms within a community, or the distribution of plant species along environmental gradients), must one pay attention to the food webs supported by those plant communities? It is fair to say that plant ecology has traditionally focused on how plant form, life history, and species composition reflect the outcome of competitive interactions and population dynamics playing out in the context of various factors in the physical environment (e.g., climate, soil, disturbance regimes). This unilaterally bottom-up view of plant ecology essentially ignores herbivory as a deterministic force in structuring vegetation. But if trophic cascades are ubiquitous and large, as we are convinced, bottom-up forcing is only half the picture.

Some authors argue that trophic cascades are idiosyncratic in occurrence and not all that important. For instance, Polis et al. (2000) suggest that in contrast to aquatic systems, “community cascades . . . are absent or rare in terrestrial habitats” (473); furthermore, they claim that “support for even species-level cascades is limited in terrestrial systems” (474). The reasons they give for these assertions are that most food webs have a reticulate and heterogeneous structure and that many prey, plants in particular, are inedible.

Biological control of agricultural pests is a widespread application of trophic cascades to solve practical problems in applied terrestrial ecology, so the second quote from Polis et al., taken literally, is false. But agricultural systems, by design, tend to be low in species diversity and other kinds of heterogeneity, and crop plants have been bred to be edible (at least to us) at the expense of spines, secondary compounds, low-quality tissues, and other antiherbivore devices. So maybe biological control is the exception that proves the rule: Trophic cascades may be ubiquitous in the artificial landscapes of agroecosystems without being significant drivers of plant community structure and dynamics in natural ecosystems.

Our reading of the literature suggests that the claims of Polis et al. (2000) are greatly overstated. This volume is replete with convincing evidence of cascades in terrestrial and aquatic systems. Moreover, it should be noted that there are limitations in most experimental studies of trophic cascades in terrestrial biomes (Holt 2000). For understandable reasons, most manipulative studies are short term. For instance, in the review by Schmitz et al. (2000), 80 percent of

the studies involved measurements over a single growing season, even though many of the target species were long-lived shrubs, trees, perennial herbs, and graminoids. The time scales of transient dynamics in trophic cascades in terrestrial systems are likely to be much longer than in many aquatic systems, where the basal producers (e.g., phytoplankton) have short generation times and so can respond very rapidly to shifts in herbivory. A small quantitative impact of herbivory observed in a single growing season in a terrestrial system that seems quite subtle, assessed, say, in terms of individual growth rates or tissue damage, could be magnified over time, for instance, by altering competitive ability. Shifts in community composition caused by altered herbivory regimes could necessitate colonization from a regional source pool, followed by shifts in local abundances, both of which could be very slow processes, especially if the vegetation is woody. Patterns in abundance as a function of trophic level along gradients reveal the importance of such within-level species sorting for elucidating natural patterns (Leibold 1996; Leibold et al. 1997). Finally, manipulative studies never remove *all* the natural enemies of herbivores. These include not just predators but parasitoids, pathogens, entomophagous nematodes, and so on. Experiments rarely run long enough so that the regional species pool of potentially important herbivores is sampled at an experimental site.

If one accepts that trophic cascades are important in natural ecosystems, applied ecologists should be deeply concerned because humans disrupt natural predator-prey systems in many ways. Generalist top vertebrate predators (e.g., the Florida panther [*Felis concolor floridiana*]) are at particular risk because of a perfect storm of multiple, correlated vulnerabilities. Top vertebrate predators tend to have low population densities and large home ranges, making them particularly vulnerable to habitat fragmentation. Moreover, low intrinsic growth rates imply weak demographic responses to increased mortality. Thus, small but sustained increases in mortality can inexorably drive such species to extinction. Because of their opportunistic diets and spatial mobility, they often come into direct contact with humans or our commensals (e.g., livestock), prompting humans to persecute them. Putting all these factors together, it is not surprising that among the species most at risk around the world are top predators such as tigers and the great sharks.

What does theoretical ecology have to say about trophic cascades? By *theory* we mean formal mathematical models that lay out explicit assumptions about the dynamic forces in ecological systems and draw out the logical consequences of those assumptions. Such models are often motivated by fine conceptual theory presented verbally, as in the stimulating papers by Fretwell (1977, 1987) and

various chapters in this volume. There is a huge body of theory on predator–prey and food web dynamics that in a broad sense is relevant to trophic cascades. However, we shall not attempt an exhaustive review but instead shall re-examine the main thrust of some key older papers to provide a convenient summary of historical perspectives that are the conceptual foundation of many empirical studies of trophic cascades. Other chapters in this volume (Chapters 4, 17, and 18) deal with current theoretical issues.

