CHAPTER 18

Theoretical Perspectives on Trophic Cascades: Current Trends and Future Directions

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What is a trophic cascade, and why do we care? Pace et al. (1999, p. 483) define a trophic cascade as "reciprocal predator–prey effects that alter the abundance, biomass, or productivity of a population, community, or trophic level across more than one link in a food web." A more specific definition is provided by Persson (1999, p. 385): A trophic cascade is a "propagation of indirect mutualisms between nonadjacent levels in a food chain." Estes et al. (2001, p. 859) state that "a trophic cascade is the progression of indirect effects by predators across successively lower trophic levels." A folk definition might be "the enemy of my enemy is my friend."

The introductory chapter of this volume included a brief history of what we might call classic theoretical models of trophic cascades, emphasizing in particular qualitative messages and implications that have yet to be addressed in detail (or at all) in empirical studies, and it touched on the importance of alternative stable states related to cascades. The other chapters of this volume are replete with dramatic case histories illustrating why we should care about trophic cascades and aim toward a deep conceptual understanding of the factors that determine variation in the strength of cascades between biomes. Ultimately, this understanding has to be grounded in an empirical basis of well-crafted observational and experimental studies, but theoretical explorations can help clarify how known processes might be expected to govern cascade strength and provide pointers for fresh directions of empirical inquiry. Here, we

provide an overview of a few likely extensions and modifications of the basic theory of trophic cascades that in our view warrant sustained attention by both theoreticians and empiricists over the next few years.

Classic food chain theory ignored many real-world complications. This is not by any means a critical observation. By recognizing what predictions change when we relax or modify assumptions in these simple models, we use these "perfect crystal" models (May 1973a) to identify axes of variation (in environmental variables or organismal traits) that can then be used to interpret differences in food web dynamics between different empirical systems. There are many directions in which one can imagine theory developing, and it is impossible to really do justice to all the possibilities in the space of this chapter. Instead, we present a few vignettes to briefly explore several important features left out of classic trophic cascade theory.

VIGNETTE 1: DIRECT PLANT–PREDATOR INTERACTIONS

The classic Lotka–Volterra food chain model (e.g., Equation 1.1 in Chapter 1 and related models such as those in Oksanen et al. 1981 and others cited in Chapter 1) assumes that to understand food chains, one can separately analyze the rate of attack of the predator on the herbivore and the rate of consumption of the plant by the herbivore and then splice these two interactions together to describe the dynamics of the full system. One current exciting area of study emphasizes the interdependence of different trophic linkages under the rubric of "trait-mediated interactions" and "interaction modification" (Bolker et al. 2003).

For instance, the rate of consumption of the plant by the herbivore may depend on traits of the herbivore that also influence its risk of predation, and these traits may respond plastically to the balance between predation risk and foraging reward. Foraging activity might itself expose an herbivore to predation, for instance because visual predators more easily cue on moving prey. In this case, herbivores should shift their behavior, feeding less when predators are perceived to be abundant and then foraging more intensely when predators are rare. There is a substantial and growing literature on the ecology of fear (Brown et al. 1999; Brown and Kotler 2004), showing both that it is a significant element in many natural predator–prey interactions and that it can provide a mechanism that mediates strong trophic cascades (Beckerman et al. 1997). Many studies suggest that trait-mediated effects are at least equal in strength to density-mediated effects (Werner and Peacor 2006; Schmitz et al. 2004). The magnitude

of trophic cascades may thus reflect the scope for plastic responses by prey to predators and by plants to herbivores as well (e.g., induced chemical or structural defenses; Van der Stap et al. 2007). Plastic responses of prey to predators may straddle generations, with far-reaching effects on density and on spatial distributions at large scales. This occurs in aphids (sap-feeding insects), which respond to the presence of natural enemies by secreting alarm pheromones, which in turn induce wingless adults to give birth to winged offspring (Kunert et al. 2005). Wings are costly, so these offspring have lower fecundity, but they more than make up for this cost because they can leave the host plant, disperse over large distances, and thus escape intensifying predation or parasitism at their birthplace. This in turn reduces aphid density on the original host plant, potentially weakening the impact of the aphid on the host in future generations. *Daphnia* (water fleas) can show a similar delayed response to chemicals released by fish; in this case the females are more likely to produce diapausing eggs when fish are sensed, allowing the offspring to escape high predator densities, not in space but in time (Slusarczyk 2005). Again, this reduces the densities of zooplankters floating in the water column, which should lower the rates of herbivory on phytoplankters in subsequent generations. Moreover, in both cases herbivores can appear at places and times at rates not strongly coupled to local production, leading to mismatches in predictions relating primary productivity to the intensity of trophic cascades (Holt 2008b). Induced defenses therefore can have complicated effects on the spatial patterning and long-term temporal dynamics of trophic cascades.

By contrast, much less attention has been given to interactions between the plant level and rates of predation. A priori, one could easily imagine that the foraging efficiency of the top predator should sensitively depend on vegetation structure and biomass. For example, Ripple et al. (2001) report that in Yellowstone predation risk for elk is elevated in aspen copses (because of the substantial risk of a fleeing elk tripping over fallen logs, dramatically hindering escape from a wolf or cougar), and so elk feed less there. In the Serengeti, lions more readily capture wildebeest by ambush in tall grass, where a lion can easily hide, than in short grass, where a large predator is more conspicuous (Packer et al. 2005; Hopcraft et al. 2005). This in turn has consequences for lion population dynamics: During the 1994 drought in the Serengeti, the wildebeest population declined severely as a result of lower food abundance. This resulted in an increase in tall grass that persisted for several years and allowed the lion population to hunt more effectively and thus to increase in its numbers (Packer et al. 2005), potentially intensifying predation on ungulates. In general, in some systems predators may more easily capture prey in thick cover than in thin.

