

Food Web Theory and Ecological Restoration

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Theory and Application

- A food web can convey many different types of information: the number of trophic levels, the pathways of energy flow, the biomass of organisms, or the most dynamically important linkages. Specifying what is meant is an essential first step.
- Simple food chain models have been useful in restoration, for example, the use of biomanipulation to improve lake water quality via trophic cascades.
- Systems often exhibit complex interactions such as apparent competition, which has deeply influenced restoration of island ecosystems affected by invasive species.
- Our intent is to highlight the potential value of 'food web thinking'—recognizing the role of predator-prey relationships—in ecological restoration.

No species exists in a vacuum. Rather, species are embedded within a network of predator-prey interactions in what Charles Darwin referred to as an “entangled bank” (Darwin 1859) and is now known more generally as a *food web*. In its most fundamental form, a food web provides insight into the feeding relationships in a system. More broadly, food webs represent a way of envisioning ecological systems that considers trophic (consumer-resource) interactions among species or groups of similar species (trophic guilds or trophic levels). Food web ecology is a constantly evolving subdiscipline of ecology, and it is important to appreciate the diversity of approaches to the study of food webs (Schoener 1989; Polis and Winemiller 1996; Montoya et al. 2006).

The term *food web structure* can have several meanings to ecologists. Food web structure can refer simply to the number of trophic levels in a food chain (fig. 11-1a), or can represent the linkages within a complex food web network (fig. 11-1b).

Food web diagrams may be used to represent the pathways of energy flow through a system (energetic webs; fig. 11-1c), or alternatively, the dynamically important linkages for regulating the abundance of other organisms (functional webs; Figure 11-1d). Additionally, food web structure sometimes refers to the distribution of biomass across different trophic levels, and ultimately how bottom-up and top-down factors regulate biomass across multiple trophic levels (fig. 11-2a,b). These diverse food web concepts serve as the basis for our discussion of food web theory and applications to ecological restoration.

Despite the intuitive importance of explicitly considering trophic connections, food web approaches are not often used in applied endeavors such as fisheries and wildlife management, conservation biology, and ecological restoration (Dobson et al. 2009; Memmott 2009). We argue that food web ecology has the potential to contribute to ecological restoration by encouraging a dynamic, interaction-driven view of ecosystems and can alert practitioners to the types of trophic interactions that have bearing on restoration outcomes (Zavaleta et al. 2001; DeCesare et al. 2010; Naiman et al. 2012). In many situations, a food web perspective will provide valuable insights into ecological restoration that would not otherwise be attained from a more static, community-based approach. For example, the reintroduction of gray wolves (*Canis lupus*) into Yellowstone Park, Wyoming, US, in the 1990s has precipitated a cascade of food web changes that has allowed the recovery of riparian vegetation from damaging effects of overgrazing by elk (*Cervus elaphus*). This has led to subsequent increases in populations of beaver (*Castor canadensis*) and bison (*Bison bison*) (Ripple and Beschta 2012), as well as implications for grizzly bear (*Ursus arctos*) foraging (Ripple et al. 2014a). Such changes only make sense by considering the cascading effects of predator-prey interactions across trophic levels.

Many of the world's ecosystems are highly degraded, and natural recovery processes are often inadequate to achieve desired goals for ecosystem recovery (Dobson et al. 2009; Hobbs et al. 2011). Ecological restoration is undertaken to hasten the recovery of damaged ecosystems, restore ecosystem function, and slow the declines of biodiversity. Ecological restoration in North America is historically rooted in plant community ecology: a perusal of the leading journals in the field such as *Ecological Restoration* and *Restoration Ecology* reveals the botanical slant of the discipline. As such, succession and community assembly theory have provided the theoretical underpinnings for restoration ecology (Weiher and Keddy 1999; Young 2000). Yet ecological restoration and species recovery may be hampered by focusing on plant communities rather than the broader suite of direct and indirect food web interactions in natural ecosystems (Aschehoug et al. 2015).