## HISTORICAL PERSPECTIVES ON THE THEORY OF TROPHIC CASCADES

All ecologists know that the world is complex. Some of us revel in that recognition (Polis 1991) and are deeply skeptical of theories based on simplifying assumptions. Others of us hope that simple models can be used like a surgeon's knife, cutting deftly through the cloying fat of complicating detail to get at the essential sinews of ecological reality. One complication that immediately arises when we contemplate theoretical studies of trophic cascades is that most food webs are highly complex (e.g., contemplate Figure 6 in Winemiller 1990), with many species locked in tangled webs of interactions. For both practical and analytical reasons, theoretical models in ecology must greatly simplify known complexities. For trophic cascades, the natural and admittedly grossly oversimplified starting point is the community module (*sensu* Holt 1997), represented by an unlinked food chain capped by a top predator that feeds on a herbivore population, which in turn is sustained by a basal plant population. (These can be viewed as single species at each level or as aggregate functional groups comprising several functionally equivalent species.)

The simplest models for unlinked food chains are based on Lotka–Volterra models, where all the per capita relationships, within and between species, are expressed by linear functional forms. May (1973a) once compared such simple models in ecology to the models of perfect crystals in physics. Perfect crystals do not exist, but developing a theory for such crystals nonetheless provides yardsticks, which can be used to gauge the consequences of various sorts of imperfections in crystal structures. In like manner, no ecologist, not even the woolliest theoretician, believes that a Lotka–Volterra model literally describes all the rich behavior of any actual ecological system, but such models may nonetheless capture some essential features that carry over to much more complex, realistic—and analytically opaque—models. Simple models give us an

accessible and tractable starting point that serves as a springboard for tackling more complex and realistic models.

We shall begin with a continuous-time, differential equation model, where each trophic level is represented by a single equation, as follows:

$$\begin{aligned}\frac{dP}{dt} &= P(b'a'N - m') \\ \frac{dN}{dt} &= N(abR - a'P - m) \\ \frac{dR}{dt} &= R(r - dR - aN)\end{aligned}\tag{1.1}$$

Here  $P$ ,  $N$ , and  $R$  are the abundances of the predator, the herbivore, and the plant, respectively;  $r$  is the intrinsic growth rate of the plant;  $d$  is a measure of its direct density dependence (e.g., competition for resources and space);  $a$  and  $a'$  are per capita attack rates;  $b$  and  $b'$  are conversion factors (relating consumption to births); and  $m$  and  $m'$  are density-independent mortality rates for the herbivore and predator, respectively.

Analyses by Stuart Pimm (1979) and various mathematicians (e.g., Hallam 1986; Freedman and Waltman 1977) in the 1970s and 1980s of the Lotka–Volterra model described by Equation 1.1 led to a number of conclusions:

- As one ascends the food chain, the conditions for persistence of each consecutive level become more stringent.
- Analysis of these persistence conditions shows that they are more likely to be met for the predator as the productivity of the plant increases (via higher  $r$  or lower  $d$ ).

In other words, this model leads to the prediction that food chain length should increase with the productivity of the basal trophic level. Basically, if primary productivity is too low, too little energy will pass through the intermediate trophic level to sustain the top level as a viable population. The prediction that food chains should tend to increase in length with increasing productivity is a general feature of many models and has been demonstrated in laboratory microcosms (Kaunzinger and Morin 1998) and at the very low productivity end of natural variation in primary production (Aunapuu et al. 2008). However, even some unproductive ecosystems seem to be able to sustain a top predator, which may persist because of factors left out of traditional models (e.g., mobility, long generation lengths, adaptations to cope with resource scarcity). It is an



open question whether, in general, natural variation in food chain length between communities is explained principally by variation in primary production or by the interplay of many distinct factors; the latter at present seems most likely (Post 2002; Holt in press).