One consequence of this is that when vegetation grows in stature, there might be an intensification in predation, leading to a reduction of herbivory, which in turn promotes further vegetation growth. This positive feedback potentially has important consequences for community dynamics. To explore this effect more formally, we can mimic an effect of vegetation on predator efficacy by making the predator attack rate in the Lotka–Volterra model (Equation 1.1 of Chapter 1) a function of vegetation biomass, as follows:

$$\frac{dP}{dt} = P[b'a'(R)N - m']$$

$$\frac{dN}{dt} = N[abR - a'(R)P - m] \tag{18.1}$$

$$\frac{dR}{dt} = R[r - dR - aN]$$

This algebraic rendition of the plant–predator interaction seems to describe the Serengeti lion–wildebeest–grass example, where grass cover has a direct effect on the predator attack rate. In the Yellowstone example, by contrast, changes in vegetation biomass alter herbivore perceptions of predation risk rather than attack rates, so the role of predation is to mediate the spatial pattern of habitat use by the herbivore rather than to increase herbivore deaths by direct consumption as in Equation 18.1. To account for this behavioral response, the "mean field" assumption of these equations would have to be expanded to account for spatial variation in perceived risk and movement between habitats. We revisit the Yellowstone case later (albeit without new algebra). Equation 18.1 is the same as the Lotka–Volterra model discussed in Chapter 1, except that we have replaced a constant attack rate by the predator on its prey with a variable attack rate that depends directly on plant biomass, R. The attack rate may either increase or decrease with R, depending on the detailed behavioral tactics used by the predator in finding and subduing its prey. An analysis of this model (Holt et al. in preparation) shows that a wide range of dynamic outcomes are possible, including unstable dynamics and alternative stable states, which are not observed in the simple Lotka–Volterra model. The introduction of a relationship between the predator attack rate and the biomass of the lowest trophic level in effect leads to a long feedback loop, and this feedback can be destabilizing. Here, we present some illustrative numerical examples rather than analytic details.

For simplicity, let us assume that there is a linear relationship between the predator attack rate and the thickness of the vegetation (truncated at 0 if necessary, because the attack rate cannot be negative):

$$a'(R) = \max(\alpha + \gamma R, 0) \qquad (18.2)$$

Figure 18.1a shows an example of alternative states in the trophic organization of a community, when there is a positive relationship between predator attack rates and vegetation cover. At one equilibrium (on the left), the predator exists stably with the herbivore. A disturbance occurs (at time 0), which knocks predator numbers down. This leads to a surge in herbivore density and a temporary increase in predator numbers, but because herbivore numbers are high, the
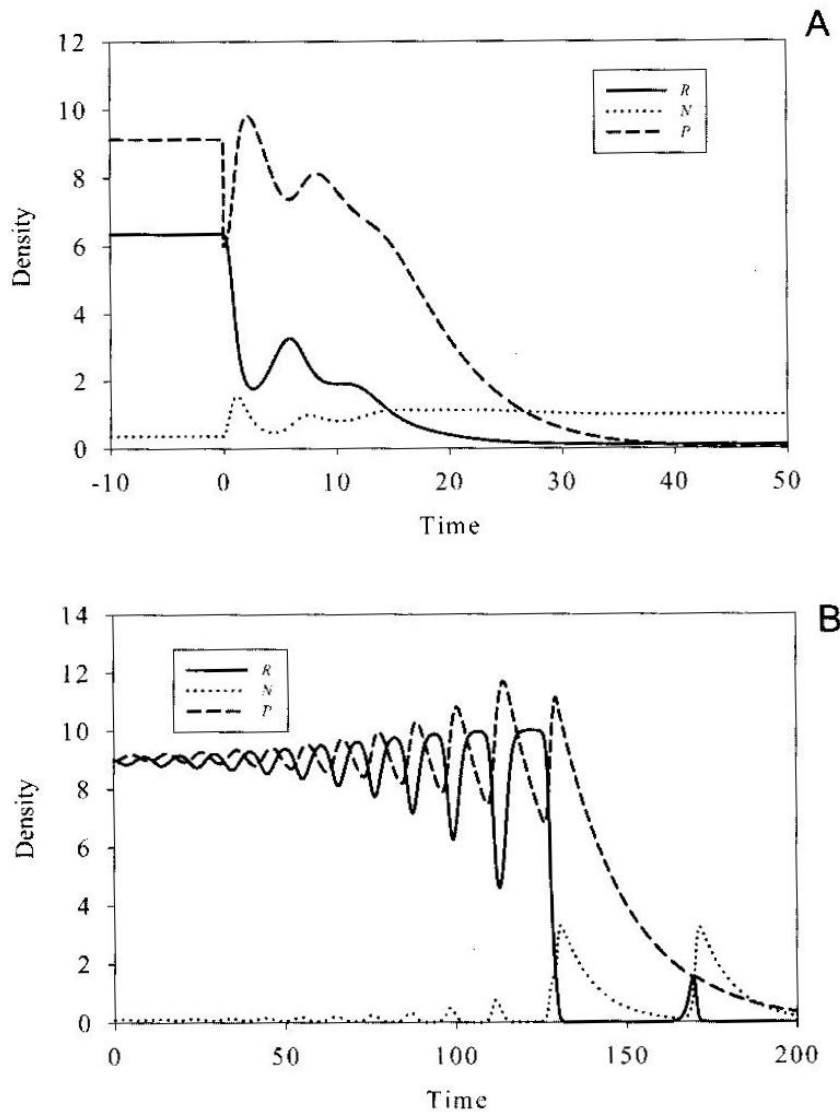

