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Predicting and Detecting Reciprocity between Indirect Ecological Interactions and Evolution

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ABSTRACT: Living nature can be thought of as a tapestry, defined not only by its constituent parts but also by how these parts are woven together. The weaving of this tapestry is a metaphor for species interactions, which can be divided into three broad classes: competitive, mutualistic, and consumptive. Direct interactions link together as more complex networks, for example, the joining of consumptive interactions into food webs. Food web dynamics are driven, in turn, by changes in the abundances of web members, whose numbers or biomass respond to bottom-up (resource limitation) and top-down (consumer limitation) forcing. The relative strengths of top-down and bottom-up forcing on the abundance of a given web member depend on its ecological context, including its topological position within the food web. Top-down effects by diverse consumers are nearly ubiquitous, in many cases influencing the structure and operation of ecosystems. While the ecological effects of such interactions are well known, far less is known of their evolutionary consequences. In this essay, we describe sundry consequences of these interaction chains on species and ecosystem processes, explain several known or suspected evolutionary effects of consumer-induced interaction chains, and identify areas where reciprocity between ecology and evolution involving the indirect effects of consumer-prey interaction chains might be further explored.

Introduction

Ecology and evolutionary biology have a long and intimate history. But how exactly are these disciplines connected? As pointed out in David Reznick's introduction to the 2011 American Society of Naturalists vice presidential symposium (Reznick 2013), two views have emerged on the time-scale of interplay between ecological and evolutionary processes: Hutchinson's (1965) highly influential perspective that ecology and evolution operate over vastly different timescales and Pimentel's (1961) less well-known view that ecological processes and evolutionary change proceed more closely in lockstep. Our knowledge of such eco-evo

interactions is currently restricted to a limited number of laboratory and field studies, reviewed elsewhere in this issue. Here we present a sampling of the large number of studies that have demonstrated how individual organisms can have a profound impact on their ecosystems. While the ecology of such interactions is well understood, their evolutionary consequences have rarely been considered. We argue that each example represents a case in which a single organism can, via its impact on an ecosystem, change the kind of selection that it and other organisms in the ecosystem experience. When viewed in this way, each of these examples represents a potential case in which Pimentel's vision of reciprocal interactions between ecology and evolution may occur. Since the literature offers hundreds of instances in which individual organisms have substantial impacts on their ecosystem and since these examples are seen in a diversity of ecosystems, we argue that there already exists a large menu of communities to choose from if one wants to search for ongoing reciprocity between ecology and evolution.

The ecological context within which species succeed or fail is an essential part of the interplay between ecology and evolution. At the most fundamental level, one would like to know the relative importance of physical (e.g., temperature, moisture, nutrients) and biological factors (i.e., species interactions) as agents of selection. Both are clearly important, although species interactions are more interesting in the context of this discussion because they offer the potential for feedback, or reciprocity, between ecological processes and evolutionary change. Species interactions can promote coevolution. Coevolution, in turn, can alter the ways in which species interact with one another and can lead back to ecological effects. Famous examples include plant-animal mutualisms that provide food or shelter for animals in return for defense, pollination, or seed dispersal services for plants, and "arms races," in which traits enhancing the defense of prey coevolve with traits enhancing resistance to those defenses in the predator (Ehrlich and Raven 1964; Futuyma and Slatkin 1983;

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Thompson 2005). Less well known are the potential evolutionary influences of interaction chains and the indirect effects (i.e., the effects of interactions between any two species with one or more intervening species) they generate on individuals, populations, communities, and ecosystems. Here we explore two dimensions of this issue: (1) the importance of indirect effects in nature and (2) the potential for reciprocity between indirect ecological interactions and their evolutionary consequences. The characterization of indirect ecological effects sets the stage for studying reciprocal interactions between ecology and evolution because indirect effects define how an organism changes its environment and hence the kind of selection that it or other species in the community experience. The question is whether the organism then evolves in response to the environment they helped to create. We focus primarily on consumptive interactions, in which one party benefits at the expense of the other, because (1) they have provided a fertile arena for the study of coevolution (Thompson 1982) and (2) they join together to form chains or webs of indirect linkages among species.

Some ecologists view populations as limited largely by the benefits conveyed by prey to their consumers, in which case the food web is seen as being under “bottom-up” control. Other ecologists view populations as limited more by the costs incurred by prey from their consumers, in which case the food web is seen as being controlled by top-down forces. In reality, both forces must occur in all food webs (Power 1992), although particular taxa or functional groups can be more limited by resources than by consumers, or vice versa.

Top-down control is particularly interesting because it can lead to the coevolution of defense and resistance in consumer-prey systems. Although variation in primary productivity and the rate and efficiency of material and energy flux upward through food webs can affect food chain length (Oksanen et al. 1981; Post et al. 2000), it is unclear how such variation might lead to qualitative changes in direct or indirect interactions within particular species pairs. This is not to say that variation in bottom-up forcing is without evolutionary consequence; rather, such evolutionary responses are more predictable (see Mooney et al. 2010 for an exception). In contrast, linear models depict alternating resource or consumer limitation from the top to the bottom of food chains under top-down control (fig. 1). The highest trophic levels (apex consumers) are predicted to be limited by resources, whereas their prey are predicted to be consumer limited. In chains with more than two trophic links, the top predator indirectly protects its prey's prey from consumption, so that the prey's prey attains densities that become resource limited. The next level (the prey's prey's prey) would be limited by consumers (Fretwell 1987). These

alternating linear chains, as well as more reticulate food webs cross-linked by omnivory, are interesting because they can generate novel modes of indirect species interactions from the building blocks of direct consumptive interactions. Examples of such effects include apparent competition (Holt 1971) and apparent mutualisms (Abrams 2000; fig. 1).

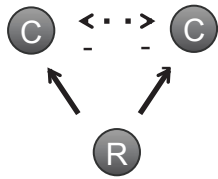
Our objective is to explore the potential for reciprocity between ecology and evolution based on the indirect effects of apex consumers. We (1) provide a brief overview of key concepts and challenges, (2) review cases of strong top-down forcing across major ecosystem types, (3) provide examples of the follow-on effects of top-down forcing from three systems we know well: kelp forests, rivers and streams, and savanna/grasslands, and (4) summarize known or suspected reciprocity between ecology and evolution that results from top-down forcing in kelp forest ecosystems. We then discuss possible evolutionary responses to known or postulated cases of apparent competition or mutualism in food web fragments and conclude with a discussion of fruitful directions for future research.

Food Web Dynamics: Concepts and Challenges

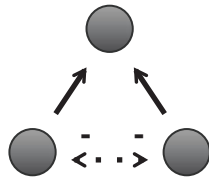
Ecologists have taken various approaches in trying to describe and understand food webs. Several important concepts and challenges have emerged along the way. One fundamental challenge is simply observing and measuring the strength of species interactions. Unlike species themselves, which can be seen, described, and enumerated, species interactions are often invisible (Janzen 1974; Estes et al. 2011). Crucial behaviors, such as the act of predation or the fear it instills in prey, are seldom witnessed by human observers. Moreover, witnessing the acts that link two species is not equivalent to measuring the population consequences of the resulting interaction. The cryptic nature of species interactions is especially problematic in steady-state systems, which are often the way we see or perceive nature (Chapin et al. 2002). Consequently, the effects of species interactions can be understood only by perturbing (or witnessing perturbations of) interacting species and their ecosystems.

Our ability to see and understand the consequences of species interactions by causing or witnessing perturbations varies with the mobility and longevity of the interacting species. Experimental perturbations have been most effective for systems with sedentary and short-lived species. Perturbations have been used to study the influences of some long-lived and highly mobile species (Estes et al. 2011), but typically these perturbations were historical accidents or management actions that fortuitously created differences in population abundance for the species of interest over large scales of space and time.

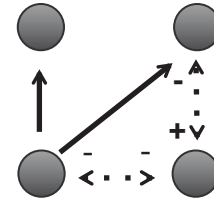
Two Trophic Levels



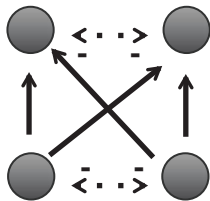
A. Exploitative competition



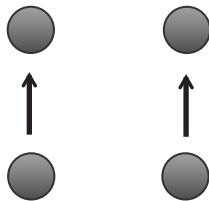
B. Apparent competition



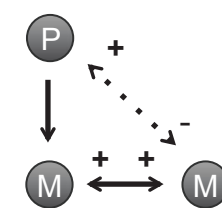
C. Square web, one generalist one specialist



D. Square web, two generalists

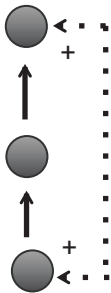


E. Decoupled food chains, two specialists

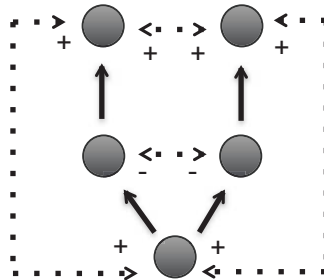


F. Direct mutualism with one parasite

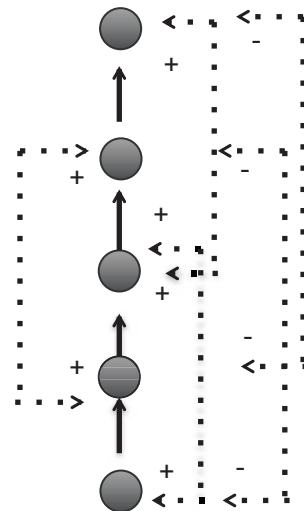
Three or more trophic levels



G. Three level food chain with one indirect protective mutualism



H. Three level food chain with multiple species at higher trophic levels



I. Five level food chain with multiple indirect mutualisms

A second challenge in understanding food webs lies in the description of their functional topology. The challenge here is in figuring out which particular pathways in the complex network of potential linkages among species are actually operational and functionally important. Species can be linked together through both direct and indirect interactions. Moreover, while direct interactions are easier to observe and understand, indirect interactions are potentially more numerous. For example, a system with n species has a maximum of ${}_n P_2$ (the number of permutations of n things taken two at a time) direct interactive pathways and $\sum_{r=3}^n {}_n P_r$ indirect pathways. Although many of these pathways may not be realized, the potential number of species interactions exceeds the number of species, the potential number of indirect interactions exceeds the number of potential direct interactions, and both of these inequalities become more pronounced as species richness increases (fig. 2).