- For this specific model, there are no alternative stable, noninvasible equilibria, so historical idiosyncrasies will not affect the ultimate community found at a site.
- Given that an equilibrium exists, it is locally and globally stable, so there is no limit cycle or chaotic dynamics.
- However, the resilience to perturbations—the time for the system to recover to its initial equilibrium after a disturbance (the shorter the recovery time, the greater the resilience)—decreases with increasing food chain length. Basically, there can be a compounding of perturbations up the food chain (Pimm 1979). So, in a certain sense, longer food chains are predicted to be dynamically more delicate in this simple model.

With these theoretical results in hand, the next step is to discern the degree to which they are general or instead reflect the many simplifying assumptions built into the Lotka–Volterra model. An important step toward generality was provided by Rosenzweig (1973), who developed a general, graphical, three-species food chain model, which in effect included nonlinear density dependence in the plant and nonlinear functional and numerical prey-dependent responses by the herbivore. He also carried out a formal local stability analysis, which led to a number of important theoretical conclusions:

- Stability requires the existence of direct density dependence (e.g., interference or competition for space) at one or more trophic levels (see also Wollkind 1976). This is a generalization that holds for all ecological models, regardless of their details.
- If higher trophic levels have weak direct density dependence, the basal level must have strong density dependence for the system to be stable.
- Intense predation can destabilize a food chain if the top predator has weak direct density dependence, as do herbivores, and the predator has a saturating functional response to its prey. This is a generalization of an insight that emerges from simple two-link predator–prey interactions when predation is effective at limiting prey numbers well below (the prey) carrying capacity (Rosenzweig 1971).
- One can construct examples in which moderate predation stabilizes an

otherwise strongly unstable plant–herbivore interaction if the top predator has direct density dependence and the herbivore only has weak direct density dependence. It is noteworthy that nearly all vertebrate top predators in terrestrial ecosystems, except possibly alligators, snakes, and a few other reptiles, have strong intraspecific density dependence mediated by direct aggression or territoriality. The very trophic apparatuses that permit vertebrate predation in the first place—sharp teeth, claws, and talons—also provide arms for intraspecific conflict or necessitate the avoidance of such conflict by spacing mechanisms such as territoriality. This permits direct density dependence in predators to buffer them from changes in their food supply, which as a byproduct can help stabilize the entire system.

A theoretical example of predation stabilizing a plant–herbivore interaction was sketched by May (1973a, 1973b), who showed using a nonlinear model that a top predator with direct density dependence could persist stably atop a three-species food chain, and the system would return to its equilibrium with damped oscillations after disturbance. When the predator is removed, the inherent instability of the plant–herbivore interaction was unleashed, leading to oscillations of such large amplitude that extinction during the population troughs would be likely.

The basic model of Rosenzweig (1973) was built upon in the celebrated exploitation ecosystem article of Oksanen et al. (1981). One of the main conclusions of that article was that the prediction from Lotka–Volterra theory relating food chain length to primary productivity was more general, and it provided a scaffolding for understanding shifts in the relative importance of top–down and bottom–up forces along environmental gradients in production.

It was not recognized until much later that the unstable dynamics in food chains noted by Rosenzweig could lead not only to cycles but also to chaotic dynamics (Hastings and Powell 1991). Chaotic dynamics can arise when each trophic link has a saturating response, so that each consumer–resource interaction on its own tends toward unstable limit cycle behavior. In a sense, the species linked in a food chain act like coupled oscillators, which reveal much more complex dynamics than do single oscillators on their own. The recognition of the potential for chaotic dynamics led to a small cottage industry of work by mathematicians on food chain models, full of recondite terms such as “codimension-two Belyakov homoclinic bifurcations” (Kuznetsov et al. 2001). Much of the ornate phenomenon analyzed in this literature has its mathematical charm, indeed elegance, but it is not immediately clear that these mathe-

mathematical details are all that relevant to natural systems. But leaving this quibble aside, some key qualitative messages do emerge from this body of mathematical work on unbranched food chain models and their exploration of instabilities that could be quite important for empirical studies, if unstable dynamics caused by coupled trophic interactions are pervasive in food webs.

First, in a wide range of circumstances, populations in a food chain may experience low densities, as the coupled system tracks a trajectory wandering over a dynamic attractor (for examples, see figures in Rinaldi et al. 2004). This means that there is often heightened extinction risk. Rinaldi et al. (2004) explored various mathematical aspects of the chaotic dynamics of the system, but for our purposes a biologically significant effect of this study (which the authors do not discuss) is that populations can plunge to very low densities, and so the food chain is likely to collapse.