Figure 18.1. Examples of tritrophic dynamics, when predation depends on the biomass of vegetation. **(a)** An example of alternative stable states in the food chain model described by Equation 18.2, with a linear increase in predator attack rates with increasing vegetation biomass. **(b)** An example of strongly unstable dynamics in a food chain. Technically, the dynamics seem to approach a heteroclinic cycle, which in practice would amount to inexorable extinction.

vegetation continues to be reduced, which leads (with a lag) to a reduction in the attack rate on the herbivore. This reduction in consumption eventually begins to drag down predator numbers. The final state of the system is one in which herbivores crop vegetation down to a low level, which increases the herbivores' ability to escape predators, and so the predators cannot persist. Figure 18.1b shows another example, where the aforementioned functional dependence of predator attacks on vegetation density leads to wildly unstable dynamics. Adding small quantities of refuges for the herbivore can moderate these oscillations without making them disappear. If the functional relationship between attack rate and vegetation is nonlinear (e.g., sigmoid, increasing with vegetation biomass but saturating) (details not shown), alternative stable states may arise, each with a full food chain. But in one state, the predator is rare (but persistent), and the plants are overexploited by herbivory, whereas in the other the predator is common, the herbivore is kept in check, and the vegetation is thickly abundant.

In other systems, prey may find cover when vegetation is thicker, so attack rates would decline with increasing vegetation biomass (Arthur et al. 2005). For instance, Ayal (2007) argues that the sparse cover of deserts makes prey more vulnerable to visually hunting, roaming predators. An effective herbivore that can sharply reduce vegetation stature or biomass can thereby increase the likelihood that it will itself be controlled in a top-down fashion by predation. It is less likely that the food chain exhibits alternative states in this case (details not shown).

There are many other ways in which a basal resource can directly influence predator dynamics. For instance, plants may provide top predators with resources directly (e.g., fruit, nectar), with benign microclimates (e.g., patches of shade for a thermoregulating lizard), or with domiciles (e.g., ants on acacias with swollen thorns). Plants that feed predators in effect exert apparent competition on herbivores (van Rijn and Sabelis 2005). Plants experiencing herbivory may exude chemicals that help lure mobile predators (Dicke and Vet 1999); if the effectiveness of this tactic varies with plant density, then a model such as Equation 18.1 can be used to describe the resulting dynamics. Depending on the detailed way in which these effects are woven into a food chain model, one may observe enhanced stability, or the reverse.

VIGNETTE 2: TROPHIC CASCADES IN SPACE

A largely unexplored issue is how trophic cascades in local communities influence dynamics at larger spatial scales, how spatial processes in turn modulate

trophic cascades at local scales, and how these processes are reflected in the emergent spatial structure of landscapes.

In the theoretical examples presented earlier, changes in vegetation biomass resulted in changes in predation rates in a homogeneous landscape. The wolf–elk–aspen example provides a case study for a spatial response by herbivores to predation risk in a heterogeneous landscape, where the heterogeneity itself emerges from the trophic interactions. In this case, a spatial patchwork mosaic of aspen groves and open habitat areas is reinforced over time by the presence of the predator. In the absence of wolves, elk could in theory produce a spatially homogeneous and open landscape with low aspen cover. With the introduction of wolves, small initial differences in aspen cover across the landscape become reinforced by elk perceptions of predation risk, as they avoid aspen patches and thus permit the growth of saplings and seedlings. In addition to leading to localized trophic cascades within aspen groves, wolf predation can thus theoretically magnify habitat heterogeneity at landscape scales, with important implications for the maintenance of biodiversity of other taxa such as bird assemblages at these scales.

If unstable dynamics readily emerge in local food web dynamics (a topic that has been one of the principal themes of the predator–prey literature over the last century), then for the food web to persist, stabilizing mechanisms not built into local interactions must exist. The most generic stabilizing factors in food webs that do not involve mechanisms of direct density dependence such as territoriality or interference all involve space, in various guises. At a very local scale, introducing absolute spatial refuges (where a limited number of prey are protected in the refuge) into any of the models discussed in Chapter 1, for victim or prey species at any trophic level, can be strongly stabilizing. This is also true for Equation 18.1. When refuges are sufficiently common, predation is expected to be weak, and trophic cascades should then be quantitatively trivial.

In the absence of refuges, space may still facilitate persistence if interactions are localized and dispersal is limited. For instance, dispersal permits colonization–extinction dynamics, so that an interaction persists at a regional scale, despite local extinctions caused by unstable food web dynamics. Even if consumers do not drive their prey locally to extinction, prey may go extinct because of disturbances. In an unlinked food chain, by assumption the top predator does not have alternative prey, and so it too should go extinct. Elsewhere (reviewed in Holt 2009), island biogeographic and metapopulation models for food chains have been developed, incorporating sequential colonizations and coupled extinctions. Here we simply recount some key conclusions from these models that are pertinent to trophic cascades.