A third challenge in understanding food webs has to do with emergent features of their topology and geometry. We distinguish here between topological attributes that would persist under continuous deformation of the network and geometric attributes that do change with continuous change in network links or nodes, including change in the interaction strengths of particular linkages or chains. Topological properties include “richness,” the number of web members, and “connectance,” the proportion of all possible pairwise interactions that are realized. From an operational perspective, a food web’s connectance depends on the number of unrealized links. Another topological network property is that of “nestedness,” the degree to which more specialist species interact only with proper subsets of those species interacting with the more generalist species (Jordano 1987; Memmott 1999; Bascompte et al. 2005; Bascompte and Jordano 2007). Geometric properties include interaction strengths of particular linkages (Paine 1992; Berlow et al. 1999) and “propagation,” the degree to which the strength of direct interactions attenuates or intensifies along interaction chains (Schoener 1993). A final geometric property of any network is “modularity,” the tendency of certain subsets of species to interact more frequently or more strongly with each other than with species in other modules. These properties add richness to food web dynamics and thus com-

plexity to the potential reciprocity between ecology and evolution.

A fourth challenge in understanding food webs is that indirect-interaction chains can add qualitative diversity to direct trophic interactions. Apparent competition (Holt 1971), which occurs when two prey species share a common consumer, is one example of this phenomenon. Under this circumstance, an increase in one of the prey can enhance the consumer through bottom-up forcing, thus reducing the second prey species through top-down forcing (fig. 1). Another well-known example is the joining together of adjacent consumer-prey interactions (both direct trophic interactions) to create indirect mutualisms between the end members of a three-species indirect interaction (fig. 1). Such mutualisms are emergent properties of certain trophic cascades (Hairston et al. 1960; Paine 1980; Terborgh and Estes 2010).

The scope of both theory and empirical work in evolutionary ecology has been limited largely to direct interactions (Pianka 2000; Schluter 2000; Thompson 2005; Mayhew 2006). However, as we have seen from the preceding brief discussion, the fabric of nature is vastly richer and more complex than this. Direct interactions among species are only a subset of nature’s dynamic infrastructure, owing to the existence of interaction chains and the novel effects of species on one another that emerge from these indirect interactions. It follows that the fabric of reciprocity between ecology and evolution may also be more complex than what would be woven from coevolutionary responses to direct species interactions alone.

Indirect Effects of Apex Consumers

Top-down forcing by predators is widespread in nature (Pace et al. 1999; Schmitz et al. 2000; Terborgh and Estes 2010; Estes et al. 2011). These effects are often manifested as trophic cascades—indirect effects of apex consumers downward across successively lower trophic levels to autotrophs or other basal species. One example of a trophic cascade is the maintenance of kelp forests in higher-latitude coastal oceans (Estes et al. 2010), where otters consume urchins that would otherwise consume kelp. Others include the prevention of algal overgrowth on coral reefs in tropical oceans (Sandin et al. 2010); the maintenance

Figure 1: Structural depictions of some of the ways that indirect interactions can arise in simple webs of five or fewer species. Solid arrows indicate direct interactions. One-headed arrows depict consumptive or other exploiter-victim interactions in which the arrow points from the resource (or victim) to its consumer (or exploiter). Dashed arrows represent indirect interactions, with the signs of these indicated. The general relationship between consumers (C) and resources (R) is shown in A only. C–E, In these square food webs, SE, NE, NW, and SW refer to species in the lower right, upper right, upper left, and lower left, respectively. F, The solid double-headed arrow depicts a direct mutualism. One mutualist is mimicked by a cheater (P). See text for further discussion.

of forests and other woody vegetation in boreal, temperate (Ripple et al. 2010), and tropical (Terborgh and Feeley 2010) terrestrial environments; the control or proliferation of periphyton (depending on food chain length) in tropical and temperate rivers (Power et al. 2008); and the control or proliferation of phytoplankton (again depending on food chain length) in lakes (Carpenter 2010) and ocean ecosystems (Shiomoto et al. 1997; Frank et al. 2005, 2011; Daskalov et al. 2007; Casini et al. 2008, 2009; see the appendix for a more detailed account of trophic cascades).

Trophic cascades can lead to a diversity of effects on other species and ecosystem processes. Examples of such indirect effects include the frequency and intensity of wild-fires (e.g., predators limit herbivores, thus increasing plants and fuel loads; Flannery 1994; Gill et al. 2009; Holdo et al. 2009; Bond 2010), methane production in terrestrial systems (Smith et al. 2010), the direction and magnitude of carbon flux between aquatic systems and the atmosphere (Schindler et al. 1997; Pershing et al. 2010), disease transmission and the frequency of epizootics (Lafferty 2004; Ostfeld and Holt 2004; Markandya et al. 2008; Bra-shares et al. 2010; Levi et al. 2012), impacts on water quality and eutrophication (Moore et al. 2007; Katz et al. 2009) and on soil composition and quality (Croll et al. 2005; Fukami et al. 2006; Dunham 2008; Frank 2008), the invasibility of ecosystems by exotic species (Kolar and Lodge 2001; Grunner 2004; Carlsson et al. 2009), and the maintenance of species diversity (Paine 1966; Crooks and Soulé 1999; Berger et al. 2001; Ripple and Beschta 2006).

Follow-On Effects of Trophic Cascades

In the preceding sections, we established the range of global environments in which trophic cascades have been documented and the diversity of follow-on influences from these trophic cascades to other ecosystem-level patterns and processes. Here we provide more detailed and mechanistic accounts of the known or suspected follow-on effects of trophic cascades in the systems we have studied and know best: kelp forests, western-US streams, and savanna/grasslands of sub-Saharan Africa.

Kelp Forests

By consuming herbivorous sea urchins, sea otters initiate a widely occurring trophic cascade that influences the distribution and abundance of kelp and other fleshy macroalgae in coastal marine ecosystems along the North Pacific rim (Estes and Duggins 1995; Watson and Estes 2011). Kelp abounds and the rate of herbivory is low in systems with ecologically effective (*sensu* Soulé et al. 2003) sea otter densities, whereas kelp is comparatively rare and the rate of herbivory is high where sea otters are below that density

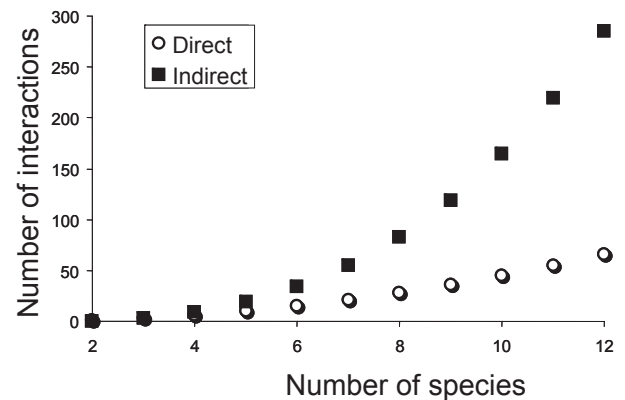


Figure 2: Changes in the maximum potential number of direct (open circles) and indirect (filled circles) pathways in webs of 2–12 species. See text for explanation of how these values were computed.

(Estes et al. 2010). The sea otter–kelp trophic cascade influences many other species and ecosystem processes. For example, we find that in areas where sea otters are rare or absent, growth rates of filter-feeding mussels and barnacles are only one-third to one-half those in areas with sea otters (Duggins et al. 1989), that kelp forest fish densities are an order of magnitude lower than in areas with sea otters (Reisewitz et al. 2005; Markel 2011), that glaucous-winged gulls shift from feeding primarily on fish where sea otters abound to feeding primarily on intertidal and shallow subtidal invertebrates (Irons et al. 1986), and that bald eagles shift from a mixed diet of fish, marine mammals, and seabirds where otters abound to feeding more singularly on seabirds (Anthony et al. 2008).