An important aspect of ecological restoration is the establishment of well-defined restoration targets, which may be structural, functional, or both (Hobbs

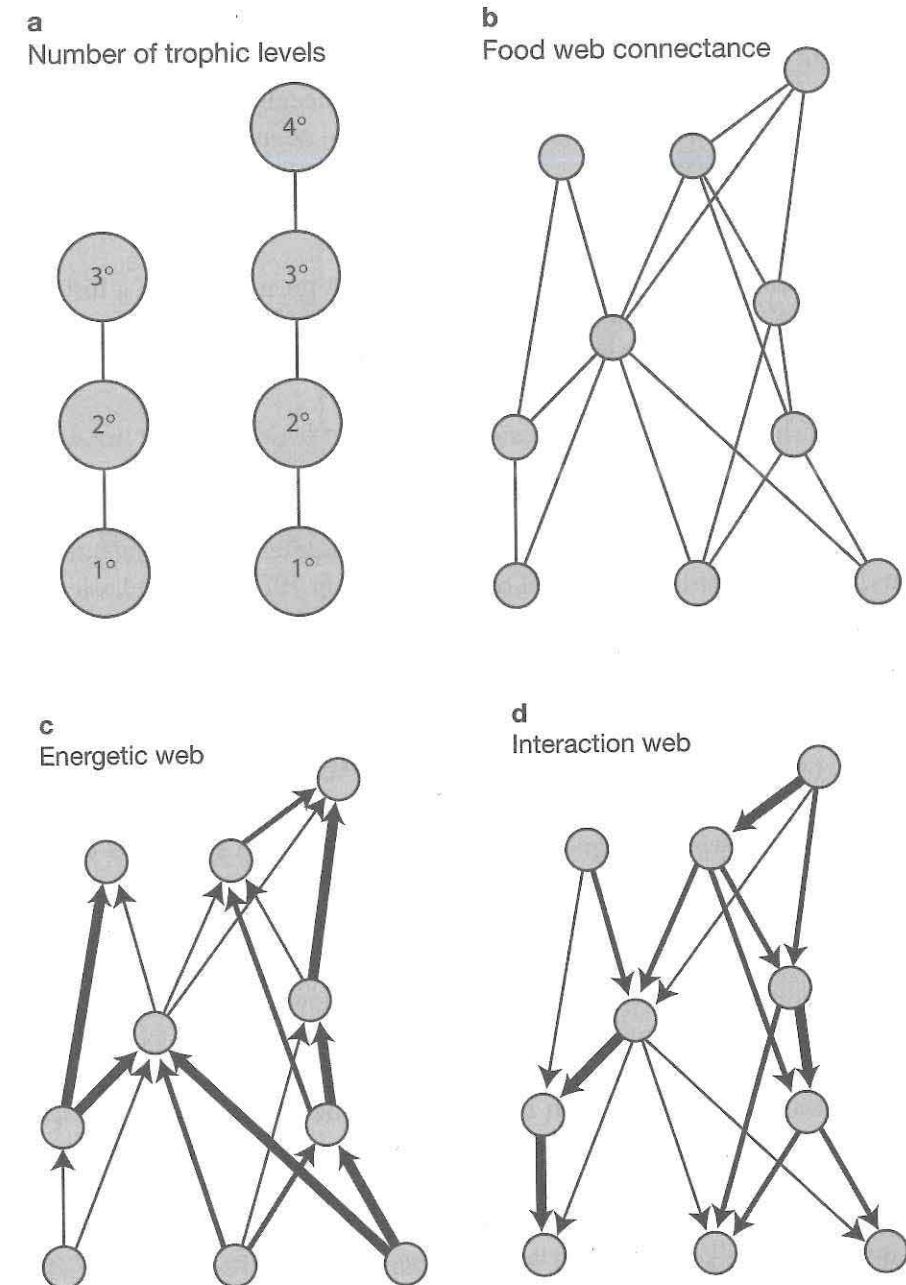


Figure 11-1. Different meaning of “trophic structure” used by food web ecologists: (a) number of trophic levels (3 versus 4 levels); (b) food web connectance, the pattern of trophic linkages among species in a complex web; (c) energetic web, depicting the pathways of energy flow; and (d) interaction web, showing the dynamically important food web linkages.

and Harris 2001). Structural and functional approaches are not mutually exclusive, and food web-based targets may incorporate both components. This chapter examines how food web theory and food web concepts more generally contribute to the planning, implementation, and evaluation of ecological restoration.

Relevant Theory—A Historical Overview

This section provides a brief overview of food web ecology from a historical perspective. For more in-depth background reading, we refer the reader to Montoya (2006); Polis and Winemiller (1996); Polis et al. (2004); McCann (2012); Schoener (1989); and De Ruiter (2005).