A broad implication of these (and related) theoretical results for empirical studies is that trophic cascades may be manifest not only in changes in average abundance but in shifts in system stability and hence, potentially, extinction rates. However, a cautionary note is that although models suggest a range of scenarios that describe unstable dynamics, such dynamics are not as often observed in nature. The rarity of unstable dynamics in nature perhaps has multiple explanations, at least one of which is the interplay of spatial heterogeneity, mobility, and the presence in most landscapes of refugia (though perhaps different ones) for predator, prey, and producer. It is likely that the spatial mobility and behavioral flexibility of large vertebrate top predators in particular can provide important buffers moderating the inherent tendencies of nonlinear food chains to exhibit extremely unstable dynamics.

Second, when the dynamics of ecological systems are unstable, their responses to perturbations or systematic shifts in environmental conditions may often be surprising, basically because unstable dynamics magnify the impact of nonlinearities in the system (Abrams 2002; see Rinaldi et al. 2004 for a food chain dynamic). Our ecological intuition is not very good at predicting what happens in nonlinear systems with unstable dynamics with multiple feedbacks playing out over different time scales, and this surprising result could be viewed as a specific example of this general truism. Counterintuitive effects emerge in many ecological models that have unstable dynamics arising from nonlinear feedbacks; the response of abundances, averaged over the trajectory of the system, to a change in a system parameter may go in exactly the opposite direction to what is expected from an examination of the system's equilibria (Abrams 2002). It is difficult to assess these predictions in field systems because in nonlinear dynamics, populations fluctuate around some kind of potential

equilibrium, but their long-term average is not in general the same as the numerical value of that equilibrium. Moreover, assessing trends in fluctuating time series in response to environmental change poses deep statistical challenges.

The bottom line of this body of theoretical work is that trophic cascades involving changes in average abundance of species at different trophic levels can also entail shifts in the dynamical behaviors of populations, such as the tendency to oscillate or the magnitude and time course of oscillations. There are some excellent examples of plant–herbivore interactions being strongly unstable in the absence of top predators. For instance, McCauley et al. (1999) showed in aquatic mesocosms that strongly unstable oscillations arose for *Daphnia* consuming algae. In a terrestrial example, voles explode on predator-free islands in the Baltic and overexploit their plant food resources. But where predators (mustelids) are present, vole populations remain bounded in their numerical fluctuations (Banks et al. 2004).

Today one seeks to understand the dynamics of two-level trophic systems (producer and consumer) through contrived experiments at micro and meso scales and field studies in such exotic places as arctic islands that lack natural predators (Aunapu et al. 2008). Our short cultural memory, as encapsulated in Pauly's (1995) notion of the shifting baseline, has blinded many modern ecologists to the fact that food-limited herbivores dominated terrestrial ecosystems over much of the world until recent times. Until humans drove them extinct, proboscideans (elephants and their relatives) and other megaherbivores ranged over all the continents except Australia and Antarctica, from the Arctic Ocean to the Southern Seas (Burney and Flannery 2005). Such large animals are immune to predation as adults and are able to increase until limited by the food supply (Owen-Smith 1988). Herd-forming migratory ungulates constitute a second class of major herbivores that are largely free of predation and consequently regulated from the bottom up (see Chapters 15 and 16, this volume). Loss of these major classes of herbivores over most of the terrestrial realm appears to have altered much of the earth's terrestrial vegetation, so the consequences have been momentous (Bond 2005).

As noted earlier, and discussed further in Chapters 17 and 18, the theory of trophic cascades has been refined and greatly advanced since publication of foundation papers by HSS, Paine, Rosenzweig, Fretwell, and Oksanen et al. One particular focus of empirical and theoretical research at present is elucidating the role of diversity at different trophic levels in modulating the strength of trophic cascades and patterns of abundance along productivity gradients. Diversity in the prey trophic level can at times moderate top-down control (Leibold et al. 1997; Stachowicz et al. 2007). Diversity in the predator level can either in-



crease top-down effects (Straub and Snyder 2008) or weaken them (Stachowicz et al. 2007). The former often reflects niche complementarity (e.g., different predators feed in different microhabitats or at different times of day). The latter is particularly likely when intraguild predation and interference between predator species is strong. This is frequently observed in biological control of agricultural pests (where it can lead to a conflict between the conservation of predator diversity and the efficacy of control; Straub et al. 2008), but is also ubiquitous in vertebrate carnivore guilds (Sergio and Hiraldo 2008; Hunter and Caro 2008). Variation in predator species diversity across time or space can thus lead to complex mosaic patterns in the strength of trophic cascades.