Kelp forests reduce the velocity of coastal currents and the intensity of wave force on the shore (Jackson 1998), both of which are thus indirectly moderated by the otter-urchin-kelp trophic cascade. Kelp forests are characterized by high photosynthetic rates and regulate considerable flux and sequestration of atmospheric carbon. Compared with a coastal ecosystem lacking sea otters, this effect is estimated to draw down CO₂ levels from the surrounding atmosphere by up to 10% through storage in living kelps alone (Wilmers et al. 2012). Numerous other indirect effects from the otter-urchin-kelp trophic cascade remain to be explored. Even so, our understanding of this system is more than adequate to argue that the indirect effects of otter predation on urchins potentially shape how they and other species adapt to the environment that predation by otters helped to create.

Western and Midwestern Rivers

Attached algae provide much, often most, of the energy fueling river food webs, even in surprisingly small, dark

headwater channels (Minshall 1978; Mayer and Likens 1987; Finlay 2001). Under favorable conditions, algae grow rapidly—doubling times of single-celled algae can be less than 1 day. Many algae, especially diatoms, are vulnerable to ingestion and digestion and are nutritious as food (Brett and Müller-Navarra 1997). Therefore, consumptive interactions among river algae, grazers, and predators can be strong and dynamic (Power et al. 1985; Power 1990). How much algae proliferate depends, as in other systems, on the length of functionally important top-down food chains. Food chain length often depends, in turn, on river discharge. Under Mediterranean seasonality, (e.g., in coastal California rivers), rainy, flood-prone winters are followed by summer droughts and relatively stable low flows. Bed-scouring floods greatly reduce abundances of predator-resistant grazers (heavily armored caddisflies) that overwinter as larvae. Algae proliferate whenever winter flooding reduces the abundance of grazers. As discharge continues to drop over the subsequent dry season, densities and biomass of animals build up (predators and early-successional, rapidly growing grazers that are vulnerable to predators), with habitat contraction, numerical recruitment (migration by fish, oviposition by invertebrates), and somatic growth. These web members assemble into food chains that have three or four trophic levels. The number depends on the abundance of grazers vulnerable to invertebrate predators but not to larger fish (Power et al. 2008). Similar algae-based food webs occur inland, in prairie-margin and Ozark streams, but under continental seasonality, so bed-scouring floods can occur during any month. Ecological recovery from flood scour is still initiated by fast-growing attached algae, which are subsequently grazed back under two- or four-level food chains unless they are protected by predators that eliminate grazers (in a three-level chain; Power et al. 1985).

Top-down interactions control not only the biomass of attached algae in rivers but also which taxa or functional groups dominate. These different attached algal groups can have different ecosystem impacts on water clarity and biogeochemical cycling. In Ozark rivers, large schools of grazing minnows (*Camptostoma anomalum*) remove diatom turfs and expose and promote growth of underlying adnate cyanobacterial felts dominated by *Calothrix* (in the Rivulariales, an order characterized by basal nitrogen-fixing heterocysts). The grazer control of diatoms is easily demonstrated when diatom turfs are exposed to *Camptostoma* in the open channel. Although overgrowth of *Calothrix* in the absence of grazing has been demonstrated to date only in replicated open-channel troughs (Power et al. 1988), black cyanobacterial felts characteristic of the stony river beds of Ozark rivers are extensive and may help maintain clarity and nutrient status in large reaches. If these felts were overgrown by *Melosira* sp., the diatom that proliferated

in enclosure troughs in the absence of grazers, then it is likely that this loosely attached, semiplanktonic diatom would cloud the water column and that the concentrations of total dissolved nitrogen would drop as benthic nitrogen fixation became increasingly light limited by both turbidity and overgrowth. In smaller prairie-margin streams, *Camptostoma* are excluded from some stream pools by largemouth or spotted bass (Power et al. 1985). In the Ozarks, *Camptostoma* appear to be released from bass predation. The reason is unknown, but possible hypotheses are that the smallmouth bass in the Ozarks are less piscivorous than largemouth or spotted bass in the prairie, that the Ozark rivers are large enough for *Camptostoma* to partition habitat with these bass or for the bass to find abundant preferred alternative prey (crayfish abound in this system), or that the bass themselves are suppressed by Ozark predators, such as mink, gar, or human anglers. Any changes that diminished the abundance or grazing impacts of this minnow might have widespread ecosystem consequences for these clear-flowing, biologically rich Ozark rivers.

In the Mediterranean rivers of coastal California, if winter floods release the dominant filamentous green alga *Cladophora glomerata* from grazing, it proliferates during the spring and early summer. Later in the summer, *Cladophora* becomes covered by epiphytic diatoms (*Epithemia* spp., *Rhopalodia* spp.) that contain nitrogen-fixing cyanobacterial endosymbionts. In these *Epithemia*-rich assemblages, areal rates of riverine nitrogen fixation increase as much as 60-fold (J. Welter, unpublished data), and rates of insect emergence increase up to 25-fold (Power et al. 2009). These changes greatly enhance productivity of these nitrogen-limited western river ecosystems (Hill and Knight 1988) and also amplify food fluxes important to watershed insectivores—spiders, birds, lizards, and bats—which concentrate and feed intensively around the river corridor during the dry season (Power et al. 2004). *Epithemia*-rich *Cladophora* fronds that drift or are introduced to the mouth of the Eel River are highly preferred over local seaweeds as food for estuarine amphipods and isopods (C. Ng, unpublished data). Therefore, top-down controls that affect algal biomass and persistence in rivers should have important influences on algae-mediated exchanges across the air-water and freshwater-marine ecosystem boundaries.

Macroalgal proliferations also greatly increase surface area and small-scale heterogeneity in redox environments for heterotrophic bacteria, which mediate important biogeochemical cycling of carbon, nitrogen, phosphorus, iron, silica, manganese, and other elements that may influence freshwater and coastal productivity near river mouths. *Cladophora* and other freshwater plants take up and concentrate heavy metals (Whitton et al. 1989) and promote the methylation of mercury (Tsui et al. 2010), rendering it

more bioavailable to food webs. Macroalgal proliferations also provide cover and contrasting thermal environments, including sun-warmed floating mats, which facilitate oviposition and subsequent development of certain river-breeding insects and frogs (Power 1990). In impounded reservoirs on the Klamath River, *Cladophora* proliferations harbor parasites and pathogens that threaten salmon (Stocking and Bartholomew 2007).

As with kelp forests, trophic cascades in rivers and streams lead to diverse ecological processes through complex interaction chains, most of which remain to be explored and understood. These changes affect physico-chemical aspects of the environment, cover and other habitat structures, and other changes in environmental context that strongly influence species interactions. All such changes created by complex biotic interactions, in turn, potentially translate to changes in the kind of selection that resident organisms experience.

African Savannas

Much of the research on trophic interactions in African savanna systems has emphasized the role of bottom-up regulation of savanna grasses and the ungulates that rely on them (Fritz and Duncan 1994; Ogotu and Owen-Smith 2003). However, a large and growing body of work has identified a multitude of pathways, both direct and indirect, through which top-down interactions shape savanna ecosystems (Sinclair et al. 2003; Waldram et al. 2008). In this discussion, we simplistically organize this work under two broad categories: (1) the effects of top-down forcing by herbivores and (2) the cascading impacts of apex predators.

Perhaps the most powerful insights regarding herbivore impacts on African savannas have come from “natural” experiments involving the temporary removal or decline of large herbivores such as elephant (*Loxodonta* sp.), buffalo (*Syncerus caffer*), and wildebeest (*Connochaetes* sp.). Correlative analyses and experimental exclosures monitored before, during, and after perturbations to elephant and buffalo populations reveal that their herbivory on trees and shrubs results in the expansion of grasslands at the expense of forest and bush habitats (Dublin et al. 1990; van Aarde and Jackson 2007; Valeix et al. 2011). This shift in habitat structure drives changes in the composition of local bird (Ogada et al. 2008), reptile (Pringle 2008), and small-mammal communities (Linzey and Kesner 1997). Grazing by massive herds of wildebeest in East Africa has a similarly powerful effect in maintaining diverse short grasslands (McNaughton 1979, 1985). By altering community composition, the indirect effects of herbivory should affect countless competitive and consumptive interactions and, ultimately, the forces of selection. For ex-

ample, conversion of forest and scrub habitat to grassland in the Serengeti, Tanzania, is associated with shifts in the dynamics of bird predation on insects, the resulting structure of insect communities, and, potentially, the antipredator strategies employed by insect prey (Sharam et al. 2009; Sinclair et al. 2010). Herbivory in African savannas also indirectly alters ecosystem processes, most notably the dynamics of fire (Bond 2010) but likely also disease prevalence (through changes in parasite and host communities; McCaughley et al. 2008) and microbial ecology (Wardle et al. 2005).

Finally, large herbivores may affect whole savanna communities through engineering effects, most notably through the maintenance and alteration of water sources (Bond 1993) but also through the movement and concentration of limiting nutrients. For example, spatially concentrated deposition of nitrogen by wildebeest increases the growth and palatability of savanna grasses (McNaughton et al. 1988), and the seemingly mundane process by which hippopotamus (*Hippopotamus amphibius*) move large volumes of terrestrially derived nutrients into aquatic habitats (i.e., consumption and defecation) is hypothesized to dramatically alter bottom-up forcing of aquatic plants and animals (Naiman and Rogers 1997; Moore 2006).