First, food chains tend to be shorter on smaller or more isolated islands or habitat patches. In addition to colonization and extinction dynamics, there can be other reasons to expect the length of food chains to be shorter on smaller islands or patches (Holt 2009). A growing body of empirical studies shows that area indeed influences the trophic organization of communities.

The upshot of this work on area effects on food chain length is that there should be predictable spatial variation in the strength of trophic cascades. On very small islands, it may be difficult for even the herbivore to persist. On somewhat larger islands, the herbivore may be present, but the predator may be absent. These are sites where one might expect to observe intense herbivory (as seen in the transient islands of Lago Guri; Terborgh et al. 2006). On yet larger islands, predators should be predictably present and moderate the impact of herbivores on their food base. So there may be a hump-shaped relationship between the average intensity of herbivory and island size, arising because of spatial variation in the likelihood of top-down trophic cascades imposed by predation.

When there are strong top-down effects of predators on herbivores, the dynamic consequences of these local cascades can feed back to larger spatial scales. Within a continent, no area may be a defined source, but instead all local sites may experience extinction over a sufficiently long time span. Population persistence then requires that occupied sites supply emigrants who can colonize empty sites fast enough to replenish these losses. In such metacommunities (Holyoak et al. 2005), alternative stable states can arise in food chain dynamics (Holt 2002). Even in simple Lotka–Volterra models, top predators with strong direct density dependence (e.g., territoriality) can stabilize otherwise strongly unstable plant–herbivore interactions (Rosenzweig 1973). What this implies is that sites with the full chain may enjoy lower herbivore extinction rates than sites without a top predator. Moreover, these sites can provide a steady supply of colonists of both the top predator and the herbivore, to colonize sites where extinctions have occurred (e.g., because of disturbances such as hurricanes). So if a landscape starts out with most sites occupied by the full food chain, overall extinction rates will be low and colonization rates high. But if instead it starts out with few sites containing the predator, and the herbivore goes extinct rapidly in the sites it occupies alone, few patches will contain the herbivore, and the predator will not be able to increase when rare. The net effect of this is that the landscape as a whole can exist in alternative states (Holt 2002, 2009).

There are many important spatial dimensions of trophic cascades other than those captured in island biogeographic and metapopulation theory. For instance, in a heterogeneous landscape, productive habitats may be juxtaposed to

unproductive habitats. If predators are mobile, the intensity of predation in the unproductive habitat may greatly exceed that expected from just local productivity because of spillover predation from the adjacent productive habitat (Holt 1984; Oksanen 1990; DeBruyn et al. 2004). This pattern of predation can lead to source–sink dynamics, which can help stabilize otherwise unstable trophic dynamics (Holt 1984). Organisms with complex life histories necessarily couple distinct habitats, leading to trophic cascades transcending ecosystem boundaries (McCoy et al. 2009). For instance, Knight et al. (2005) reported that fish in Florida ponds greatly depressed larval dragonfly abundances compared with fishless ponds. This in turn was reflected in the abundance of adult dragonflies buzzing around those ponds, which in turn influenced the abundance of insects such as bees and butterflies (due to both direct mortality and behavioral avoidance). Also, allochthonous resources can provide a spatial subsidy for consumers, sustaining resident predators at numbers well above that expected from local production, which can strengthen trophic cascades inflicted on resident herbivores in the recipient habitats (Polis et al. 1997). An important objective of research on trophic cascades should be to firmly integrate food web interactions and spatial ecological dynamics so as to better gauge the causes and consequences of spatial variation in the strength of cascades.

VIGNETTE 3: PATHOGENS AND FIRE AS MODULATORS OF TROPHIC CASCADES AND LANDSCAPE PATTERNS

Elsewhere in this volume, Sinclair et al. and Bond explore both the role of rinderpest as a trigger for a trophic cascade in the Serengeti and the role of fire as a "consumer" and determinant of vegetation biomass in the savanna biome. The Serengeti presents a situation in which a consumer (the wildebeest) is able to circumvent the regulatory pressure of predation by being highly mobile in large herds, diluting predation (Fryxell et al. 1988). This allows wildebeest to increase to high numbers, where it is regulated by its food resources (Mduma et al. 1999). The top-down impact of wildebeest herbivory on plant biomass is one of the principal drivers of temporal dynamics and spatial patterning in the Serengeti ecosystem (Holdo et al. 2009a, 2009b, in press). The consumer–resource equilibrium between this dominant herbivore and its resource base was disrupted by the emergence of rinderpest more than a century ago and then reestablished only after rinderpest eradication by deliberate human intervention (Sinclair 1979; Dobson 1995; Holdo et al. 2009b). Fire has played a key role in this cascade, which features not only the vertical propagation of trophic

perturbations (the classic model) but also lateral effects between two resource guilds, grasses and trees (Holdo et al. 2009b). Trees and grasses compete in savannas (Scholes and Archer 1997), and fire often acts as a consumer that can mediate this competitive interaction by affecting the slow-growing but competitively dominant trees to a greater extent than the fast-growing grasses, which in turn feed the fire—a striking if nonstandard example of apparent competition (Holt 1977). Fire in effect is a transient megaherbivore, which can inflict massive changes on vegetation, independent of any higher-up top-down controls. The wildebeest population explosion that followed from rinderpest eradication in the 1960s led to a reduction in grass cover, a decline in fire, and an expansion of the tree population (Packer et al. 2005; Sinclair et al. 2007; Holdo et al. 2009b).

