Trophic Downgrading of Planet Earth

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Until recently, large apex consumers were ubiquitous across the globe and had been for millions of years. The loss of these animals may be humankind's most pervasive influence on nature. Although such losses are widely viewed as an ethical and aesthetic problem, recent research reveals extensive cascading effects of their disappearance in marine, terrestrial, and freshwater ecosystems worldwide. This empirical work supports long-standing theory about the role of top-down forcing in ecosystems but also highlights the unanticipated impacts of trophic cascades on processes as diverse as the dynamics of disease, wildfire, carbon sequestration, invasive species, and biogeochemical cycles. These findings emphasize the urgent need for interdisciplinary research to forecast the effects of trophic downgrading on process, function, and resilience in global ecosystems.

The history of life on Earth is punctuated by several mass extinction events (2), during which global biological diversity was sharply reduced. These events were followed by novel changes in the evolution of surviving species and the structure and function of their ecosystems. Our planet is presently in the early to middle stages of a sixth mass extinction (3), which, like those before it, will separate evolutionary winners from losers. However, this event differs from those that preceded it in two fundamental ways: (i) Modern extinctions are largely being caused by a single species, *Homo sapiens*, and (ii) from its onset in the late Pleistocene, the sixth mass extinction has been characterized by the loss of larger-bodied animals in general and of apex consumers in particular (4, 5).

The loss of apex consumers is arguably humankind's most pervasive influence on the natural world. This is true in part because it has occurred globally and in part because extinctions are by their very nature perpetual, whereas most other environmental impacts are potentially reversible on decadal to millenial time scales. Recent research suggests that the disappearance of these animals reverberates further than previously anticipated (6–8), with far-reaching effects on processes as diverse as the dynamics of disease; fire; carbon sequestration; invasive species; and biogeochemical exchanges among Earth's soil, water, and atmosphere.

Here, we review contemporary findings on the consequences of removing large apex consumers from nature—a process we refer to as trophic downgrading. Specifically, we highlight the ecological theory that predicts trophic downgrading, consider why these effects have been difficult to observe, and summarize the key empirical evidence for trophic downgrading, much of which has appeared in the literature since the beginning of the 21st century. In

> "What escapes the eye ... is a much more insidious kind of extinction: the extinction of ecological interactions"
>
> Daniel H. Janzen (1)

so doing, we demonstrate the influence of predation and herbivory across global ecosystems and bring to light the far-reaching impacts of trophic downgrading on the structure and dynamics of these systems. These findings suggest that trophic downgrading acts additively and synergistically with other anthropogenic impacts on nature, such as climate and land use change, habitat loss, and pollution.
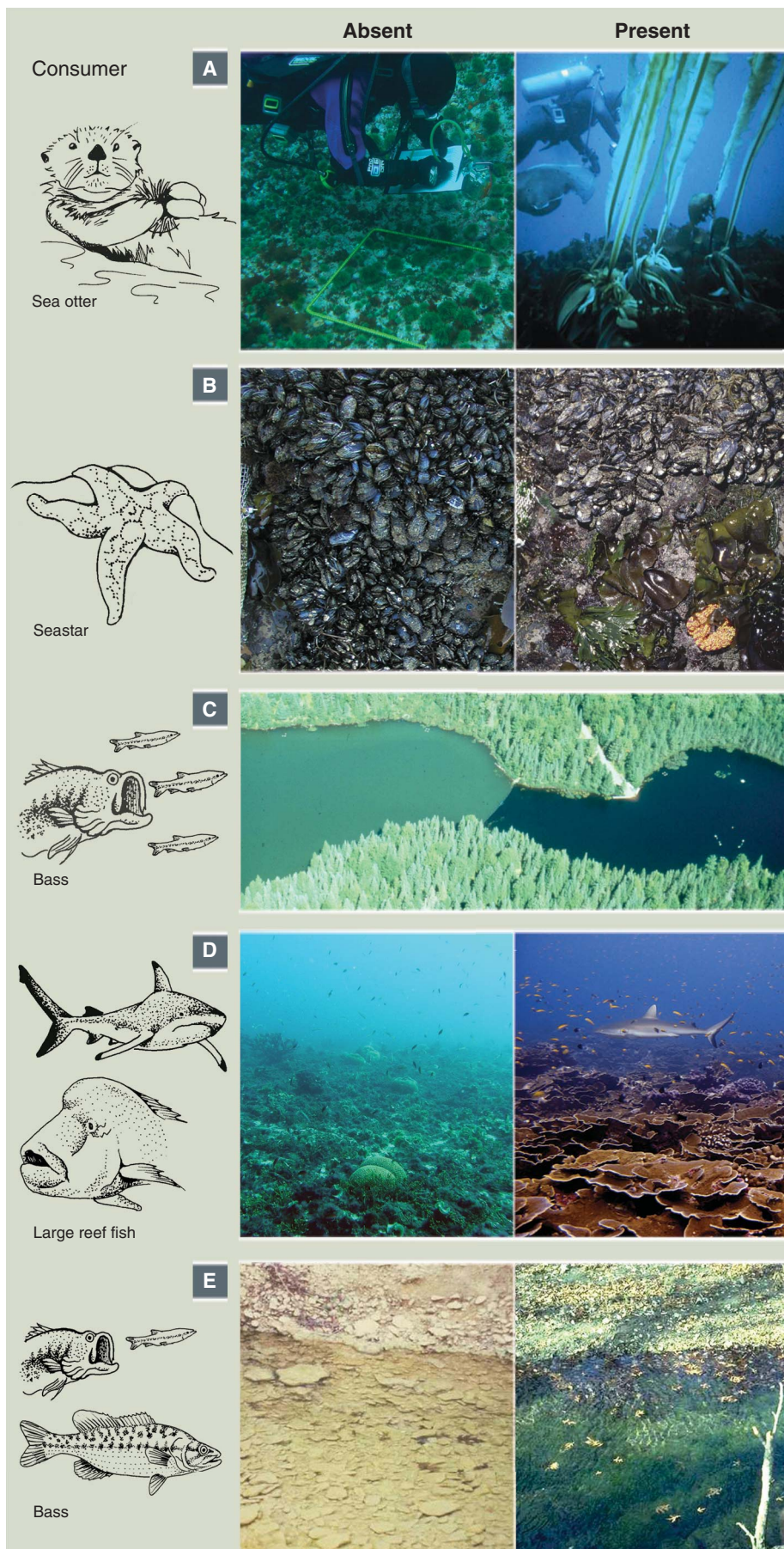
Foundations in Theory