The complexity of consumptive interactions in African savannas becomes apparent when one considers that the far-reaching direct and indirect effects of herbivores described above are themselves mediated by top-down impacts of carnivores on herbivore abundance and dispersion. A large literature documents experimental and correlative evidence of large carnivores affecting herbivore populations through consumption of prey (Georgiadis et al. 2007; Owen-Smith and Mills 2008) and also by altering habitat selection and grouping behavior of herbivores responding to the risk of predation (Hopcraft et al. 2005; Valeix et al. 2009). Other research highlights the role of predation in creating patterns of simultaneous top-down and bottom-up forcing across diverse prey assemblages in savannas (Sinclair et al. 2003; Radloff and Du Toit 2004). Recent studies of predator-prey dynamics in African savannas also illuminate the cascading consequences of the decline of apex predators for savanna communities. The decline of lions in West African savannas is associated both temporally and spatially with increases in mesopredator abundance (Brashares 2003). One mesopredator in particular, the olive baboon (*Papio anubis*), has increased by an order of magnitude in some protected savanna areas and, through predation, is implicated in the decline of birds and smaller primate species (Prugh et al. 2009; Brashares et al. 2010). Baboon eruptions are also anecdotally linked to the spread of exotic trees and increases in human-wildlife conflict and parasite transmission (Brashares et al. 2010). This example, along with other accounts of me-

sopredator release and niche expansion in African savannas (e.g., Lloyd 2007), shows the powerful role of apex predators in these ecosystems. The profound effects of herbivores and carnivores on ecosystem structure further shows how their presence or absence might shape selection imposed on other members of the community.

Eco-Evo Interplays

The preceding sections establish diverse indirect effects of consumers on other members of their associated food webs. To what extent might these indirect effects result in evolutionary change, and how might any such evolutionary effects feed back on the ecology of the system? In the following sections, we explore these questions. We adapt a simple theory of trophic interactions to consider where one might begin to look for the indirect evolutionary effects of trophic cascades in any food web. Then, for the specific case of kelp forest systems, we summarize the supporting evidence and explain how these purported evolutionary processes appear to feed back on ecology in the form of variation in the distribution and abundance of plants and herbivores.

The Theory

Schoener (1993) systematically considered the range of indirect interactions that can arise in simple webs (up to five web members) in which the only direct connections are between consumers and resources. We follow his sequence of indirect ecological interactions (depicted in figs. 23.3–23.5 of Schoener 1993), add one further example involving parasitism of a direct mutualism, and consider which of these indirect interactions have documented, likely, or potential evolutionary consequences for one or more of the participants.

Most published reports of evolutionary responses to indirect interactions come from observations of character displacement that are interpreted as adaptive responses to exploitative competition (fig. 1A). Resources consumed by competitors in sympatry are more distinct than resources used by the same consumer species when they live in allopatry. Feeding structures (gill rakers, beaks, photosynthetic pigments) diverge correspondingly, with morphometric or chemical characters overlapping more when species do not share common habitats. Evidence of character displacement has been observed in a wide range of traits and taxa, such as fish body form and gill-raker spacing (Schluter and McPhail 1992), bird beak depth (Grant 1986), and possibly even light-harvesting pigments of cyanobacteria (West and Scanlan 1999). The decades-long and highly temporally resolved studies of the Grants and their coworkers have documented that exploitative com-

petition in sympatry has led to evolution by natural selection that changed the bill depths of and the size of seeds taken by Galapagos finches and that the selective advantage and frequency of particular trait states (bill depths) can vary with year-to-year changes in environmental regimes (rainy periods vs. drought) over relatively short time periods (Grant and Grant 2006).

Apparent competition (sensu Holt 1971, the indirect adverse interactions of different prey species mediated through a shared predator, parasite, or pathogen; fig. 1B) should be frequent in nature but has been demonstrated in relatively few field studies (Schoener 1993). In theory, selection arising from shared predators might cause these prey to diverge in their evolved traits (Holt 1971; Abrams 2000). In practice, such outcomes might be difficult to distinguish from direct effects or alternative selection pathways. Schluter (2000) considered the effects that apparent competition might have on prey species sharing a common enemy, pointing out that these range from apparent competition to apparent mutualism (Abrams 2000) if the alternative prey dilutes predation pressure, which has been observed over short timescales that increase the importance of behavioral over numerical responses by predators to prey supplements (Sabo and Power 2002). Rundle et al. (2003) experimentally examined character divergence of intermediate stickleback morphs exposed to distinct benthic or marine (similar to limnetic) competitors under enhanced versus reduced predation from trout and predatory insects. They found more divergence (in gill-raker count) with predator augmentation, even though exploitative competition was stronger in the predator-reduction treatments, as evidenced by reduced growth rates of all stickleback types when released from predators. This divergence could be interpreted as a response to selection by apparent competition, but the authors favor a different interpretation. Given the lack of selection for enhanced predator defenses (armor) and the tighter relationship of divergence to overall mortality (which was also high in reduced-predator treatments) than to manipulated predation, the authors found it more likely that divergence arose either because predators enhanced behavioral habitat partitioning between more benthic and more limnetic morphs or because diet partitioning weakened under high densities and extreme exploitative competition, with starving morphs forced into whichever habitat had the most food even if it was not the one in which they were more efficient. Increased diet overlap as food availability declined from the rainy season to the dry season has been documented for very dense fish starving in drying stream pools in natural tropical fresh waters (Lowe-McConnell 1975). In the first case, behavioral habitat partitioning might be more parsimoniously interpreted as selection in response to direct predation. Conceivably, this behavioral

partitioning could be considered a response to apparent competition if alternative prey consistently enhanced densities of the shared predator, but this effect would likely be hard to distinguish from other factors that might also enhance local predation rates.

In another study focused on predator effects on competing prey, Vamosi and Schluter (2004) examined defense traits (armor, pelvic-girdle reinforcement, spines, body shape) in the same allopatric and sympatric populations of lake stickleback in which Schluter and McPhail (1992) had detected character displacement in gill rakers. Limnetic stickleback, subject to vertebrate predation, were consistently more armored than benthic species, whose more important predators are invertebrates that are not deterred by armor. There was, overall, more divergence in defensive traits between sympatric benthic and limnetic sticklebacks than between randomly paired allopatric populations. However, overall armor, spine length, and other defensive character states, averaged over both species, were significantly reduced when fish lived in sympatry. Vamosi and Schluter (2004) offered as one interpretation for these results that habitats for both morphs were more distinct in sympatry but that benthic forms may have enjoyed somewhat reduced predation from vertebrate predators (apparent mutualism; Abrams 2000).

Apparent competition may be of societal importance in fisheries in which hatchery and wild stocks interact. Huge numbers of hatchery-reared salmonids attract and support predator populations (terns, seals, and human fishers; Kareiva et al. 2000) that also prey on wild salmon. The wild stocks would likely not be subject to such strong predation in the absence of hatchery fish. We are not aware of any documented evolutionary response by wild salmon to apparent competition from hatchery fish. One predicted response could be to diverge, if possible, from hatchery fish in the timing of out-migrations as smolts or returns as breeding adults, to partition “enemy-free space” (Jeffries and Lawton 1984, 1985) with hatchery stocks. This divergence might be possible for wild salmon if periods when hatchery stocks return or out-migrate have been focused to narrow windows of time by artificial selection (via practices in which only the early portion of the run is captured for breeding). The out-migration times of wild spring chinook (*Onchorychus tshawytscha*) through the Lower Granite Dam on the Snake River were much more spread out and mostly later (May–June) than the spiked peak out-migration in April by hatchery spring chinook (Matthews et al. 1990, cited in Waples 1991). It is not known whether selection has affected wild out-migration passage times relative to those of hatchery fish. The considerable phenotypic variation in wild chinook passage times could, however, permit such divergence, which would offer some relief from putative apparent competition from predators

attracted to hatchery-inflated stocks in the lower Snake or Columbia Rivers and at the mouth of the Columbia. Conversely, extensive gene flow between wild and hatchery stocks might prevent evolutionary divergence of wild stocks from apparent hatchery-reared competitors.

In a square food web with one specialist consumer (fig. 1C), Schoener (1993) identifies an indirect benefit for the SE (“southeast” or lower-right-node) prey from the NE (“northeast” or upper-right-node) predator that reduces its apparent competitor’s population. If these resource populations also competed exploitatively or directly, this positive effect could be augmented. The SE prey, in turn, has a negative impact on the NE predator by supporting the consumer’s exploitative competitor, the NW (“northwest” or upper-left-node) predator. Selection could favor spatiotemporal tracking of the NE predator by the SE prey. Association, which the prey might initially seek for protection, could evolve into a more direct facilitative interaction that might counter the expected evolutionary tendency of the NE predator to avoid (or suppress) the SE prey and its indirect adverse impact. Cleaner services, for example, might arise in smaller fishes that sought enemy-free (or competitor-free) space around larger client fishes. On the other hand, if selective forces by the indirect adverse effect of this prey on the NE consumer first molded the evolutionary path, then these forces might change the interaction to that depicted in figure 1D, in which the NE consumer broadens its diet to consume, or otherwise suppress, the SE prey.