This transient trophic cascade from rinderpest to wildebeest down to vegetation, modulated by fire, exemplifies several broadly applicable themes. Trophic cascades have traditionally been viewed through the conceptual lenses of classic food web ecology, which focuses on the feeding relationships, escape tactics, and so on of the macroorganisms that to our eyes dominate natural ecosystems. Yet there is increasing evidence that hidden players—microorganisms—left out of the usual food web diagram can have enormous impacts on how communities are structured and ecosystems function (Thompson et al. 2001). Pathogens themselves may generate trophic cascades, as did rinderpest in the Serengeti.

Pathogens can also modify the strength of trophic interactions in more subtle ways, for instance by making prey easier to catch, which could magnify the ability of a predator to generate a trophic cascade, or by keeping in check the numerical responses of predators and thereby weakening cascades. Another very significant but nonstandard cascading effect of top predators may be via the modulation of disease dynamics in hosts that are also prey. An epidemiological consequence of top predator removal may be the unleashing of host–pathogen interactions at lower trophic levels and disease emergence both within and across host species (Hudson et al. 1992; Packer et al. 2003; Ostfeld and Holt 2004). Consider a prey species harboring a specialist pathogen, and assume that this prey species is also attacked by a generalist predator. Abstractly, this is an example of intraguild predation. Predators attack infected hosts, and so they can be predators directly on the pathogen. But predators can also attack healthy hosts, and so in a sense they compete with the infection for access to the resources in those host bodies. What is the effect of predator removal on the incidence of infected prey? In a wide range of epidemiological models, predator removal increases disease incidence (the fraction of hosts infected) and

sometimes paradoxically can lead to a decrease in total host numbers. The latter can occur if predators preferentially pick off infected prey (e.g., because they are easier to catch) and if the pathogen can strongly regulate its host by both a reduction in fecundity and elevation in mortality for infected individuals (Packer et al. 2003). By shifting mortality regimes in a host species and increasing the prevalence of disease, predator removal can also lead to unstable host–pathogen dynamics and recurrent epidemics (Hochberg et al. 1990; Dwyer et al. 2004). All these mechanisms can then have knock-on effects on the resource populations used by the host species. If the pathogen is not completely specialized to a given host species, top predator removal can increase spillover infection onto alternative hosts, paving the way for cascading extinctions as resistant host species suppress vulnerable host species.

Various real-world complications can change these predictions in interesting ways. For instance, if a host has a strong immune response and strong negative density dependence in recruitment, somewhat paradoxically, modest amounts of predation can actually *boost* disease prevalence. The reason this occurs is that density-dependent compensation in reproduction leads to an increase in the supply rate of fresh, young, susceptible hosts (Holt and Roy 2007; Roy and Holt 2008), which can feed the infection. Moreover, in some systems parasites exploit both prey and predators to complete their life cycles. Models of such systems suggest that the emergent interactions can be very unstable (Fenton and Rands 2006).

VIGNETTE 4: EFFECTS OF DIVERSITY, IN SPECIES AND IN INTERACTIONS

One obvious limitation of models such as Equation 18.1 is that they assume that there is just a single species at each trophic level. This is a far cry from reality. Adding diversity to these models makes them more realistic and also much more complicated. This is a huge topic, and we cannot pretend to do justice to it here.

With multiple species on each level, one has to consider the interplay of trophic cascades and the conditions for species coexistence within trophic levels. Figure 18.2 shows a schematic example. At the top we see the typical effect of removing a top predator in an unlinked food chain: The herbivore increases (at least as a transient), and the basal level decreases. This is the classic view of a cascade. At the bottom, we have assumed that two plant species are present. If these species differ in their sensitivity to herbivory, the less sensitive can sustain
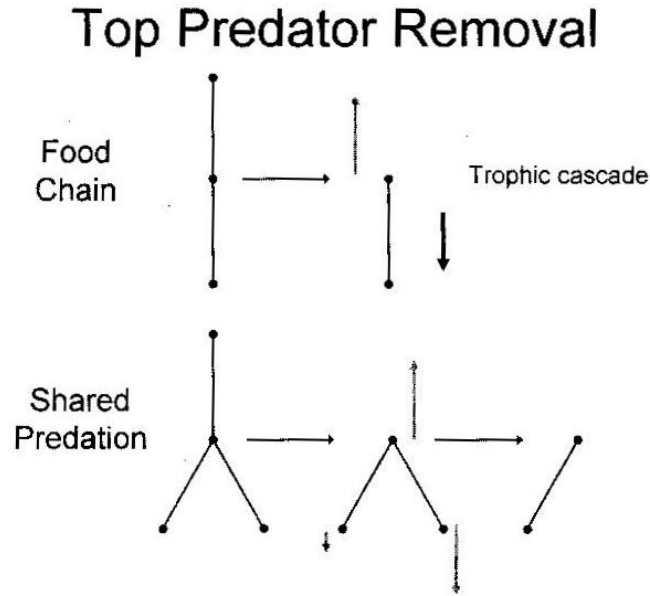
Top Predator Removal

Figure 18.2. Schematic depiction of a trophic cascade, when there is just one basal plant species present (top) or two (bottom). In the latter case, one consequence of the cascade may be extinction of a plant species due to intensified apparent competition.

the herbivore after release from predation, so that as the herbivore surges in numbers it greatly depresses the more vulnerable plant species. Because the herbivore is sustained at some level by the more resistant plant species, it can overexploit the vulnerable plant species to the point of extinction. This apparent competition effect is likely to be significant whenever multiple species are present at lower trophic levels. Considering interactions between consumer species, removal of a top predator can lead to an increase in intermediate predators (mesocarnivore release), with devastating consequences for prey species of the released predators (Crooks and Soulé 1999). Increasing the diversity of predators or prey also permits a rich array of additional interactions to occur, because of behavioral shifts or interference among species (Prasad and Snyder 2006).