Ecological theory has long predicted that major shifts in ecosystems can follow changes in the abundance and distribution of apex consumers (9, 10). Three key elements of that theory provide the foundation for interpreting recurrent patterns suggestive of trophic downgrading in more recent empirical work across ecosystems. First is the idea that an ecosystem may be shaped by apex consumers, which dates back more than a century but was popularized in the 1960s (9). This concept was later formalized as the dynamic notion of "trophic cascades," broadly defined as the propagation of impacts by consumers on their prey downward through food webs (11). Theoretical work on factors that control ecosystem state resulted in a second key advance, the recognition of "alternative stable states." The topology of ecosystem dynamics is now understood to be nonlinear and convoluted, resulting in distinct basins of attraction.

Alternative stable states occur when perturbations of sufficient magnitude and direction push ecosystems from one basin of attraction to another (12). Tipping points (also known as thresholds or breakpoints), around which abrupt changes in ecosystem structure and function (a.k.a. phase shifts) occur, often characterize transitions between alternative stable states. Ecosystem phase shifts can also display hysteresis, a phenomenon in which the locations of tipping points between states differ with the directionality of change (13). A third key concept, connectivity, holds that ecosystems are built around interaction webs within which every species potentially can influence many other species. Such interactions, which include both biological processes (e.g., predation, competition, and mutualism) and physicochemical processes (e.g., the nourishing or limiting influences of water, temperature, and nutrients), link species together at an array of spatial scales (from millimeters to thousands of kilometers) in a highly complex network.

Taken together, these relatively simple concepts set the stage for the idea of trophic downgrading.

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Fig. 1. Landscape-level effects of trophic cascades from five selected freshwater and marine ecosystems. (**A**) Shallow seafloor community at Amchitka Island (Aleutian archipelago) before (1971; photo credit: P. K. Dayton) and after (2009) the collapse of sea otter populations. Sea otters enhance kelp abundance (right) by limiting herbivorous sea urchins (left) (*20*). (**B**) A plot in the rocky intertidal zone of central California before (September 2001, right) and after (August 2003, left) seastar (*Pisaster ochraceous*) exclusion. *Pisaster* increases species diversity by preventing competitive dominance of mussels. [Photo credits: D. Hart] (**C**) Long Lake (Michigan) with largemouth bass present (right) and experimentally removed (left). Bass indirectly reduce phytoplankton (thereby increasing water clarity) by limiting smaller zooplanktivorous fishes, thus causing zooplankton to increase and phytoplankton to decline (*26*). (**D**) Coral reef ecosystems of uninhabited Jarvis Island (right, unfished) and neighboring Kiritimati Island (left, with an active reef fishery). Fishing alters the patterns of predation and herbivory, leading to shifted benthic dynamics, with the competitive advantage of reef-building corals and coralline algae diminished in concert with removal of large fish (*66*). (**E**) Pools in Brier Creek, a prairie margin stream in south-central Oklahoma with (right) and lacking (left) largemouth and spotted bass. The predatory bass extirpate herbivorous minnows, promoting the growth of benthic algae (*67*).