In a square web with two generalist consumers (fig. 1D), there are two adverse indirect interactions: exploitative competition between the consumers and apparent competition between the prey. This could lead to niche partitioning between the consumers, as discussed above, and to mutual avoidance of the apparent competitors (the prey), as discussed under the enemy-free-space hypothesis (Jeffries and Lawton 1984, 1985; Abrams 2000). Given the complexities of outcomes of sharing predators for prey species, however, alternative evolutionary pathways—arising, for example, from apparent mutualisms between the prey—could also develop.

These interactions, depicted in and discussed for figure 1C and 1D, could decouple the web if they led to niche partitioning and consequently to diet specialization in the two consumers (fig. 1E; Schoener 1993). Apparent competition may have played an underappreciated role in reinforcing character or habitat divergence among exploitative competitors, as discussed by Rundle et al. (2003).

Direct mutualisms (+/+ in fig. 1F) often involve providing a fruit, nectar, or fat-body resource to a plant’s disperser or protector. The costs of providing this reward are more than offset by the fitness benefits for the provisioning mutualist from pollination, seed dispersal, or

protective services. In some cases, the only costs to the host seem to be time (e.g., clients for cleaner fishes). Many (probably most) successful mutualisms, however, are parasitized by “cheaters,” shown in the NW corner of figure 1F. The coevolutionary consequences of this parasitism could be to hone the original mutualism: the client fish and true cleaner wrasse would evolve coloration or signaling that would distinguish mutualist from parasite; a flower would evolve morphologically to facilitate selective entry by the true pollinator and to thwart entry by nectar burglars; the pollinator would learn to discriminate the rewarding milkweed flower from the cheating, nectar-free orchid. If a parasite “won” this coevolutionary arms race, both mutualists (if the relationship was obligate) would decline or become extinct, taking the specialist parasite with them. Therefore, the examples of mutualisms we see may be those in which refinement of cues and adaptations have thwarted debilitating parasitism, at least for the time being. Models exploring these types of interactions have found that certain competitive interactions among mutualistic and parasitic exploiters can lead somewhat counterintuitively to stable equilibria (Morris et al. 2003; Jones et al. 2009).

As discussed above, tritrophic interactions (three-level trophic cascades; fig. 1G, 1H) are well known in ecology and have major impacts on the distribution and abundance of green biomass in terrestrial, freshwater, and marine biomes (Fretwell 1987; Pace et al. 1999; Terborgh and Estes 2010; Estes et al. 2011). In general, we would expect this interaction to relax selection for defense of the basal resource against its consumers. If one resource supplies two consumers, each preyed on by a specialist (fig. 1H), then these top predators would enjoy an indirect mutualism driven both by their effects in protecting the basal resource and by reducing the competitor of the other predator’s prey. As food chains lengthen (fig. 1I), indirect adverse interactions, as well as more indirect mutualisms, arise, and the proportion of indirect interactions increases, relative to that of direct interactions (see also Schoener 1993).

A Test of the Theory in Kelp Forests

Most of the potential evolutionary influences discussed above remain to be demonstrated. However, Steinberg et al. (1995) explored the prediction that three-level trophic cascades relax selection for the coevolution of defense and resistance in plants and herbivores by contrasting kelp forest ecosystems in the northeast and southwest Pacific oceans. They chose this particular contrast because while both regions support diverse brown algal floras and contain similar guilds of macroinvertebrate herbivores, the presence of sea otters in the northeast Pacific has created

a three-trophic-level system, whereas the long-standing absence of sea otters or other predators of comparable influence makes the southwest Pacific a two-trophic-level system. This is not to say that predators are absent from Southern Hemisphere kelp forests (e.g., Babcock et al. 1999) but only that their interaction strengths are less than those of sea otters in the North Pacific. This purported functional disparity in food chain length between the northeast and southwest Pacific oceans is assumed to have prevailed through at least the Pleistocene (Estes and Steinberg 1988), thus leading to the prediction that Southern Hemisphere brown algae should have evolved stronger defenses against herbivory than their Northern Hemisphere counterparts.

To test this idea, it was first necessary to ascertain how algae defend themselves against herbivores. There are four main possibilities: through changes in life history, morphology, behavior, and chemistry. Behavior was not considered because sedentary macrophytes lack both nervous and muscular systems and thus the ability to behave in the traditional sense. Although heteromorphic life histories are known to provide seasonal refuges from intense herbivory in some marine algae (Lubchenco and Cubitt 1980), the sporophyte life stage of most species from both the Northern and Southern Hemispheres is relatively long. Morphology was similarly excluded because of the absence of any obvious morphological differences between Northern and Southern Hemisphere algal species. This left chemical composition as the likely response mechanism, a process supported by numerous studies showing a defensive role of marine algal secondary metabolites against their herbivores (Hay and Fenical 1988; Hay 2009). An assessment of potential secondary compounds in brown algae pointed toward phlorotannins (Targett and Arnold 1998), and a survey comparing phlorotannin levels in the common brown algal species of the Southern and Northern Hemispheres revealed a roughly 10-fold greater concentration of these compounds in the Southern Hemisphere (Steinberg 1989).

These findings are consistent with the hypothesis that Southern Hemisphere algae evolved under a greater intensity of herbivory than did their Northern Hemisphere counterparts. This hypothesis was tested further in two ways: (1) by measuring in situ plant tissue loss to herbivory in Northern Hemisphere kelp forests with sea otters, in Northern Hemisphere kelp forests lacking sea otters, and in Southern Hemisphere kelp forests and (2) by evaluating the abilities of Northern and Southern Hemisphere herbivores (sea urchins and gastropods) to resist phlorotannins. The in situ grazing assays revealed no significant algal tissue loss to herbivory in Northern Hemisphere kelp forests with sea otters ($<1\% \text{ day}^{-1}$), high levels of algal tissue loss to herbivory in Northern Hemisphere kelp forests

lacking sea otters ($\approx 80\%$ day⁻¹), and relatively low but significant levels of algal tissue loss to herbivory in Southern Hemisphere kelp forests (5%–7% day⁻¹). Feeding assays of the herbivores on diets in which phlorotannin concentrations were varied experimentally further demonstrated that Southern Hemisphere herbivores were less deterred by these compounds than their Northern Hemisphere counterparts (Steinberg et al. 1995). In some trials, phlorotannins in agar blocks were actually a feeding attractant for Southern Hemisphere grazers.

Steinberg et al. (1995) interpreted these results as follows. The two-trophic-level structure of Southern Hemisphere kelp forests led to the coevolution of defense and resistance in the plants and their herbivores. The addition of sea otters as a third trophic level in the Northern Hemisphere, by reducing the abundance of herbivores and thus the intensity of herbivory, broke the evolutionary arms race between the plants and their herbivores, thus reducing selection for increased defenses in the plants and selection for increased resistance to those defenses in the herbivores. Under these conditions, competition among northern seaweeds for light (“competitive overtopping”; Schluter 2000) might select against allocations to defense that slowed growth rates.

This evolutionary scenario explains several other characteristics of species and species interactions in kelp forests of the North Pacific Ocean. One of these is a depth gradient in the intensity of herbivory and associated shifts in a trade-off between plant defense and competitive ability in Aleutian Islands kelps. As air-breathing divers, sea otters become less efficient predators in deeper water, resulting in an increased abundance of sea urchins and a greater intensity of herbivory with depth (Estes et al. 1978). This gradient, in turn, selects for a kelp flora with poorly defended but competitively superior species in shallow water and better defended but competitively inferior species in deeper water (Dayton 1975; Estes and Steinberg 1988).

Another characteristic feature of Northern Hemisphere kelp forests that is explainable by this evolutionary scenario is the urchins’ tendency to shift abruptly to deforested sea urchin barrens when their natural predators (sea otters, lobsters, and various fishes) are removed (Steneck et al. 2002). The likely explanation for this phase shift is that the poorly defended Northern Hemisphere kelps easily succumb to elevated intensities of herbivory. Although deforestation by herbivores also occurs in Southern Hemisphere kelp forests (Babcock et al. 1999), the purportedly different strengths of coevolution between plants and their herbivores has led to strikingly different patterns of spatial association/disassociation between kelps and their herbivores in Northern and Southern Hemisphere kelp forests (fig. 3). Abundant kelps do not co-occur with abundant herbivores in Northern Hemisphere kelp forests, as in-

dicated by the strongly hyperbolic functional relationship between kelp and herbivore abundance in the lower panels of figure 3. In contrast, Southern Hemisphere plants and herbivores commonly co-occur at high densities.

Steinberg et al.’s (1995) evolutionary scenario might further explain the phylogeography and evolution of dugongid sirenians, which became kelp eaters as they radiated into high-latitude oceans with the onset of Late Cenozoic polar cooling (Domning 1978). A poorly defended and thus more highly nutritious kelp flora would have drawn these kelp-eating marine mammals into the North Pacific Ocean, while the better-defended and thus less nutritious kelp floras of the Southern Hemisphere would have had the opposite effect (Estes and Steinberg 1988).