Even when species within a trophic level coexist, heterogeneity in their properties can lead to shifts in how trophic level abundances change along productivity gradients (Chase et al. 2000). For instance, some experimental studies show that an increase in herbivore diversity can lead to a reduction in the indirect impact of top predators on plant biomass (Duffy et al. 2005). In arthropod systems, the outcome of trophic cascades may also strongly depend on the specificity of the signal provided by a target herbivore and the diversity of herbivores facing the predator or parasitoid. Vos et al. (2001) showed that a specialist parasitoid wasp that specifically targets one herbivore species can also be at-

tracted to plants damaged by other herbivores. The presence of the other herbivores therefore can have a negative effect on the interaction strength between the parasitoid and its host; this tends to stabilize their dynamics by lowering average attack rates on the host this specialist parasitoid needs. However, Vos et al.'s model also showed that there may be a threshold diversity at which the interaction strength is reduced to such an extent that the parasitoid goes extinct. If trophic cascades in arthropod communities emerge from the concatenation of many specialist predator–prey or host–parasitoid interactions, then an increase in herbivore diversity may lower the overall strength of trophic cascades. The patterning of specialization and generalization in trophic relationships is of course central to the quantitative description of food webs. An important task for future work is to understand how the details of this trophic patterning in food webs influences the likely strength of trophic cascades.

There are many examples of responses to chemical cues from species at nonadjacent trophic levels, leading to surprising impacts on trophic cascades. For example, hyperparasitoid wasps at the fourth trophic level exude chemicals to which their host's hosts (aphids) respond by having greater fecundity, probably because they spend less time on defensive behavior and more on feeding (van Veen et al. 2001). In this case, the population growth rate of the herbivore is dependent on the density of its enemy's enemy, and having a top predator present intensifies herbivory on the plant.

Another complication is that top predators can be omnivores and intraguild predators, feeding on the same resources as do the intermediate consumers. Empirical studies show that adding diversity to the predator trophic level can both weaken (Finke and Denno 2004) and strengthen (Byrnes et al. 2006) trophic cascades, and theory can help illuminate why these disparate effects are observed. For instance, some predators might be able to use other predators as prey (intraguild predation). Models of intraguild predation (Holt and Polis 1997) predict that if the intermediate consumer does not have its own exclusive resources, to persist it must be superior at exploiting the shared resource. This implies that top predator removal will lead to a decline in the basal resource species. Moreover, intraguild predation can alter patterns of abundance along gradients in productivity. Figure 18.3 shows an example from a model where both the top predator (IG predator) and intermediate predator (IG prey) share a resource (shared prey), but the IG prey also has an exclusive resource (exclusive prey). Along a gradient in productivity, the IG prey is first absent, then increases, but then decreases once the IG predator is present. At intermediate levels of productivity, total predator abundance (adding intraguild predator and intraguild prey) declines with productivity, and the basal resource increases in
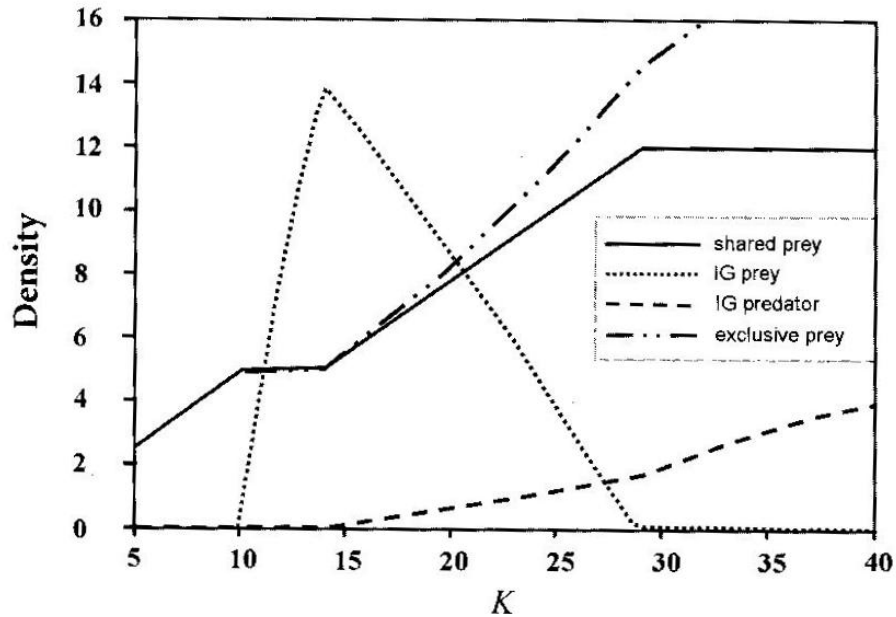
Figure 18.3. Patterns in abundance along a gradient in productivity, for a food chain in which there is intraguild (IG) predation, and alternative prey for both the top and intermediate predator. At high productivity, the intermediate consumer is excluded. In the zone where the two consumers coexist, the patterns in abundance by trophic level differ from the classic step pattern predicted in a simple, unlinked food chain (as in Oksanen et al. 1981). (Modified from Holt and Huxel 2007)

biomass because of the negative effect of the top predator on the intermediate species (see Holt and Huxel 2007 for more details). These effects differ from those predicted by classic food chain models (Oksanen et al. 1981) because there are shifts in species composition and relative abundance within trophic levels along the productivity gradient.