The loss of apex consumers reduces food chain length, thus altering the intensity of herbivory and the abundance and composition of plants in largely predictable ways (*10*). The transitions in ecosystems that characterize such changes are often abrupt, are sometimes difficult to reverse, and commonly lead to radically different patterns and pathways of energy and material flux and sequestration.

The Cryptic Nature of Trophic Downgrading

The omnipresence of top-down control in ecosystems is not widely appreciated because several of its key components are difficult to observe. The main reason for this is that species interactions, which are invisible under static or equilibrial conditions, must be perturbed if one is to witness and describe them. Even with such perturbations, responses to the loss or addition of a species may require years or decades to become evident because of the long generation times of some species. Adding to these difficulties is the fact that populations of large apex consumers have long been reduced or extirpated from much of the world. The irony of this latter situation is that we often cannot unequivocally see the effects of large apex consumers until after they have been lost from an ecosystem, at which point the capacity to restore top-down control has also been lost. Another difficulty is that many of the processes associated with trophic downgrading occur on scales of tens to thousands of square kilometers, whereas most empirical studies of species interactions have been done on small or weakly motile species

with short generation times that could be manipulated at small spatial scales. Although some influences of apex consumers (e.g., trophic cascades) seen in experiments scale up to systems with larger or more mobile species (*14*), others are harder to discern at small spatial and temporal scales (e.g., many of the indirect effects of trophic cascades on ecosystem processes described below). As a result, we have an incomplete and distorted picture of the influences of apex consumers across much of the natural world.

The Widespread Occurrence of Trophic Cascades

Despite these challenges, trophic cascades have now been documented in all of the world's major biomes—from the poles to the tropics and in terrestrial, freshwater, and marine systems (table S1). Top-down forcing and trophic cascades often have striking effects on the abundance and species composition of autotrophs, leading to regime shifts and alternative states of ecosystems (*15*). When the impacts of apex consumers are reduced or removed or when systems are examined over sufficiently large scales of space and time, their influences are often obvious (Figs. 1 and 2). Although purposeful manipulations have produced the most statistically robust evidence, "natural experiments" (i.e., perturbations caused by population declines, extinctions, reintroductions, invasions, and various forms of natural resource management) corroborate the essential role of top-down interactions in structuring ecosystems involving species such as killer whales (*Orcinus orca*) (*16*), lions (*Panthera leo*) (*17*), wolves (*Canis lupus*) and cougars (*Puma concolor*) (*18*), the great sharks (*19*), sea otters (*Enhydra lutris*) (*20*), diverse mesopredators (*21*), and megaherbivores (*22*). Although the extent and quality of evidence differs among species and systems, top-down effects over spatial scales that are amenable to experimentation have proven robust to alternative explanations (*23*).

The impacts of trophic cascades on communities are far-reaching, yet the strength of these impacts will likely differ among species and ecosystems. For example, empirical research in Serengeti, Tanzania, showed that the presence or absence of apex predators had little short-term effect on resident megaherbivores [elephant (*Loxodonta africana*), hippopotamus (*Hippopotamus amphibius*), and rhinoceros (*Diceros bicornis*)] because these herbivores were virtually invulnerable to predation (*24*). Conversely, predation accounted for nearly all mortality in smaller herbivores [oribi (*Ourebia ourebi*), Thompson's gazelle (*Eudorcas thomsonii*), and impala (*Aepyceros melampus*)], and these species showed dramatic increases in abundance and distribution after the local extinction of predators. Thus, top-down forcing in this system is more apparent in some species than others, at least when it is studied on relatively short time scales, although the aggregate ecological impact of apex consumers here, as elsewhere, remains great (*24*).

Other than the inclusion of top-down forcing, there is no rule of thumb on the interplay between apex consumers and autotrophs in intact ecosys-

tems. This is largely a consequence of natural variation in food chain length (*10*). In some cases, the influence of apex consumers is to suppress herbivory and to increase the abundance and production of autotrophs. The sea otter/kelp forest system in the North Pacific Ocean (*20*) (Fig. 1A) and the wolf/ungulate/forest system in temperate and boreal North America (*25*) (Fig. 2C) function in this manner. Apex consumers in other

systems reduce the abundance and production of autotrophs. The largemouth bass/planktivore/zooplankton/phytoplankton system in U.S. Midwestern lakes (*26*) (Fig. 1C) functions in such a manner.