Similar arguments have been advanced to explain the evolution of large body size in abalones (Estes et al. 2005). Abalones have radiated from the tropics (where all extinct and extant species are small) to higher-latitude kelp forest systems (where they have become much larger). This general increase in body size is likely a response to the increased production of cool, higher-latitude oceans. Although this bottom-up force probably explains why large abalones occur in various kelp forest systems, the largest species evolved in the North Pacific Ocean, where a strong three-level trophic cascade would have selected for a poorly defended (and thus more nutritious) kelp flora. An alternative explanation for very large body size in North Pacific abalones might be that they achieve a refuge from predation in size, but this is not the case, because sea otters are easily capable of killing and consuming the largest abalones.

These collective findings and ideas suggest an intimate but complex reciprocity between ecology and evolution in kelp forest systems. Indirect ecological interactions originating from sea otters and their immediate ancestors appear to have led to evolutionary responses in herbivores and plants, leading, in turn, to feedback effects on the distribution and abundance of numerous species.

Where Else to Look?

We have argued (1) that indirect ecological interactions among species are both complex and widespread in nature, (2) that indirect interactions can lead to evolutionary responses in much the same way as do direct interactions, and (3) that feedbacks from indirect evolutionary responses can have important ecological consequences. Although accounts of complex interplays between ecology and evolution (as described above for kelp forest systems) are rare (Mooney and Singer 2012), they do occur elsewhere in nature, as exemplified by work on sticklebacks (Harmon et al. 2009), Trinidadian guppies (Bassar et al. 2010), Caribbean lizards (Schoener 1988), ant-plant mutualisms (Janzen 1966; Rico-Gray and Oliveira 2007),

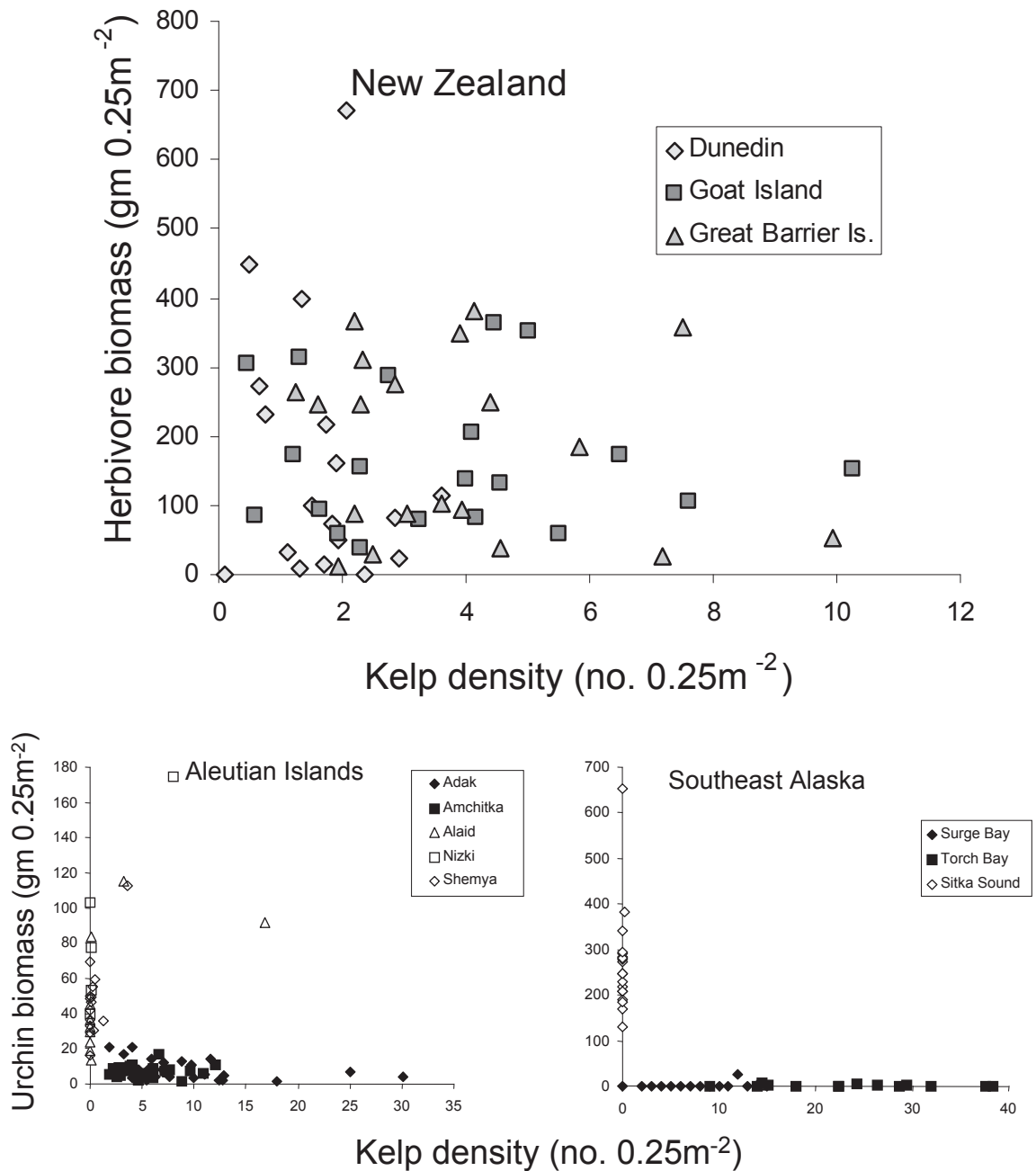


Figure 3: Bivariate plots of kelp density versus herbivore biomass at various sites (symbols) from kelp forests in Australia/New Zealand (*top*) and western North America (*bottom*). The bottom panels are reproduced from Estes and Duggins (1995).

crossbills (Mezquida and Benkman 2005), and aphid-milkweed interactions (Mooney et al. 2010). The dearth of examples could be because such processes are rare (unlikely, we think) or because they remain largely unstudied. If the latter is true, then how and where might one look for them? The answer to how is straightforward in principle—that is, by contrasting the characteristics of species

and the patterns of species abundance between systems in which a suspected driver is present or absent. This might be done experimentally or retrospectively (Schoener 2010). Models of indirect effects, such as those in figure 1, provide guidelines as to what to look for.

The answer to the question of where to look could be “almost anywhere,” since such indirect interactions appear

to be ubiquitous. Three specific areas seem especially fruitful for further research.

Following the sea otter–kelp forest example described above, we might expect plant defenses to vary predictably as a function of food chain length, such that the defenses are better developed in systems with an even number of trophic levels. There are numerous potential opportunities for testing this prediction in arenas where predation risk changes predictably over space: grazing halos around reefs; similar depleted areas grazed by pika, pocket mice, or other central-place grazers that venture only so far from cover; or margins of rivers, ponds, and lakes, where grazer exposure to terrestrial or aquatic predators changes abruptly with depth.

Another fruitful place to look for a complex reciprocity between ecology and evolution might be in the interplay between predators, prey, and pathogens. Predators commonly reduce the abundance or alter the behavior of their prey, in turn influencing the manner in which their prey (as hosts) interact with parasites and pathogens. Much as predators influence the coevolution of defense and resistance in plant–herbivore systems, they might also influence the coevolution of immunity and virulence in host–parasite systems.

A third potentially interesting arena for further research is in the interplay among predators, herbivores, plants, and wildfire. By reducing herbivores, predators can increase plant abundance, thus increasing fuel loads and the frequency and intensity of wildfires. The frequency and intensity of fire, in turn, should influence life-history evolution in plants, thus further influencing the manner in which plants and fire interact across landscapes.

These suggestions may seem far-fetched. But are they any more far-fetched than the idea that sea otters and their immediate ancestors influenced the evolution of body size in abalones (Estes et al. 2005) or the phylogeography of Stellar's sea cow (Estes and Steinberg 1988)? Indirect ecological effects of apex consumers and top-down forcing are commonplace in the natural world. These interactions increase the complexity of the potential interplay between ecology and evolution, regardless of the timescale over which this interplay operates.

Conclusions

We end with several general conclusions concerning the interplay between ecology and evolution. First, species interactions in general and consumer–prey interactions in particular form complex networks structured by variation in such features as interaction strengths among particular pairs of species; the degree of connectivity, nestedness, and modularity of the network; the length and configuration of interaction chains; and the degree to which direct spe-

cies interactions attenuate or amplify as they move along the chain (Schoener 1993).

Second, indirect effects of apex consumers occur in diverse ecosystems and appear to be a nearly ubiquitous feature of the natural world. This conclusion is based on a growing list of examples from terrestrial, marine, and freshwater ecosystems from the poles to the tropics.

Third, these complex interactions can lead to evolutionary responses with important feedbacks to ecology. Although such interactions and feedbacks can change rapidly with changes in spatial and temporal context (Power et al. 1996), increasing research documents equally nimble changes in evolutionary responses to environmental change (Grant and Grant 2006; Thompson and Cunningham 2002; Schoener 2010). Whenever ecological outcomes change the frequency of heritable traits of populations, evolution has occurred. Predator-mediated changes in behavior and density of prey will, without a doubt, affect traits that in turn influence fitness components (differential mortality or fecundity) of organisms linked to prey in interaction webs. On the basis of the sheer number of potential indirect effects (fig. 2) and the possibility that at least the more proximate of indirect effects can have strong impacts on abundances and persistence of species, the interplay between ecology and evolution resulting from indirect species interactions is likely significant, if somewhat harder to detect than that resulting from direct interactions. Nonetheless, such complex eco-evo interactions have been, are currently, and will continue to be important threads in weaving the fabric of nature.