Published food web diagrams date back to at least 1880 and the work of Lorenzo Camerano (Cohen 1994). Early food web diagrams based feeding relationships on a diverse range of sources, including scientist intuition. Nevertheless, these abstractions were invaluable for the development of ideas about the direct and indirect interdependence of organisms (Elton 1927). In his classic book *Animal Ecology*, Elton (1927) presented food webs ("food-cycles") as collections of vertically size-structured food chains, whereby links represented feeding interactions. Elton also stressed the idea that abundance in food webs is a pyramid of numbers in which animals at the base of the food chain are more abundant than those at the top.

Lindeman's study (1942) of a small Minnesota lake marked a next major advance in food web ecology. Lindeman viewed the lake biota as a chain of energy transformations—energy was "produced" via photosynthesis, a portion was converted to herbivore biomass, and transfers continued on up the food chain (Lindeman 1942). Production decreased at successive trophic levels due to metabolic inefficiencies at each trophic link. In this view, primary production limited higher trophic level production, suggesting 'bottom-up control of the distribution of biomass in food webs (fig. 11-2a). This work provided the operational structure for modern food web research by introducing the concept of trophic levels and the use of energy as a currency. One implication of this work was that available energy could limit the number of trophic levels (Pimm 1982; Power 1992), an idea that can serve as a basis for assessing whether the energetic needs of higher consumers are likely to be met within a restored ecosystem. Lindeman's ideas also raise the issue of whether variables such as food chain length provide meaningful restoration endpoints.

Two decades later, Hairston et al. (1960) argued that terrestrial food chains have three functional trophic levels—predators keep herbivores in check, thus allowing plant biomass to accumulate. The top-down perspective offered by Hairston et al. (1960) was predicated on the idea that predators control the abundance of

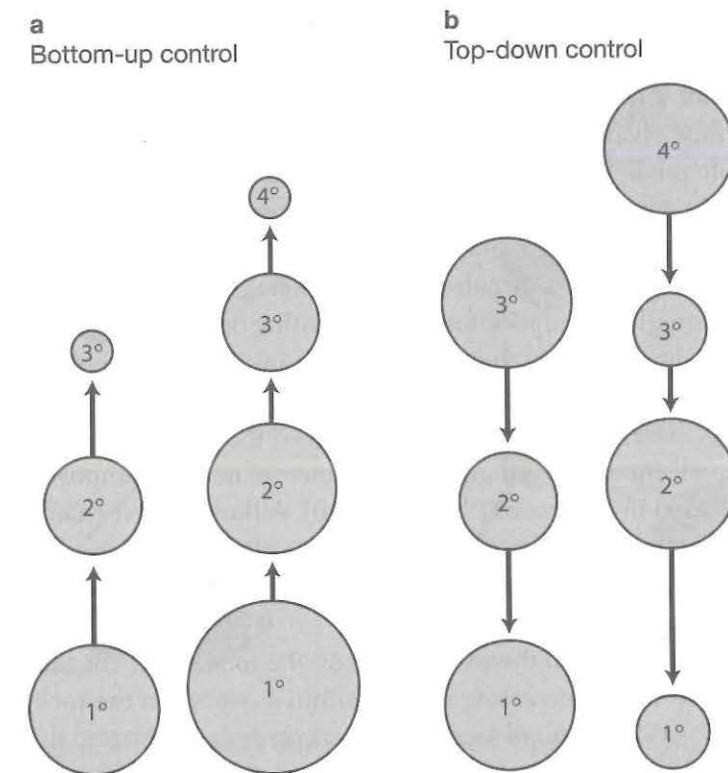


Figure 11-2. Bottom-up versus top-down control of the distribution of biomass at different trophic levels. Note that compartment size indicates trophic level biomass: (a) In the case of bottom-up control, primary production is the basis for higher trophic levels. Increasing primary production allows higher biomass at subsequent trophic levels, and possibly the support of additional trophic levels. (b) In the case of top-down control, predation plays a role in determining the distribution of biomass across trophic levels. In a three-level system, herbivores (2°) are suppressed by predators (3°), which allows accumulation of plant (1°) biomass. Addition of 4° controls the biomass of 3° . As a result, herbivore biomass (2°) increases, leading to a reduction in plant biomass (1°).

their prey, and that these effects subsequently cascade down food chains to impact primary producers (fig. 11-2b). This proposition ran counter to the dominant paradigm that nutrients and/or environmental factors limited plant communities and biomass, which, in turn, constrained higher trophic levels (compare fig. 11-2a, b). Hairston et al. (1960) has since inspired research directed toward the role of predators and resources as determinants of the abundance of trophic levels in a variety of ecosystem types (Polis and Strong 1996; Schmitz 2010). To illustrate, if top-down factors dominate, removal of predators from a three-level system should produce an increase in herbivore biomass, and a decrease in plant biomass. Alternatively,

if removal of predators does not cause an increase in herbivore biomass, this indicates bottom-up control, and we might expect that increasing plant productivity would produce an increase in herbivore and predator biomass.