Effects on Ecosystem Processes

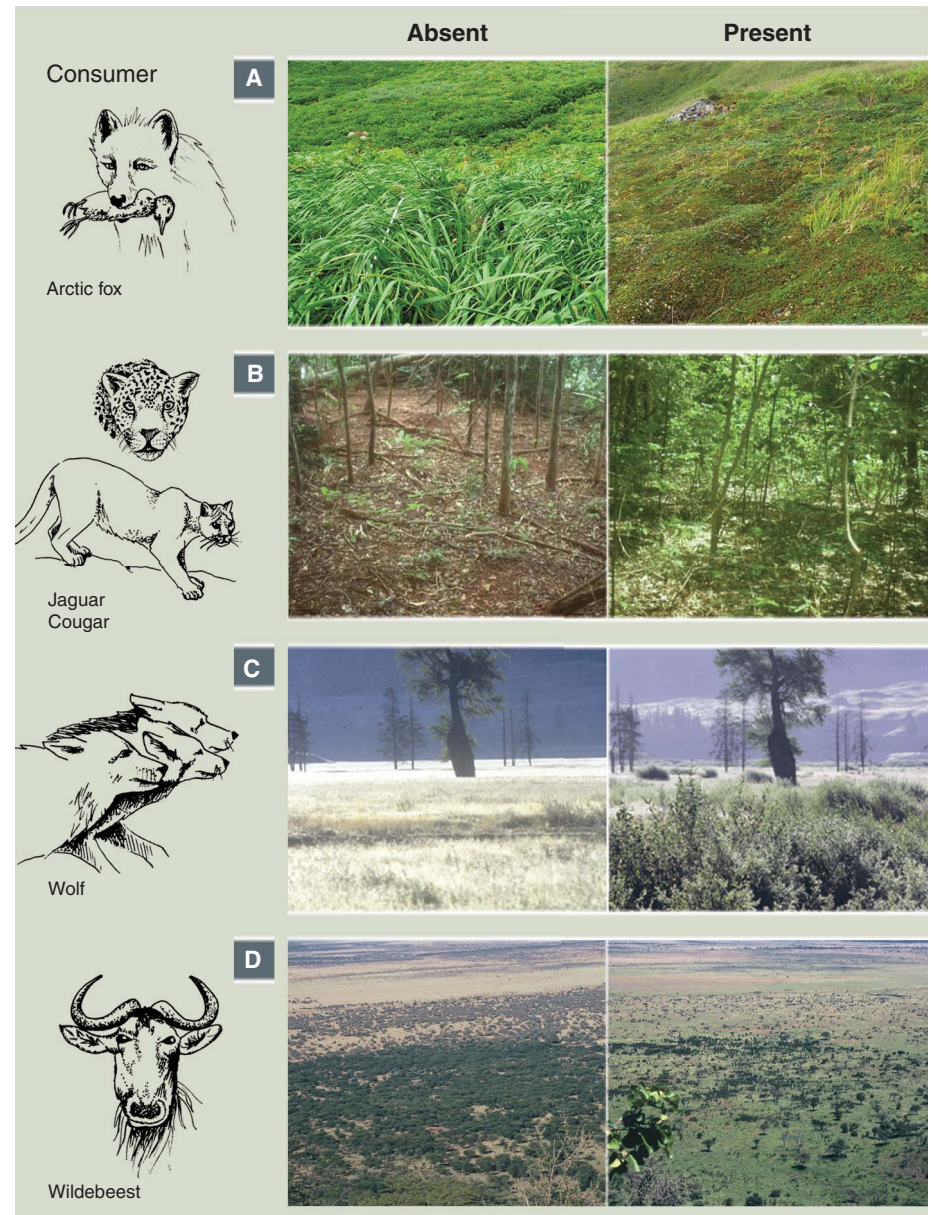Apart from small oceanic islands, all regions of our planet supported a megafauna before the

Fig. 2. Landscape-level effects of trophic cascades from four terrestrial ecosystems. (**A**) Upland habitat of islands with (right) and without (left) Arctic foxes in the Aleutian archipelago. Foxes drive terrestrial ecosystems from grasslands to tundra by limiting seabirds and thereby reducing nutrient inputs from sea to land (*47*). (**B**) Venezuelan forests on small islands of Lago Guri (left: jaguar, cougar, and harpy eagles absent) and mainland forest (right, predators present). A diverse herbivore guild erupted with the loss of predators from the island, thereby reducing plant recruitment and survival (*68*). (**C**) Riparian habitat near the confluence of Soda Butte Creek with the Lamar River (Yellowstone National Park) illustrating the stature of willow plants during suppression (left, 1997) from long-term elk browsing and their release from elk browsing (right, 2001) after wolf reintroductions of 1995 and 1996 (*25*). (**D**) Decline of woody vegetation in Serengeti after eradication of rinderpest (by early 1960s) and the recovery of native ungulates (by middle 1980s). Left, 1986; right, 2003 (*69*).

rise of *Homo sapiens* (*4*, *27*). The apex consumers influence their associated ecosystems through top-down forcing and trophic cascades, which in turn often lead to myriad effects on other species and ecosystem processes (Figs. 3 and 4). Here, we describe some of the known or suspected indirect effects of losing these apex consumers.