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APPENDIX

Supporting Materials

Consumptive interactions link together to form indirect-interaction chains and complex networks. The following brief review demonstrates the wide occurrence of trophic cascades in terrestrial, freshwater, and marine ecosystems.

Terrestrial Ecosystems

The clearest evidence of terrestrial trophic cascades comes from the experimental manipulation of small predators. Removals of spiders from old-field systems in the north-eastern United States (Schmitz 2006, 2008), birds from deciduous North American trees (Marquis and Whelan 1994), and lizards from small Bahamian islets (Schoener and Spiller 1996, 1999) provide unequivocal evidence of the indirect effects of predators on plants. Numerous studies demonstrate strong limiting effects of irrupting or high-density populations of large herbivores or seed predators on plant assemblages (Schmitz et al. 2000; Schmitz 2008; Terborgh and Estes 2010). Such effects, which are often caused, in turn, by the loss of large predators, are known from subarctic to tropical biomes in the Old and New World, Australia, and many of the larger oceanic and land-bridge islands (Terborgh and Estes 2010; Estes et al. 2011).

Changes recorded on the recently created land-bridge islands of the Lago Guri impoundment, Venezuela, establish the essential role of predation and top-down forcing in tropical forest systems. Those islands that were too small to support resident predators and too isolated to be reached by predators residing on the mainland or on larger islands experienced population irruptions of a diverse herbivore guild, including howler monkeys, leafcutter ants, and various rodents. Increasing herbivory resulted in high rates of seedling and sapling mortality, recruitment failure in many plant species, and a landscape-level shift from dense forests to parklands with a reduced overstory and practically no subcanopy (Terborgh et al. 2006).

Similar processes occur widely in temperate and boreal forests in which cervids (deer, elk, moose, and caribou) are the principal large herbivores. On the Canadian mainland, where large predators have persisted, cervid biomass is consistently less than 100 kg/km², regardless of the productivity of the province. In the United States, where large predators have been extirpated, cervid biomass is consistently higher and increases along gradients of increasing primary productivity, reaching 1,000 kg/km² in the most productive states (Crête 1999). Following extirpation of wolves, grizzly bears, and cougars from the United States, cervids and beavers have altered patterns of forest regeneration, markedly reducing the diversity of herbaceous plant communities and exposing stream banks to increased erosion (McShea et al. 1997; Ripple and Beschta 2006; Waller and Rooney 2008). Similar impacts of overabundant ungulates have been documented in other parts of the developed world now lacking large carnivores (Ripple et al. 2010). These effects are best known from various US national parks, where the loss of large predators a few decades ago has left a characteristic signal of reduced growth rate (McLaren and Peterson 1994) or recruitment

failure (Beschta and Ripple 2009; Kauffman et al. 2010; Ripple et al. 2010) in the dominant tree species.

Productive low-arctic scrublands appear to be dynamically comparable to forests: predatory mammals and birds regulate herbivores, and their exclusion leads to severe reduction of plant biomass and elimination of erect woody plants, regardless of their palatability. The new dominants are herbaceous and trailing woody plants (Aunapuu et al. 2008; Dahlgren et al. 2009). Similar plants prevail on the tundra proper (Tihomirov 1959). This view is supported by quantitative empirical studies and experiments (Batzli et al. 1980; Oksanen 1983; Moen et al. 1993; Olofsson et al. 2004a, 2009; Aunapuu et al. 2008). A likely reason for the inability of predators to regulate the herbivores of the tundra proper is its low primary productivity, creating a situation where the vegetation cannot sustain herbivore densities high enough to support predators (Oksanen et al. 1981; Oksanen and Oksanen 2000).

The role of herbivory is less prominent in the precipitation-poor Beringian tundra (northeast Siberia and interior Alaska), where the scantiness of snow is unfavorable for small mammals. According to Zimov et al. (1995), the current lack of strong grazing pressure in Beringia is a consequence of the end-of-Pleistocene overkill of big arctic mammals, which changed a previously graminoid-dominated arctic steppe to moss-lichen-dwarf shrub tundra. As predicted by Zimov et al. (1995), the arctic steppe can be restored by intense reindeer grazing (Olofsson et al. 2001, 2004b). Moreover, the recovery of wild reindeer and musk oxen has dramatically changed the composition of the tundra vegetation and influenced its response to global warming (Manseau et al. 1996; Crête and Doucet 1998; Hansen et al. 2007; Post and Pedersen 2008; Olofsson et al. 2009), indicating that if the two surviving big arctic herbivores are allowed to recover, they could change the Beringian biome from mossy tundra to grassed steppe (Zimov et al. 1995).

Along the arctic coasts, the proximity of nutrient-poor terrestrial ecosystems and productive sea generates a strong interaction of an entirely different kind. Birds exploiting marine resources must breed on land, where their populations are dense enough to support predators, which can also regulate small, herbivorous mammals (Reid et al. 1995). Thus, marine birds aggregate to cliffs, where the nutrient transfer from sea to land is often sufficient to change dwarf shrub heaths to productive grass-herb meadows. On oceanic islands, which predators cannot reach and where the ratio of feeding to breeding habitats is high, entire islands can be embraced by this "bird cliff effect." Introduction of predators changes these meadows to heaths (Croll et al. 2005).

Freshwater Ecosystems

Freshwater ecosystems, both flowing (rivers and streams) and still (lakes and ponds), have been important arenas for understanding food web dynamics because of the relatively short generation times of lower-trophic-level species (in contrast with trees and ungulates in forest systems, for example) and their clearly circumscribed physical borders, which make them well suited for comparative and experimental analyses. Impacts of apex consumers are known in freshwaters from the lowland tropics to high elevations and high latitudes. Evidence comes both from purposeful experimental manipulations in which naturally occurring consumers have been added or removed and from time series following the introductions of exotic species.

Cascading effects of apex consumers in lakes were perhaps first reported (at least in Western scientific literature) in large village ponds dug into the floodplain of the Elbe River in what is now the Czech Republic. Hrbaček et al. (1961) documented strong responses in phytoplankton, zooplankton, water chemistry, and ecosystem metabolism following changes in fish species stocked in these ponds. Subsequently, cascading effects of top predators, usually fish, have been observed and experimentally induced in ponds and lakes throughout Europe and North America (Brooks and Dodson 1965; Persson et al. 1992; Carpenter et al. 1985, 1987). These trophic cascades typically are mediated by fish predation on grazing zooplankton. Large grazing zooplankters, especially *Daphnia*, potentially control phytoplankton, the main primary producers in pelagic lake habitats. When piscivorous fish eat zooplanktivorous fish, grazing zooplankters are released from predation and can clear lake water columns of phytoplankton in weeks or months. Without piscivores, zooplanktivorous fish (often minnows in temperate lakes) suppress these grazers, and phytoplankton builds up to turn lakes green. These cascades motivated the “biomanipulation” of fish to improve water quality (Shapiro et al. 1975; Hansson et al. 1998; Lathrop et al. 2002).

Trophic cascades also link predatory fish, through prey, to attached algae in rivers. As in lakes and marine and terrestrial settings, apex riverine consumers either release (Power et al. 1985; Flecker and Townsend 1994; McIntosh and Townsend 1996) or suppress (Power 1990; Wootton and Power 1993) algal biomass, depending on whether food chains have odd or even numbers of functional trophic levels (Fretwell 1977). As with lakes, top-down impacts of predators in rivers vary across space and time. In the Eel River of northern California, predatory fish (juvenile steelhead *Oncorhynchus mykiss*) indirectly control algal biomass by consuming herbivorous insects, but only under normal winter flood–summer drought hydrologic

regimes. Following flood disturbance, fast-growing edible (early-successional) grazers recover first, during the biologically productive summer low-flow season, and feed juvenile steelhead and other river fish. During prolonged periods without flood scour (i.e., following drought winters or in artificially regulated channels), predator-resistant armored caddisflies increase their densities, sequester algae, and curtail energy flow up the food web to fish, also severing the top-down cascade linking fish to algal biomass (Wootton and Power 1993; Power et al. 2008).

Food chain dynamics in aquatic systems are characterized by a strong size structure, in which larger individuals occupy higher trophic positions, with many species increasing their trophic positions as they grow older or larger. Ontogenetic changes in diet and predator vulnerabilities of freshwater fishes and their ecological consequences have been well studied (e.g., Mittelbach et al. 1988; Persson and De Roos 2003). Many prey fishes that have outgrown their gape-limited predators continue to compete with smaller, vulnerable conspecifics for food resources. In such situations, predation on young prey can free adult conspecifics from competition, so they reproduce at higher rates. An example of this phenomenon is provided by the work of Persson et al. (2007) in Lake Takvatn, an unproductive lake in northern Norway, where the top predator, brown trout (*Salmo trutta*), had been overharvested in the early 1900s. Prey (arctic charr *Salvelinus alpinus*) were introduced around 1930, but in the absence of effective trout predation, the charr grew to a dense population dominated by stunted, food-limited adults that reproduced at low rates. By 1980, severely food-limited brown trout had almost disappeared from the lake. Counterintuitively, a massive culling of their charr prey (from 1984 to 1989) allowed brown trout to rebound as apex predators, after which they were able to hold the charr population in check at about half its precull abundance. At this lower density, adult charr were not food limited and produced a plentiful supply of offspring to support the trout. A more productive trout fishery has persisted for more than 20 years as an alternative stable state (Persson et al. 2007). Like the scouring winter floods in the Eel River (Power et al. 2008), the culling of charr in Lake Takvatn rejuvenated the food web to one in which predators can exert strong top-down control, but through a density-dependent population mechanism rather than a community-level reset of succession.