Simple food chain models have played an important role in ecology by generating testable predictions and are often consistent with observations from natural systems (Terborgh and Estes 2010). However, trophic levels can also be heterogeneous, and the addition of grazers to a system may cause a compensatory shift toward grazer-tolerant plants rather than an overall biomass reduction (Leibold 1989). Interestingly, descriptive food webs focusing on network structure offer the paradoxically different view that food webs are immensely complex—with hundreds of species and trophic links, rampant omnivory, and intraguild predation (Dunne et al. 2002; Bascompte 2009). Moreover, the prevalence of behavioral or “trait-mediated” interactions highlights the power of nonconsumptive effects (e.g., fear of predators) in food webs (Schmitz 2010). Although food chain models undoubtedly simplify trophic interactions, they are often useful, and it is important to consider when and whether additional complexities are important in driving system dynamics.

One way that food web theory has built on the food chain concept is through the study of subsets of interacting species within a system. In the rocky intertidal, Robert Paine’s (1966) seminal food web experiments demonstrated that predation by the Ochre sea star (*Pisaster ochraceus*) on competitively dominant prey reduced competition for space, thereby allowing persistence of inferior competitors. This work highlighted the role of predators in maintaining prey diversity by mediating interspecific competition (fig. 11-3a). Paine labeled *Pisaster* a keystone species due to its role in structuring the community. The implication was that a few species play central roles in structuring ecosystems (Lawton 2000).

The question of what governs the stability of ecosystems has long been a key motivating question in ecology (Elton 1927). Early food web studies depicted relatively static interactions among organisms that were presumed to fluctuate near equilibrium. Today our view of food webs is more dynamic in both the nature of interactions and the consequences of these interactions for organisms. Although ecosystems often persist in a specific state for long periods of time, it is also recognized that shifts in species interactions can lead to rapid and potentially undesirable changes in ecosystems (chap. 2). Furthermore, positive feedbacks can make systems resilient against attempts to reverse these undesirable changes (Scheffer et al. 2001; Suding and Hobbs 2009). Indeed, restoration ecologists have written extensively about the role that feedbacks play in restoration design—often the actions needed involve reinforcing or weakening a feedback in order to shift the system toward the more desirable state, for example, Zedler (2013).

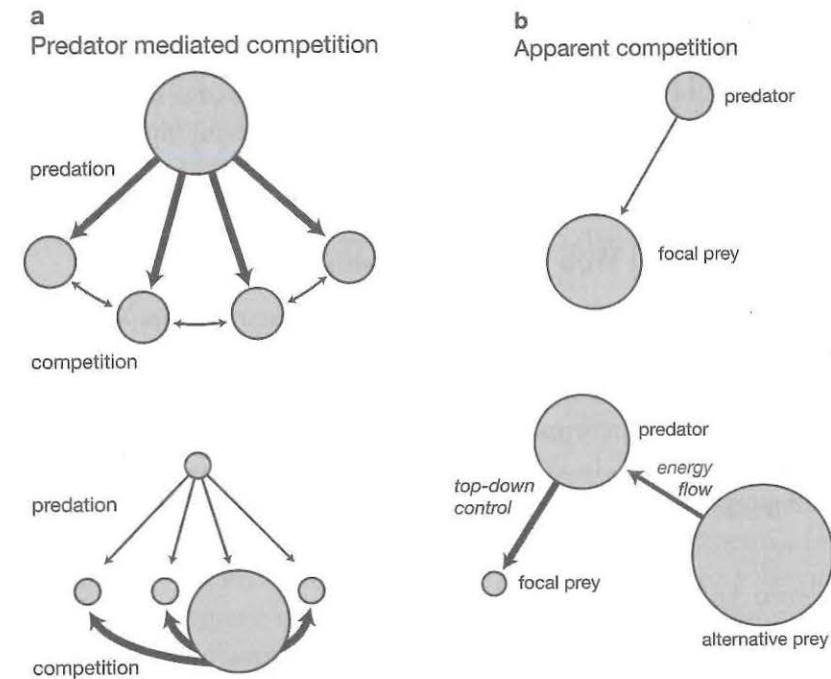


Figure 11-3. Examples of complex food web interactions. Upward arrows represent energy flow pathways; downward arrows represent top-down control. Arrow width represents the strength of the trophic linkage. (a) Predator-mediated competition. High-predator biomass suppresses densities of prey taxa, reducing competition among prey. Reduction of predator biomass allows increased prey biomass, thereby increasing competition among prey and domination by the superior competitor taxa. (b) Apparent competition. The predator consumes the focal prey (top panel). Addition of a highly productive alternative prey increases predator biomass, causing greater predation rates on the focal prey than in the absence of alternative prey (bottom panel). The consequence is elevated predator biomass and decreased biomass of focal prey.