Herbivory and wildfire. Wildfires burn up to 500 million ha of the global landscape annually, consuming an estimated 8700 Tg of dry plant biomass, releasing roughly 4000 Tg of carbon to the atmosphere, and costing billions of dollars in fire suppression and property loss (*28*). The frequency and extent of wildfire have been largely attributed to a warming and drying climate and fuel accumulation from protective wildland management practices. However, the global distribution and biomass of vegetation are poorly predicted by temperature and rainfall (*29*), and recent analyses suggest that interdependencies among predation (including disease), herbivory, plant communities, and fire may better explain the dynamics of vegetation. Such interdependencies are well illustrated in East Africa, where the introduction of rinderpest in the late 1800s decimated many native ungulate populations, including wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*). Reductions of these large herbivores caused an increase in plant biomass, which fueled wildfires during the dry season. Rinderpest was eliminated from East Africa in the 1960s through an extensive vaccination and control program. Because of this, wildebeest and buffalo populations had recovered to what was thought to be historically high levels by the early 1980s. The resulting increase in herbivory drove these systems from shrublands to grasslands, thus decreasing the fuel loads and reducing the frequency and intensity of wildfires (*30*) (Fig. 4). Other examples of the interplay between megafauna and wildfire are the increase in fire frequency after the late Pleistocene/early Holocene decline of megaherbivores in Australia (*31*) and the northeastern United States (*32*).

Disease. The apparent rise of infectious diseases across much of the globe is commonly attributed to climate change, eutrophication, and habitat deterioration. Although these factors are undoubtedly important, links also exist between disease and predation (*33*). For example, the reduction of lions and leopards from parts of sub-Saharan Africa has led to population outbreaks and changes in behavior of olive baboons (*Papio anubis*). The baboons, in turn, have been drawn into increasing contact with people because of their attraction to crops and other human food resources. The increased baboon densities and their expanded interface with human populations have led to higher rates of intestinal parasites in baboons and the humans who live in close proximity to them (*17*). A similar result, involving different species and processes, occurred in India, where the decline of vultures also led to increased health risks from rabies and anthrax (*34*). Further examples of the interplay between predation and disease exist for
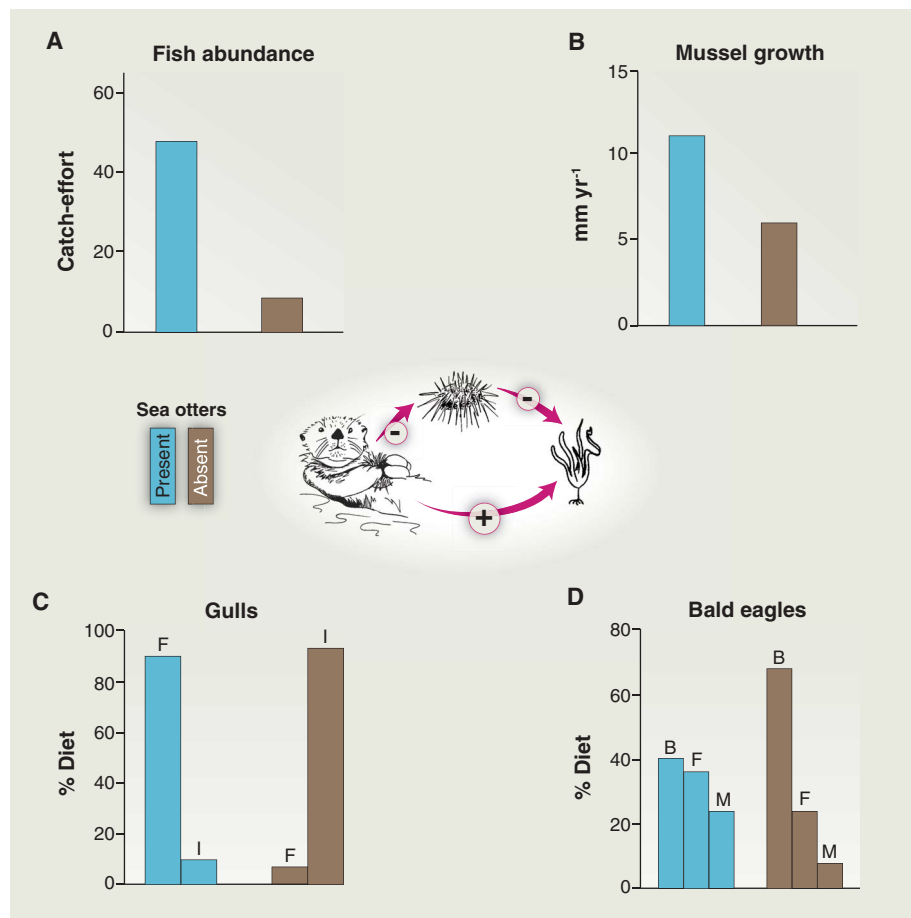