The basic processes of top-down control are understood and have received ample empirical support from a global array of ecosystems, as will be documented in this book. The field now stands at a new threshold, one that promises enormous dividends in enhanced understanding of the way in which ecosystems work. The new plateau of understanding rests on the concepts of alternative states, positive feedback loops, catastrophic regime shifts, and hysteresis (Scheffer et al. 2001).

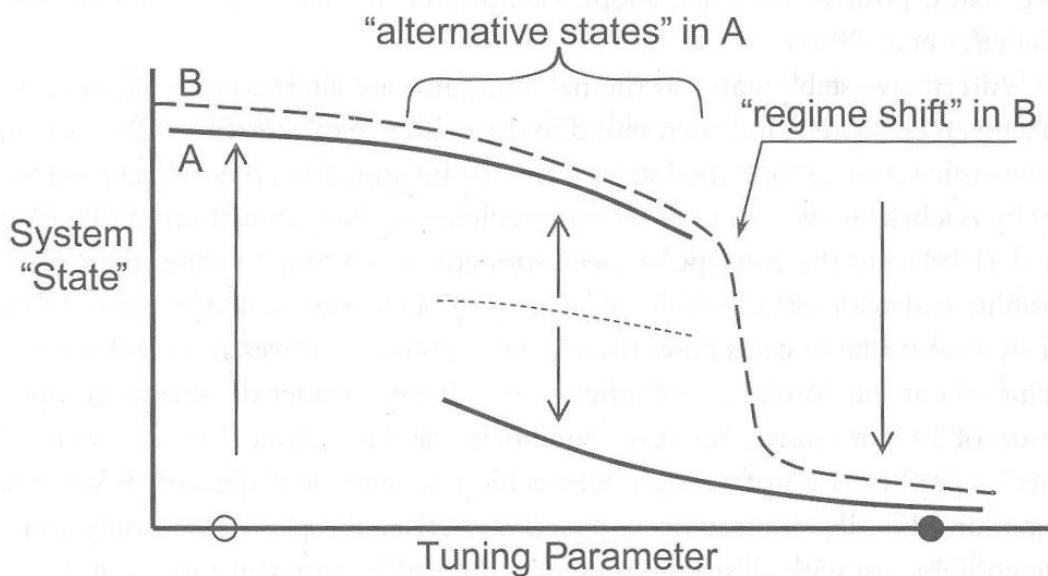
Alternative stable states, as the name implies, are alternative configurations of a given ecosystem and correspond to the existence of alternative attractors in a dynamic system. Alternative states were first imagined as a theoretical possibility by Richard Lewontin in 1969 and predicted in the formulation of Oksanen et al. (1981), but the concept has been strengthened through further theoretical insights and widespread empirical support. As Lewontin noted, the possibility of alternative stable states raises the specter that history leaves an indelible footprint on current community configurations. If we consider the species composition of a community, alternative equilibria may be generated from a regional species pool because of strong interspecific interactions. If the Lotka–Volterra equations describe community interactions between  $n$  species, then only a single equilibrium with all species present can possibly exist. But this set of  $n$  species may contain a number of subsets that, when present and established, are able to prevent invasion by species left out of this subset. When alternative stable states exist, the sequence of colonization events matters greatly in determining the final community configuration. But if interactions within or between species are strongly nonlinear (i.e., non-Lotka–Volterra models), then alternative stable states can exist, even with all the same players being present.

A fundamental objective of ecological science is to understand how ecosystem properties and community structure track major external variables and how ecosystems respond to different kinds of perturbations. Community ecologists distinguish between two kinds of perturbations: pulse perturbations and



press (Bender et al. 1984). In the former, one imagines that there is a single, sharp perturbation to the system, such as a quick culling of a dominant species (without driving it to extinction), whereas in the latter the perturbation is sustained over an indefinite time horizon. A press perturbation in effect takes an original system and transforms it into a new system. The question is how much of the structure of the original system carries over to the new system.