The diversity-stability debate is a well-known research theme related to food webs (McCann 2000). Early studies noted that species-poor ecosystems were more likely to undergo severe fluctuations. For example, monocultures appear more susceptible to pest outbreaks, and islands are more susceptible to species invasion (Elton 1958). These observations led to the conventional wisdom that more species and more complex food webs beget stability (MacArthur 1955). In contrast, May (1973) found that species-rich mathematical food web models were less stable than simple models, thereby challenging ecologists to more carefully consider how food web configuration affects stability (Rooney and McCann 2012). Recent research considers the importance of interaction strengths. Theory suggests that

weak food web interactions can dampen oscillations among strongly interacting organisms (Rooney and McCann 2012). Understanding the connections between food web structure and stability remains an active area of research that has relevance for ecological restoration (McCann 2000; Thebault and Fontaine 2010; Saint-Béat et al. 2015).

Application of Food Web Theory to Restoration Ecology

Restoration ecology has historically been based on a succession-driven, bottom-up view of ecosystems that has not generally incorporated food web perspectives. Even if restoration targets do not specifically involve the reestablishment of trophic linkages per se, there may be value in food web approaches because the dynamics of any species or community depend critically on interactions within and among prey and predators.

Food Chain Approaches

The loss of apex predators from aquatic and terrestrial environments is perhaps one of humanities most pervasive influences (Estes et al. 2011; Ripple et al. 2014b). Numerous studies demonstrate that changes at the top of the food web can have powerful cascading effects, with implications for process, function, and resilience of ecosystems (Estes et al. 2011). Top-down effects and predation are widely recognized as key processes in the maintenance of biodiversity and ecosystem function (Terborgh and Estes 2010; Estes et al. 2011), highlighting the value of restoring or maintaining predation regimes as a component of ecological restoration. Below, are several examples where ecosystem restoration was viewed through the lens of a food chain model.

The importance of simple food chain interactions in ecosystem restoration has been well described for aquatic ecosystems. Human-induced eutrophication caused by nutrient loading is a critical problem affecting lakes, resulting in algal blooms, oxygen depletion, and loss of submersed aquatic vegetation (Carpenter et al. 1998). Although nutrient reductions are an obvious approach for improving water quality, food web manipulations can also play a role. The trophic cascade hypothesis was conceived to explain unexplained variance in relationships between nutrient levels and phytoplankton (algae) biomass in lakes, by postulating that changes in predator abundance can "cascade" down the food chain to affect phytoplankton (Carpenter et al. 1985). This realization led to the use of biomanipulation, particularly piscivorous (fish-eating) fish stocking as a lake restoration tool (Hansson et al. 1998). Temperate lakes generally function as four trophic level systems comprising phytoplankton, zooplankton, planktivorous fish, and pis-

civorous fish (Carpenter et al. 1985). Protecting or augmenting populations of piscivores can reduce planktivore biomass, releasing zooplankton from predation, thereby increasing zooplankton grazing rates and decreasing algal biomass. One important way that humans may have amplified the effects of eutrophication has been the reduction of piscivorous fishes due to overfishing and habitat alteration (Post et al. 2002). Along these same lines, restoration of filter-feeding bivalves and oyster reefs offer a means of improving water quality (Beck et al. 2011; Gedan et al. 2014).

In Atlantic Coast salt marshes, predation has traditionally been assumed to be unimportant in regulating marsh plant (*Spartina*) productivity. This view has been challenged by work in mid-Atlantic U.S. marshes demonstrating an important role of periwinkle (*Littoraria*) herbivory in regulating *Spartina* production and biomass (Silliman and Bertness 2002). This suggests that efforts to restore salt marsh communities may benefit from not only restoring hydrology and improving abiotic conditions for plant growth (i.e., nutrient enhancements), but may also be hastened by efforts to manipulate food webs or by tolerating the spread of nonnative predators (green crabs) that prey on marsh grass herbivores (Bertness and Coverdale 2013). For example, augmenting or protecting blue crabs, a major predator of *Littoraria*, appears to benefit *Spartina* restoration efforts (Silliman and Bertness 2002).