Fig. 3. Trophic cascade from sea otters to sea urchins to kelp (center) has myriad effects on other species and ecological processes. The increase in kelp enhances the abundance of kelp forest fish (**A**) (*70*). Enhanced kelp production increases the amount of particulate organic carbon in coastal ocean waters, thus increasing the growth rate of filter-feeding mussels (**B**) (*71*). The presence or absence of sea otters influences the diet of other consumers in the coastal ecosystems (**C** and **D**). In systems with abundant sea otters, Glaucous winged-gulls (*Larus glaucescens*) consume mostly fish (F), whereas in systems lacking sea otters, gulls consume mostly macroinvertebrates (I) (**C**) (*72*). When sea otters were abundant in the Aleutian archipelago, bald eagles (*Haliaeetus leucocephalus*) fed on fish (F), mammals (M), and birds (B) in roughly equal amounts. The loss of sea otters from this system led to a stronger reliance by the eagles on seabirds (**D**) (*73*). Blue bars from system with sea otters; brown bars from system without sea otters.

aquatic systems. The establishment of no-take marine reserves in the Channel Islands of southern California led to increases in the size and abundance of spiny lobsters (*Panulirus interruptus*) and declines in population densities of sea urchins, which are preyed on by the lobsters. The reduced urchin densities thwarted the spread of disease among individual sea urchins, which led to a lowered frequency of epidemics of sea urchin wasting disease within the reserves (*35*) (Fig. 4). In freshwater systems, the localized rise and fall of human malaria is associated with the impacts of predatory fishes on planktivores, which are in turn important consumers of mosquito larvae (*36*).

Physical and chemical influences. The influences of industrialization and agriculture on Earth's physical environments and geochemical processes are widely known. However, the contributing effects of changes in the distribution and abundance of apex consumers to the physical and chemical nature of our biosphere—the atmosphere,

soils, and water—are understudied and largely unappreciated. Even so, important connections between these entities have become apparent in the few instances where people have looked.

The atmosphere. Linkages between apex consumers and the atmosphere are known or suspected in freshwater, marine, and terrestrial ecosystems. Trophic cascades associated with the presence or absence of apex predatory fishes in lakes can affect phytoplankton density, in turn affecting the rate of primary production, the uptake rate of CO_2, and the direction of carbon flux between lakes and the atmosphere. Where apex predatory fishes are present in sufficient numbers, they reduce the abundance of smaller planktivorous minnows, thus releasing zooplankton from limitation by planktivores and increasing consumption rates of phytoplankton by zooplankton (Fig. 1B). This trophic cascade causes lakes to switch from net sinks for atmospheric CO_2 when predatory fishes are absent to net sources of atmospheric CO_2 when

these fishes are present (*37*) (Fig. 4). Similar processes occur in the oceans and on land. Industrial whaling during the 20th century transferred some 105 million tons of carbon from great whales to the atmosphere (*38*), and even today whale feces return various limiting nutrients from the aphotic to photic zones, thereby directly enhancing primary productivity (*39*, *40*) and its influence on carbon flux and sequestration. From land, the demise of Pleistocene megaherbivores may have contributed to or even largely accounted for the reduced atmospheric methane concentration and the resulting abrupt 9°C temperature decline that defines the Younger-Dryas period (*41*).

Soils. Leaf-eating herbivores profoundly influence soils and their associated biota through altered plant allocation patterns of carbon and nutrients to the roots and rhizosphere, changing the quantity and quality of litter that plants return to the soil. Ungulate herbivores further influence soils through trampling, compaction, and the return of dung and urine. The collective influence of these processes is often an effect on species composition of the vegetation and altered successional pathways (*42*, *43*). Predators of these herbivores and the trophic cascades they set in motion reverse these belowground effects (*44*). For example, the reintroduction of wolves to Yellowstone National Park has reduced the positive indirect effects of ungulates on soil nitrogen mineralization and potentially the nitrogen supply for plant growth (*45*). In contrast, introduced rats (*46*) and arctic foxes (Fig. 4) (*47*) have reduced soil fertility and plant nutrition on high-latitude islands by disrupting seabirds and their sea-to-land nutrient subsidies, with striking effects on plant community composition.