The influences of exotic species, while usually undesirable, have also informed the understanding of large consumers in freshwater ecosystems. Native beavers (*Castor canadensis*) once created rich riverine and wetland habitats for fish, riparian vegetation, and associated wildlife throughout North America, but these functions have been largely extirpated by overharvest of beavers for their fur,

by the destruction of riparian vegetation from overgrazing, and by land conversion. Beavers were introduced into southern Chile in 1946, where they spread and damaged native flora, made up of plants, such as *Nothofagus*, that have not coevolved to withstand beaver impacts, as have their North American counterparts. Exotic beavers are killing expanses of native forest and other vegetation and facilitating the spread of invasive exotic plants into formerly pristine ecosystems of southern Chile (Anderson et al. 2006, 2009). Nutrias (*Myocastor coypus*) might be considered South America's revenge. Introduced to Louisiana from South America in the 1930s, they have spread invasively throughout the Mississippi Gulf coast and are greatly damaging marsh vegetation, including island-colonizing trees, essential for land building (Fuller et al. 1985; Carter et al. 1999). Sea lampreys (*Petromyzon marinus*) invaded the North American Great Lakes via creation of the St. Lawrence seaway in the late 1800s, where they subsequently exploded to devastate Great Lakes fisheries (J. Kitchell, cited in Burton 2010). The Nile perch (*Lates nilotica*) was introduced into Lake Victoria in Africa, where it caused the extinction of hundreds of endemic haplochromine cichlids (Kaufman 1992; Vershuren et al. 2002). In Lake Gatún, central Panama, Zaret and Paine (1973) attributed the loss of much of the native fish fauna, including small top minnows that potentially controlled mosquito larvae, to the introduction of the peacock bass *Cichla ocellaris*. The risk for humans of contracting malaria has been related to predator impacts in fresh waters (Zaret and Paine 1973; Mather and That 1984, cited in Roger et al. 1991).

Ocean Ecosystems

The exploitation of large vertebrates throughout the world's oceans has substantially changed the functioning of marine ecosystems (Pauly et al. 1998; Jackson et al. 2001; Estes et al. 2006; Roberts 2007). The evidence of such effects from coastal oceans is wide-ranging and compelling but that from the vast neritic and oceanic realms is more circumstantial (Baum and Worm 2009; Essington 2010).

Coastal marine habitat can be broadly categorized as consolidated substrates (rock and coral reefs), seagrass meadows, or soft sediment (sand and mud). Limiting influences by herbivores on autotrophs and predators on herbivores are widely known for each of these habitat types, from the tropics (Sandin et al. 2010) to higher latitudes (Estes et al. 2010).

Much like tropical forests, tropical reefs are characterized by enormous species diversity. The influences of both herbivory (mostly by fishes and sea urchins) and predation (by invertebrates, sharks, and other large fishes) on reefs

and seagrass meadows are well documented (Sandin et al. 2010). "Grazing halos," bands of bare sand that separate Caribbean patch reefs from surrounding turtle grass meadows, are caused by herbivorous fishes and sea urchins that shelter in the reefs by day and venture forth to feed by night (Randall 1965). Observational (Williams and Polunin 2001; Mumby et al. 2006; Newman et al. 2006) and experimental (Smith et al. 2001; Thacker et al. 2001; McClanahan et al. 2003; Burkepile and Hay 2006; Hughes et al. 2007) studies have elucidated a primary role of herbivores in limiting autotrophs on coral reefs in the Atlantic, Pacific, and Indian Oceans. Cryptic coloration (Hixon 1991; McFarland 1991), schooling (Alexander 1974; Magurran 1990; Sandin and Pacala 2005), and refuging (Ogden et al. 1973; Hixon and Beets 1993; Friedlander and Parrish 1998) are widespread evolutionary responses that reduce the risk of predation for reef dwellers. Strong demographic effects of predators have been shown or suggested at numerous locations (Hixon and Carr 1997; Caddy and Rodhouse 1998; Chiappone et al. 2003; Graham et al. 2003; Burkepile and Hay 2007). Predator-prey and herbivore-autotrophic interactions link together as trophic cascades in the Caribbean (Hughes 1994), the Gulf of Mexico (Heck et al. 2000), the western tropical Pacific (Dulvy et al. 2004), and the Indian Ocean (McClanahan 2005; O'Leary and McClanahan 2010). The destruction of coral reefs through such processes as algal overgrowth and predation by the crown-of-thorns starfish is thought to be caused in significant part by the disruption of trophic cascades (Sandin et al. 2010).

The loss or reduction of great sharks from eastern-US coastal oceans and estuaries has triggered a trophic cascade in which the great sharks' prey (smaller sharks, skates, and rays) have irrupted, thus sharply reducing populations of the infaunal bivalve mollusks that are preyed on by these smaller elasmobranchs, in turn causing the collapse and closure of various clam fisheries (Myers et al. 2007). Decline of filter-feeding bivalves may have caused phytoplankton to increase, thus reducing water clarity and quality (Jackson et al. 2001; Kirby 2004).

Consumer effects are especially well studied in temperate-to-boreal kelp forest systems (Estes et al. 2010). The collapse of overfished cod was primarily responsible for reduced intensities of predation on (Witman and Sebens 1992; Vadas and Steneck 1995) and resulting increases of both shrimp (Worm and Myers 2003) and lobsters (Steneck and Wilson 2001) in the western North Atlantic. Relaxation of cod predation led to population irruptions by herbivorous sea urchins and kelp deforestation in the Gulf of Maine (and probably elsewhere) in the western North Atlantic (Steneck et al. 2004).

Kelp forests are maintained in southern California by various consumers, including benthic predatory fishes

(Nelson and Vance 1979; Cowen 1983), lobsters (Lafferty 2004; Tegner and Dayton 2000), and zooplanktivorous fishes (Davenport and Anderson 2007). At higher latitudes, a trophic cascade from sea otters to sea urchins to kelp occurs from at least the western Aleutian Islands (Estes and Duggins 1995) through British Columbia (Watson and Estes 2011).

Similar patterns and processes also occur in higher-latitude coastal marine systems of the Southern Hemisphere (Steneck et al. 2002). Predation by recovering populations of fishes and lobsters has led to sea urchin reductions and kelp recovery in New Zealand marine reserves (Babcock et al. 1999). Kelp forests have recently collapsed in parts of Tasmania because of the interactive influences of overfishing predatory lobsters and the southward range expansion of a warm-temperate sea urchin (Ling et al. 2009). In South Africa, the loss of predatory lobsters (apparently because of an anoxic event) led to an increase in a predatory whelk (previously preyed on by lobsters) and a predator-prey role reversal, in which predation by groups of these whelks overwhelmed colonizing lobsters, preventing their establishment (Barkai and McQuaid 1988).

Evidence of trophic cascades in pelagic ocean ecosystems is sparser but increasing (Baum and Worm 2009; Essington 2010). In nearly all cases, the key data come from time-series measurements associated with the natural fluctuations of predators or their depletion in fisheries. The reduction of finfish by fisheries in the Black Sea has led to an increase in small planktivorous fishes, a reduction in zooplankton, an increase in phytoplankton, and ultimately a regime shift to a system dominated by gelatinous plankton (Daskalov et al. 2007). Cod declines from overfishing across much of the North Atlantic Ocean have been closely followed by increases in their prey—shrimp (Worm and Myers 2003), crabs (Frank et al. 2005), and zooplanktivorous fishes—in turn leading to reduced zooplankton abundance followed by increasing phytoplankton and oceanic chlorophyll concentrations (Frank et al. 2005, 2011; Casini et al. 2008, 2009).

The extirpation of great whales from the world's oceans has removed their impacts in food webs as consumers of krill, squid, and forage fish; as prey to apex predators such as giant sharks and killer whales; as carcasses delivering high concentrations of lipids and other nutrients to the sea floor in an otherwise nutrient-impoverished deep sea (Estes et al. 2006); and as vectors of various nutrients from deep waters to the photic zone (Nicol et al. 2010; Roman and McCarthy 2010). The ecological consequences of these changes are striking and diverse. Before industrial whaling, the great whales are estimated to have co-opted more than 60% of the total net primary production by the North Pacific Ocean (Croll et al. 2006). The reduction of great

whales in the Southern Ocean caused or contributed to a dietary switch in Adélie penguins from fish to krill (Emslie and Patterson 2007), and whale reductions in the North Pacific appear to have caused their foremost predators—killer whales—to expand their diets to include seals, sea lions, and sea otters, thereby driving populations of these prey to collapse (Springer et al. 2003).

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