The importance of food chain dynamics are being revealed for terrestrial systems (Ripple et al. 2014b). The rapid suburban development in coastal canyons of southern California has diminished and fragmented natural habitats. The mesopredator release hypothesis was proposed to explain the dramatic decline of scrub-breeding birds in these fragments. Crooks and Soulé (1999) reported that coyotes (*Canis latrans*), the top predator in the system, have been extirpated from all but the largest habitat patches. Sites lacking coyote support large numbers of mesopredators (raccoon, grey fox, striped skunk, opossum, domestic cat), which are effective predators on birds and other small vertebrates. An increase in abundance of mesopredators following coyote extirpation in habitat patches explains the recent avifauna declines in these habitat fragments. Based on this work, efforts to restore the avifauna would benefit from managing bird predators, perhaps in combination with efforts to improve bird habitat.

Reintroduction of wolves (*Canis lupus*) into the Greater Yellowstone Ecosystem in the 1990s provided unique insights into the role of food web interactions in structuring the ecosystem. Riparian ecosystems in the Greater Yellowstone Ecosystem (and much of the western United States) have undergone declines over the past century (Beschta and Ripple 2009). An important aspect of this decline has been the recruitment failure of riparian trees such as native cottonwoods and aspens. While a number of explanations have been examined, food web interactions

appear to play a key role in maintaining riparian vegetation structure (Beschta and Ripple 2009; Painter et al. 2015). Wolves were extirpated from Yellowstone in the 1920s, which coincided with riparian tree recruitment failure. The reintroduction of wolves has reduced abundance and altered the foraging behavior of elk (*Cervus canadensis*). Woody plants are now recovering from past unimpeded browsing by herbivores (Beschta and Ripple 2009; Painter et al. 2015). Regeneration of riparian vegetation is having far-reaching implications for the broader ecosystem, including increases in beaver, bison, and avifaunal communities (Ripple and Beschta 2012). Reduction of elk has also led to an increase in berry-producing shrubs, which appears to be benefitting grizzly bears (Ripple et al. 2014a). Finally, there are consequences for aquatic ecosystems, including stabilization of streambanks and strengthened linkages between riparian and riverine habitats (Beschta and Ripple 2012).

Complex Interactions

The above examples illustrate how simple food chains provide useful models for informing ecological restoration. Yet chain-like interactions do not accurately describe many systems, which are often considerably more complex. Here we illustrate the value of recognizing predator-mediated competition (fig. 11-3a) and apparent competition (fig. 11-3b) in a restoration context. In addition to food webs being complex, energy and nutrients also move across habitat boundaries, and can have important dynamic implications (Polis et al. 2004; Richardson and Sato 2015). Top-down control can be dampened or reinforced by resource subsidies from outside the focal habitat, which can cascade to lower trophic levels (Baxter et al. 2005; Richardson and Sato 2015). Recognition of the importance of landscape context and cross-habitat linkages represents an important conceptual shift in food web ecology, with implications for the provisioning of ecosystem services and ecological restoration (Richardson and Sato 2015).

An example of apparent competition in natural systems is the introduction of the brown tree snake (*Boiga irregularis*) to Guam (Savidge 1987). This introduction has caused the near complete elimination of the island avifauna. A simple predator-prey (snake-bird) model would predict snake populations to decline following local extirpation of the avifauna. But *Boiga* are generalist predators, readily consuming alternative prey such as small mammals and lizards. Because of this, *Boiga* has maintained high population densities, even after eliminating bird populations. In effect, the availability of alternative prey sustained high *Boiga* populations through the avifaunal crash, thereby preventing avifaunal recovery.

Islands provide strong evidence for the importance of food web interactions when conducting ecosystem-level restoration. The eight California Channel Is-

lands off the coast of southern California have been the subject of intensive restoration efforts. During much of the nineteenth and twentieth centuries, Santa Cruz Island supported nonnative populations of cattle, sheep and pigs, which adversely impacted the native plant community. Restorationists initiated a program to eradicate cattle and sheep. Following the decline of these two nonnative herbivores, European fennel (*Foeniculum vulgare*) rapidly became the dominant plant species on the island (Zavaleta et al. 2001). This improved the plant forage base for feral pigs, resulting in an increase in pig numbers. Feral pigs have subsequently devastated native plant communities as a result of their digging and grubbing (Power 2001). These interactions would not have been predicted from a simple herbivore-plant model, as they involve direct and indirect interactions among a mix of native and nonnative plants and herbivores.