In complex communities, predators can influence the strength of many interactions beyond just plant–herbivore interactions, and sometimes these alternative pathways may be more significant than the classic trophic cascade. In the fish–dragonfly example sketched earlier (Knight et al. 2005), the bees and butterflies were all important pollinators for several species of flowering plants growing near the pond margins, and these plants proved to be more pollen limited (i.e., had lower seed set) near ponds without fish (and thus with abundant dragonflies) than near ponds with fish. Follow-up work is needed to determine whether these effects on plant reproduction lead to changes in local plant abundance and community structure. But even if there is no change in local abundance, it is clear that plant populations adjacent to fishless ponds with lower seed production will be poor sources of propagules in a metapopulation context.

Mutualisms and facilitation are ubiquitous features of communities, and changes in trophic cascades, via shifts in top predators, can have large effects on mutualism interaction webs (Knight et al. 2006). This could have ramifying influences both on local dynamics (e.g., on plant reproduction) and on landscape connectivity via dispersal. This topic has barely been touched in the empirical or theoretical literature.

VIGNETTE 5: THE INTERPLAY OF TEMPORAL VARIATION AND TROPHIC CASCADES

Most theory to date on trophic cascades has assumed that species interactions play out in constant environments. Yet temporal variability and disturbances can have large impacts on the strength of interspecific interactions, including trophic cascades. For instance, Spiller and Schoener (2007) report that at their Bahama study site a hurricane greatly amplified the impact of herbivores on plants because of an overall reduction in predation by lizards, which were hammered by the storm and lagged in their numerical recovery. Seasonal variation in food supply can constrain consumer dynamics, thus freeing the resource base from consumption in certain phases of the year and potentially destabilizing food chain dynamics (Oksanen 1990). A localized pulse at the base of a resource chain could lead to increases in herbivores, which in turn attract predators from a surrounding landscape. After depleting the local patch of its resources, the predators could then spread out over neighboring habitats, which would then experience transient spikes in predation and thus the strength of trophic cascades (Holt 2008b). Understanding how temporal variation and disturbance translate into temporal and spatial variation in the impact of trophic cascades is an important challenge for both theoretical and empirical studies.

VIGNETTE 6: *HOMO SAPIENS*, THE "UBER"-TOP PREDATOR?

Across the globe, humans have decimated top vertebrate predators, with ramifying consequences for ecosystem structure and human interactions (Stolzenburg 2008). Sometimes, humans themselves are significant predators, acting in many ways as the dominant determinant of top-down cascades. The Serengeti again provides a potential example of this role. Humans can hunt wildebeest and other ungulates for local consumption and the bushmeat market. Using a spatially explicit simulation model, Holdo et al. (in press) showed that increased

wildebeest hunting in the Serengeti as a result of the expanding human population is predicted to have strong knock-on effects on the amount of fire and ultimately tree cover in the Serengeti. Moreover, these effects are likely to propagate across space because of the spatial coupling effect of wildebeest movement across the system. This spatial propagation can be demonstrated through simulations of the system with and without wildebeest present (Holdo et al. 2009a). Figure 18.4 shows the predicted long-term (based on a 100-year time horizon) state of the Serengeti ecosystem with and without wildebeest (i.e., with human hunting kept to a low level and allowed to increase in an unbounded manner). When wildebeest are absent from the system (top panels), standing grass biomass is high, fires are frequent, and tree cover is uniformly low. When wildebeest are present (bottom panels), the intensity and timing of grazing in relation to rainfall create a distinctive pattern of fire occurrence across the landscape, and this in turn has a dominant effect on the amount and distribution of tree cover (Figure 18.4). Intense predation on wildebeest by humans is predicted ultimately to affect not only the total amount of tree cover present but also the pattern of its spatial distribution.

CONCLUSIONS

Theory in ecology helps to clarify our understanding of the often surprising effects that emerge because of the nonlinear feedbacks inherent in ecological systems. Much of what we have presented here can be viewed as statements of hypotheses that warrant much closer examination by empiricists. There are a number of important issues we have not discussed, such as how theory might help us understand the seeming contrast between terrestrial and aquatic ecosystems in the strength and ubiquity of trophic cascades, and how evolutionary dynamics can modify trophic cascades. To end this chapter, let us reprise some of the main themes we have presented here and in Chapter 1 as a kind of road map that may be helpful in guiding future empirical studies of trophic cascades.