Water. Large consumers influence the composition and quality of both fresh and salt water through a variety of mechanisms. For example, the collapse of large demersal fish led to a 20% reduction in silica supply to pelagic diatoms in the Baltic Sea (*48*). In rivers, mass spawning by salmon suspends sediments, thus increasing downstream sediment transport (*49*) (Fig. 4). This flushing of stream bed sediments by the spawning fish and the increased circulation of fresh water through the gravel interstices of the stream bed have positive feedbacks on salmon populations by increasing oxygen for incubating eggs and fry and decreasing the frequency with which bed-mobilizing floods kill salmon in these early life stages (*50*). Similarly, in terrestrial systems wolves protect riparian trees and shrubs from over-browsing by large ungulates, in turn shading and cooling the adjacent streams, reducing stream bank erosion, and providing cover for fish and other aquatic life (*51*, *52*).

Invasive species. A common feature of many successful invasive species is that they have left behind their natural predators and freed themselves from top-down control (*53*). Likewise, the loss of native predators leaves ecosystems more vulnerable to invasion by nonnative species (*54*). There are many examples of hypersuccessful invasions due to the absence or loss of top-down

control in aquatic and terrestrial systems. The experimental exclusion of native birds from small areas in Hawaii resulted in an up to 80-fold increase in nonnative spider density (*55*) (Fig. 4). Other examples include the spread of the invasive brown tree snake (*Boiga irregularis*) on the otherwise vertebrate predator–free island of Guam (*56*), the facilitating influence of reduced fish predation on the invasion of zebra mussels (*Dreissena polymorpha*) in the Mississippi River (*57*), and reduced abundance and spread of the introduced European green crab (*Carcinus maenas*) by predation from native blue crabs (*Callinectes sapidus*) in eastern North America (*58*).

Biodiversity. Earth's biodiversity (defined here as both species diversity and the associated functional diversity) is increasingly confined to formal protected areas. Although the establishment of protected areas mitigates certain threats to biodiversity—habitat loss and fragmentation, over-exploitation, and the spread of invasive species—when large apex consumers are missing, protected areas often fail to function as intended. The link between apex consumers and species diversity can occur via a number of interaction pathways, for example, by blocking competitive exclusion [predatory seastars in the rocky intertidal (*59*)], mesopredator release [coyotes (*Canis latrans*) maintaining small vertebrate species in chaparral habitats (Fig. 4) (*60*)], and indirect habitat effects [e.g., the loss of small vertebrates from over-grazed and degraded riparian habitats after the
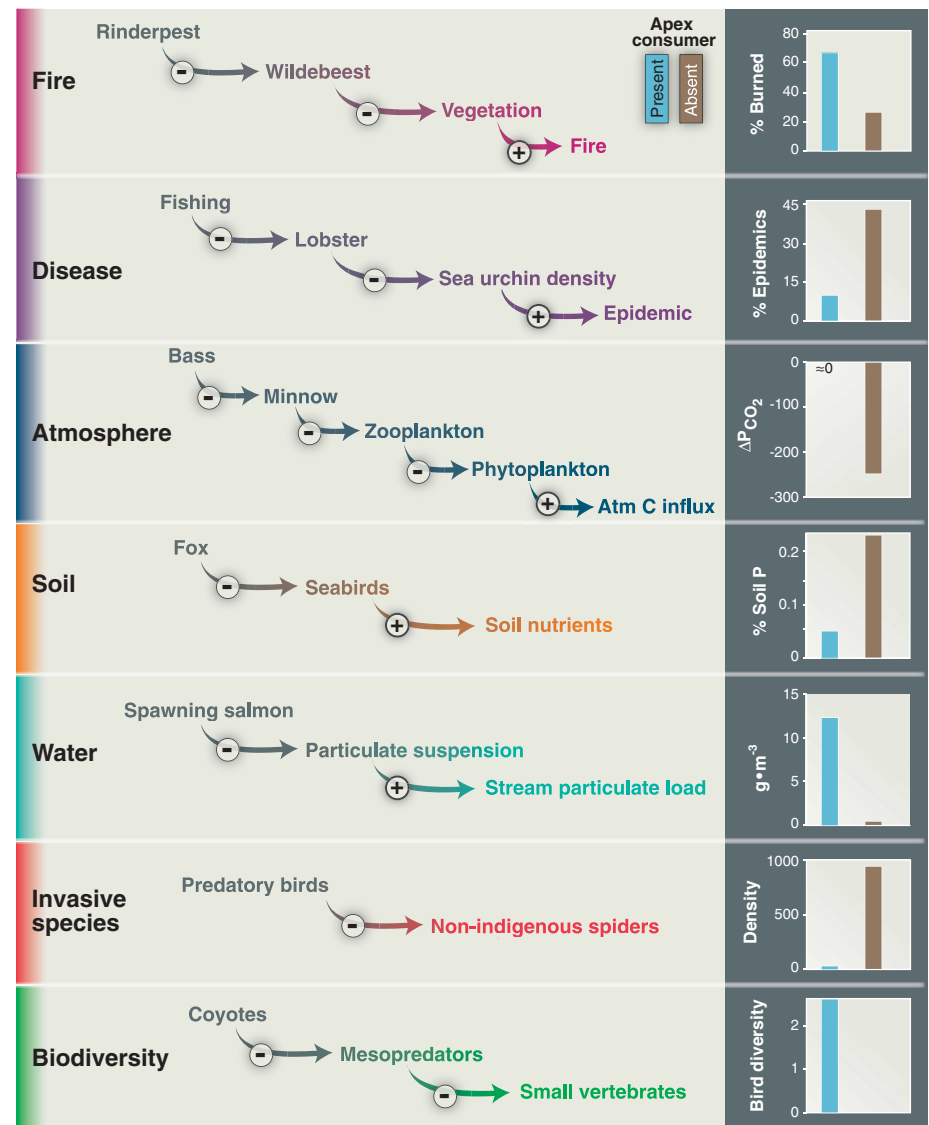