Figure 1.1 (modified from Scheffer et al. 2001) helps clarify two kinds of responses one can observe to either press or pulse perturbations. We imagine there is a state variable we are interested in (e.g., abundance of a focal species), and there is a parameter of the system that can be directly perturbed (e.g., by experimental manipulation). Systems labeled “A” and “B” in Figure 1.1 both have nonlinear positive and negative feedbacks defining how they respond to press and pulse perturbations and how they settle into an equilibrium (or more than one) for any given fixed value of the key parameter. If we abruptly increase



**Figure 1.1.** A schematic depiction of the concepts of regime shifts, alternative states, and hysteresis. Two ecosystems, A and B, are shown, where the equilibrational states of those systems vary with a tuning parameter, an independent variable extrinsic to the system (e.g., nitrogen loading in a lake, or *Pisaster* abundance in a small patch of the intertidal zone trod by Bob Paine). The equilibria are locally stable; small perturbations tend to return to the equilibrium, where the system started. In both cases, a large change (from the open to closed circles) in the tuning parameter implies a large change in state. The nonlinear forces in B are such that the system stays largely in one state or another, with an abrupt transition between them. But for every value of the tuning parameter, the system settles into just one state. For A, there is a zone of alternative stable states, and where the system ends up depends on where it started out.

the value of the parameter from low (open circle) to high (closed circle) values and leave it there (a pulse perturbation), we expect equal changes in both systems. But if we change the system between these values and do so slowly (so each system stays near equilibrium), we see different responses in the two systems. In B, there is a sharp shift in state. Such shifts have been called regime shifts in the literature. But note that at any given value of the parameter, there is a single resulting system state.

In system A, there also can be sharp transitions. But in contrast to system B, the value at which the system changes depends on the direction of change in the parameter. Over a certain range of parameter values, it is necessary to know where the system started to know where it is. This dynamic structure is called hysteresis. Moreover, in this parameter range, pulse perturbations that change the state of the system can lead to abrupt shifts rather than a tendency to return back to where it started.

The state of any ecological system is not really a mathematical point, a hypothetical equilibrium of fixed and unchanging abundances, but rather (in the jargon of dynamic systems) an attractor, a bounded regime within which fluctuations—which are always present in the natural world, albeit to differing degrees—are contained. Dynamic systems driven by nonlinear interactions can have multiple attractors, alternative states toward which their trajectories tend, depending on where they start. A very important issue in ecology is understanding when systems have alternative states and when they do not. We believe this is of primary significance when we reflect on the potential importance of trophic cascades, particularly in the context of conservation and restoration.

Trophic cascades can involve regime shifts and potentially even alternative stable states. When a stable trophic system is powerfully perturbed in a press fashion, say by addition or removal of a top level, the remaining system can be destabilized and enters a transient state. Adding a top predator (e.g., largemouth bass) to a pond containing only planktivorous fish, zooplankton, and phytoplankton results in major shifts at lower levels. Bass reduce the density of planktivorous fish, releasing zooplankton to increase, whereupon abundant zooplankton filter out phytoplankton, a process that clarifies the water column. All this takes place over a period of months to a year. During the transition, the system is rapidly changing.

In other systems, the transitions arising from such perturbations may play out over centuries or even millennia. An upsurge in herbivory on seedlings in a temperate forest may have no obvious impact on the structure of the forest until several centuries have passed, as recruitment of a different suite of species replaces the occasional but inevitable death of canopy dominants. It can be very

difficult to distinguish between true alternative stable states and sluggish transitions between reversible states.

The simplest way for nonlinearities to be introduced is for species to experience strong positive intraspecific density dependence at low densities (Allee effects; for a recent review, see Courchamp et al. 2008). This in turn can arise from intrinsic factors. For instance, sexual outcrossing species may find it difficult to find mates at low densities. Well-established species in communities may not be able to recover if their numbers plummet to very low levels. So all communities comprising sexual species thus can contain subsets of alternative, more depauperate communities, where reestablishment of species that have gone locally extinct may be difficult.