Food web interactions involving predators on Santa Cruz Island also have restoration significance (Roemer et al. 2001; Roemer et al. 2002). Santa Cruz Island historically supported two carnivores—the endemic (and endangered) island fox and the island spotted skunk. Introduction of feral pigs in the mid-nineteenth century expanded the prey resource base, ultimately allowing the island to be colonized by golden eagles from the mainland. Golden eagles became significant fox predators, and the endemic island fox declined dramatically (Roemer et al. 2002). In turn, skunk populations increased due to competitive release from island fox. Recognizing these more complex food web interactions was key to the subsequent restoration of these island ecosystems (Knowlton et al. 2007). Ultimately, both pigs and eagles had to be removed to allow recovery of the endemic island fox (Collins et al. 2009).

Melero et al. (2014) cautions that restoration of multiple-invaded ecosystems should explicitly consider the interactions between nonnative predators and prey. Following escape from fur farms, American mink (*Neovison vison*) are now established in many areas outside of North America. Crayfish comprise a large portion of mink diets, and mink often reach higher population densities in areas with high invasive crayfish densities. The authors argue that mink will be harder and more costly to eradicate in areas where consumption of nonnative crayfish elevates mink densities. The authors recommend use of information on interactions among nonnative species in the planning of restoration and ecosystem management.

Spatially Linked Food Webs

Because islands are isolated, they tend to be free from the heavy influence of landscape context that can complicate restoration at mainland sites. In addition, islands are conducive to whole-ecosystem experimental approaches to restoration, allowing comparisons between experimental and reference ecosystems (Donlan et al.

2002). Yet the majority of restoration projects occur on mainland systems, meaning that restoration sites are not isolated, but rather are nested within a broader landscape context (Ehrenfeld and Toth 1997). For example, while the boundaries of a wetland restoration site may be easily delimited, this target ecosystem is connected in diverse ways to its surrounding landscape. Nutrients and consumers may be imported or exported from the wetland via streams, while mobile consumers (mammals, birds, insects) move across the wetland boundary. Consumers may be dependent on the restoration site to satisfy some needs, and areas outside the restoration site for others (i.e., feeding grounds, reproductive areas, refuge from predators). While resource managers may have some control over what happens within the boundaries of the restoration site, the broader linkages to the surrounding landscape are likely beyond their control. A food web approach recognizes linkages beyond the boundaries of the restoration site, and includes the broader landscape and ecosystem context of ecological restoration (Ehrenfeld and Toth 1997; Richardson and Sato 2015).

A dramatic example in which the dynamics of distinct habitats are linked by mobile consumers is that of snow geese (*Chen caerulescens*), which migrate between arctic breeding grounds in Canada and wintering grounds in the central United States. (Jefferies 2000; Jefferies et al. 2004). Intensification of agriculture and fertilizer use in the central United States during the past century has shifted snow geese wintering grounds from coastal marshes to agricultural areas. This has subsidized snow goose populations, allowing a 5% annual increase in the population. The effects of this population explosion are readily evident in the coastal breeding habitats around Hudson Bay, Canada, approximately 5,000 km from their winter feeding grounds, producing what has been described as a spatially subsidized trophic cascade (Jefferies et al. 2004). Goose overabundance has intensified grazing and grubbing in breeding grounds. Local impacts range from decreased plant cover and productivity, to the transformation of intertidal salt marshes to bare mudflats—a process involving positive feedback mechanisms analogous to that of desertification (Jefferies 2000; Jefferies et al. 2004). Subsequent changes in ecosystem processes, as well as increased reproductive success of arctic foxes (Giroux et al. 2012), and declines in bird and insect communities have been documented (Jefferies et al. 2004). Restoration of breeding ground habitat would likely necessitate wholesale changes in agricultural management practices in the United States, an unlikely prospect considering the remoteness of the impacted habitat and the vast spatial separation between the two areas. This is a clear example of how the dynamics of spatially separated habitats can be linked (chap. 4), and highlights the need to better understand landscape-level food web linkages (Polis et al. 2004).