Fig. 4. Examples of the indirect effects of apex consumers and top-down forcing on diverse ecosystem processes, including wildfires (*30*); disease (*35*); composition of atmosphere (*37*), soil (*47*), and fresh water (*49*); invadability by exotic species (*55*); and species diversity (*60*). Interaction web linkages by which these processes are connected to apex consumers are shown in the center. Magnitude of effect is shown in graphs on right. Blue bars are data from systems containing the apex consumer; brown bars are data from systems lacking the apex consumer. Data replotted from original sources (cited above), except raw data on native bird diversity in chaparral habitats provided by K. Crooks.

loss of cougars (61) or wolves and grizzly bears (*Ursus arctos*) (62) from temperate and boreal forests of western North America].

Tree recruitment failure and the eventual transformation of forests to heaths and grasslands because of increased ungulate herbivory illustrates the influence of large apex consumers on functional diversity. This process is most clearly seen by contrasting areas where apex consumers have been absent for differing lengths of time. In North America, where wolves and other large carnivores were not extirpated until the early 20th century, the effects of their loss on plants is evident only as the recruitment failure of the younger trees. Because of the longevity of adult trees, the older individuals persist in what superficially appears to be a normally functioning forest ecosystem. These effects are best known from various U.S. National Parks, where the loss of large predators a few decades ago has left a characteristic signal of reduced tree growth rate (63) or recruitment failure (64) in the dominant tree species. A longer time horizon can be obtained from the Canadian island of Anticosti, where white-tailed deer (*Odocoileus virginianus*) have persisted in the absence of predators for more than a century, causing the successive elimination of saplings of less and less palatable trees and shrubs and increasing graminoid dominance in the understory (65). The Scottish island of Rùm, from which wolves have been absent for 250 to 500 years, provides a view of the likely final outcome of predator loss and elevated herbivory in many temperate forests. Rùm has transitioned over this same period from a forested environment to a treeless island.

These examples support the conclusion that disruptions of trophic cascades due to the decline of predation constitute a threat to biodiversity from within for which the best management solution is likely the restoration of effective predation regimes.

A Paradigm Shift in Ecology

The accumulation of theoretical and empirical evidence calls for an altered perspective on top-down forcing in ecosystem dynamics. Many practicing ecologists still view large animals in general, and apex consumers in particular, as ecological passengers riding atop the trophic pyramid but having little impact on the structure below. The influences of these animals, although acknowledged in particular cases, are generally regarded as anomalous, occurring in some systems but not in many others. This perception has generally led to the requirement of independent study and confirmation for each species and system before the null hypothesis that they serve no important ecological role can be rejected. We argue that the burden of proof be shifted to show, for any ecosystem, that consumers do (or did) not exert strong cascading effects.

Conclusions

Unanticipated changes in the distribution and abundance of key species have often been attributed in some unspecified manner to the "complexity of nature." We propose that many of the ecological surprises that have confronted society over past centuries—pandemics, population collapses of species we value and eruptions of those we do not, major shifts in ecosystem states, and losses of diverse ecosystem services—were caused or facilitated by altered top-down forcing regimes associated with the loss of native apex consumers or the introduction of exotics. Our repeated failure to predict and moderate these events results not only from the complexity of nature but from fundamental misunderstandings of their root causes. Except for controlling predators to enhance fish, wild game, and livestock, resource managers commonly base their actions on the assumption that physical processes are the ultimate driver of ecological change. Bottom-up forces are ubiquitous and fundamental, and they are necessary to account for the responses of ecosystems to perturbations, but they are not sufficient. Top-down forcing must be included in conceptual overviews if there is to be any real hope of understanding and managing the workings of nature.

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