Allee effects can also arise from trophic interactions, and this theoretically plausible effect may be more pertinent to the theme of trophic cascades. Type III functional responses by generalist predators are accelerating at low prey numbers (which can be stabilizing if prey are kept in check at low levels) but saturating at high levels, which means that high densities of prey can escape predator control. This process has been suggested as an explanation for outbreaks of rodent populations (Sinclair et al. 1990), shifting between a stable low-density state and another stable high-density state, permitted by transient pulses in food availability for the rodents. Although a number of examples of this effect have been suggested, it has been difficult to definitively show that this plausible process actually occurs (Sinclair 2003). Sinclair and Metzger (2009) note one example in Kruger National Park, where initially high numbers of wildebeest were reduced by culling. After culling, their numbers continued to decrease because of lion predation. This pattern suggests that two alternative states describe the nonlinear dynamics of the full system. However, it is difficult to convince skeptics on this point, in part because it is difficult to perform experiments at the appropriate spatial and temporal scales.

Transitions between alternative states or regime shifts may be fast or very slow and may be triggered by a variety of abiotic or biotic perturbations. A particularly familiar type of press perturbation is the addition or deletion of a top trophic level. Examples involving keystone predators, the starfish *Pisaster* and the largemouth bass, were discussed earlier. Other examples come from the marine realm, where overfishing has led to the collapse of many fish stocks to the point of commercial extinction. Van Leeuwen et al. (2008) point out that even though fishing has been totally banned for many of these stocks, the fish populations show no sign of recovering. They note that the literature contains many plausible mechanisms that can stabilize a fish population, once abundant, to low levels after a crash. For instance, the decrease in cod numbers may have led to an upsurge in planktivore abundance. Because these planktivores can prey on cod

eggs and can compete with cod larvae for food resources, this can check population growth in the cod.

For a terrestrial example, one can point to ecosystems dependent on fire. Fire is a physical driver of alternative states that operates with positive feedbacks and hysteresis. Fire-adapted vegetation typically includes plants that dry out aboveground, creating fuel, while remaining viable belowground. If fires are frequent enough, such plants tend to dominate the vegetation of coarse, porous soils or regions subject to long, hot dry seasons. For example, vast portions of the southeastern United States were once occupied by the fire-dependent longleaf pine (*Pinus palustris*)–wiregrass (*Aristida stricta*) association. Wiregrass provided the fuel. Modern Americans have imposed fire suppression over much of this region, allowing forests of oak and other pine species to grow up in place of longleaf pine. Moist, shady oak forests, lacking a grassy ground layer, burn reluctantly and infrequently and are stable to occasional cool ground fires. Restoration of the longleaf pine system entails opening up the oak canopy and burning frequently, typically every 2–5 years. Thus, a high fire frequency is needed for the oak–longleaf pine transition, whereas a much lower frequency is needed for the reverse, pine–oak transition.

The knowledge that ecosystems can assume alternative states and that these alternative states are, in principle, reversible presents managers with a powerful tool for ecological restoration. With respect to fire ecology, the reversibility of alternative states and the conditions needed to stabilize them are quite well understood. In contrast, reversing the eutrophication of ponds and streams is a challenge fraught with difficulties (Chapter 4, this volume). As for trophic cascades mediated by biotic forcing, there are some encouraging initial signs in the recovery of kelp forests following the return of sea otters to various parts of their historical range in the North Pacific (Estes and Duggins 1995) and in the recovery of willows, cottonwoods, and aspens in Yellowstone and Jasper national parks following wolf restoration (Beschta 2003; Beschta and Ripple 2007a, 2007b). We believe an important future dimension of restoration ecology lies in the manipulation of trophic cascades, a prospect that will require managers to reexamine existing methods.

The intent of this chapter has been to introduce the reader to the basic concepts of what trophic cascades are and how they operate and to provide a thumbnail history of some of the basic approaches that have been taken to develop a theory of trophic cascades. Additional layers of complexity and detail will be introduced and discussed in later chapters.

The broad purpose of this volume is to provide an overview of the importance of large apex predators in maintaining trophic cascades across global ecosystems. The book is organized into four parts. The first consists of Chapters 2–

6, covering aquatic ecosystems. Terrestrial ecosystems from the Arctic to the tropics are covered in the second part (Chapters 7–12). The five chapters of the third part (Chapters 13–17) cover topics that cut across the divide between aquatic and terrestrial systems. And the final part (Chapters 18–21) presents a synthesis of concepts and evidence to make the case that trophic cascades regulate the organization, dynamics, and diversity of all natural ecosystems.

In the final synthetic chapter, we conclude that trophic cascades are the key to understanding how ecosystems function. And if this should prove true, ecology will finally have found its holy grail: the power to predict the responses of ecosystems to many kinds of abiotic and biotic perturbations.