- We need to characterize the effects of trophic cascades not just on average abundances of populations, guilds, and entire communities but on dynamic stability, which influences extinction risks and thus the stability and durability of entire food webs.
- Linking trophic cascades to spatial ecology—ranging from metacommunity dynamics, to spatial subsidy and spillover effects, to behavioral redistributions, to ontogenetic habitat shifts—is a large and important
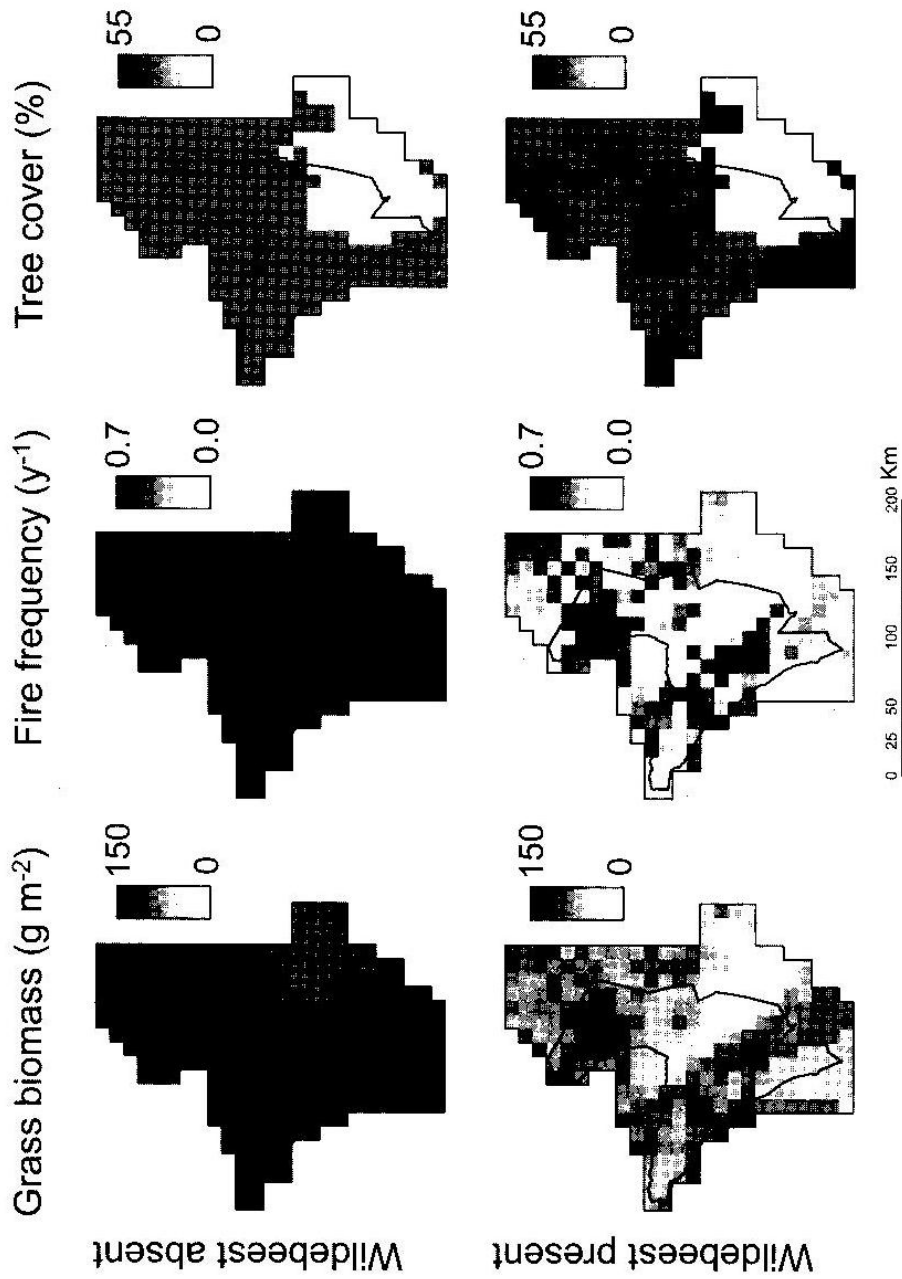
Figure 18.4. Spatial distribution of standing grass biomass, fire frequency, and tree cover with (bottom panels) and without (top panels) wildebeest in the Serengeti ecosystem after a 100-year simulation. The Serengeti ecosystem is defined here as the range of the wildebeest migration and comprises about 30,000 square kilometers, simulated in a lattice at 10- by 10-kilometer resolution (Holdo et al. 2009a). The simulation results shown here assume for simplicity that no elephants are present.

challenge. The real impact of predators may not be so much that they increase local plant biomass but that they indirectly enhance plant reproductive output, which in turn sustains metapopulations via colonization at broad spatial scales.

- Trophic cascades have many "nonstandard" dimensions, including the ecology of fear, trait modifications, and influences of vegetation on predation rates, that have yet to be fully explored, either theoretically or empirically.

- Trophic cascades can severely affect mutualism and facilitation webs and shift host–pathogen interactions in many ways. All of these effects may loom larger than the traditional emphasis on changes in levels of herbivory.

- Theoretical analyses of multispecies interactions—intraguild predation, apparent competition, keystone consumption, competitive guild interactions—can be used to elucidate many of the complexities of trophic cascades in both natural and disturbed or managed ecosystems. A particularly important complexity is the ways in which temporal variation and disturbance regimes influence the pattern of spatiotemporal variation in the strength of trophic cascades.

The other chapters in this volume recount dramatic examples of how top predators affect the structure and functioning of natural ecosystems, particularly through their influence on the intensity of herbivory. The theoretical ideas sketched in this chapter suggest that top predators could have far more pervasive impacts on community structure and dynamics than currently believed. To us, this makes a compelling case that conservation, harvesting, and land management strategies should have as a primary focus the retention and protection of the full panoply of top predators so at risk today.

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