In agricultural systems, arthropod predators such as lady beetles, wasps, and spi-

ders are important mobile consumers. The essence of biological control of insect pests in forest or agricultural systems relies on predators inducing trophic cascades to increase crop yields. Yet, modern agricultural landscapes are often dominated by large expanses of intensively managed annual crops, where it can be difficult for predators to maintain adequate populations to suppress pests (Tschamntke et al. 2012). Restoration of nonagricultural (“natural”) habitats as reservoirs for predators in the landscape (Landis et al. 2000) relies on the concept that food webs in unmanaged, nonagricultural areas are linked to agricultural habitats through the movement of mobile predators. In sum, restoration of ecosystem services such as biological control or pollination in agricultural landscapes can be enhanced by understanding the factors that affect landscape-level food webs linkages (Dreyer and Gratton 2014).

Invasions and Reintroductions

Biological invasions are of global concern because of mounting economic and ecological costs (Lodge et al. 2006). Nonnative species can pose major barriers to achieving restoration goals, which are often focused on native species and communities. Yet with accumulating numbers of introduced species, eradication may not be compatible with restoration goals due to food web interactions involving native and nonnative species (case study box 11-1). In addition, nonnative species are not always considered harmful. In the Laurentian Great Lakes, nonnative species have adversely affected native biodiversity, though food chains comprising introduced species now support valuable sport fisheries, and the native predators in these systems are reliant on nonnative prey (Eby et al. 2006). Indeed, nonnative species are sometimes used for achieving desired restoration goals and providing ecosystem functions (Schlaepfer et al. 2011). This does not negate the adverse impacts of invasive species, and reliance on nonnative species warrants thoughtful consideration of costs, benefits, and other constraints to restoration (Schlaepfer et al. 2011).

Once established, many undesirable invasive species are difficult to control since they tend to be *r*-strategists, with high reproductive rates, broad environmental tolerances, and high dispersal abilities (Elton 1958). In addition, systems subject to anthropogenic disturbance, the very sites that often require restoration, tend to be more invasible (Chytry et al. 2008). Invasive species may themselves be an agent of disturbance that can promote further invasions, leading to what has been termed invasional meltdown (Simberloff and Von Holle 1999; chap. 8). A meta-analysis evaluating interactions among invasive animals highlighted the fact that combinations of invasive species can interact to either amplify or mitigate each other's impacts in ecosystems (Jackson 2015). The challenges that invasive

Case Study Box 11-1
Invasive Species on Islands
Apparent Competition and Hyperpredation

Oceanic Islands: The native biota of many island ecosystems evolved in the absence of strong competition and predation, and as a result, islands are often rich in endemic species. Consequently, these insular systems tend to be deeply affected by introduction of non-native species, particularly mammals. Conventional wisdom would suggest that the undesired invasive should simply be controlled as a part of ecological restoration. Yet addition of these invasive species can lead to complex food webs comprising a mix of interacting native and invasive species spanning multiple trophic levels. This creates opportunities for unexpected consequences of invasive species management and control.

Supporting theory: Apparent competition

Bob Holt and colleagues (1977; 1994) greatly advanced the theory of apparent competition, defined as two species interacting indirectly through a shared common predator. As an example, consumption of prey A benefits the predator, thereby leading to increased predation rates on prey B.

Expected outcomes and progress: Numerous studies have highlighted the role of complex interactions such as apparent competition in ecological restoration. Smith and Quin (1996) found that declines of Australian island-dwelling mammals were most severe on islands containing both nonnative predators (cats, foxes) and nonnative prey (rabbits, mice). To explain this, they suggested "hyperpredation," whereby nonnative predators were maintained at high levels due to consumption of nonnative prey, thereby increasing predation on native prey. There have since been several examples: introduction of feral pigs increased predation by native eagles on an endangered fox in the California Channel Islands, and introduced rabbits increase mammal predation on native dryland lizards in New Zealand. Apparent competition and other complex food web interactions are increasingly considered as a factor in species endangerment, and for conservation efforts more broadly.

References: Holt 1977; Holt and Lawton 1994; Smith and Quin 1996.

species pose for large-scale restoration efforts is well illustrated in the Columbia River Basin where recent calls have suggested that it would be prudent to identify and maintain the most productive and resilient food webs (i.e., those food webs with the capacity to buffer and recover from mild perturbations). Such food webs may contain both native and nonnative species that collectively retain function, productivity, and resilience into the future (Naiman et al. 2012).

Several salmonid species have been widely introduced throughout the world. These species have generally been viewed as "desirable" nonnatives since they provide valuable recreational fisheries. As the broader ecosystem and food web

consequences of these introductions have been documented, this perspective is shifting toward a more cautious view of nonnative salmonid introductions (Cucherousset and Olden 2011). A notable example of food web interactions involving nonnative salmonids and native species in a restoration context can be seen in the Colorado River below Glen Canyon Dam in the southwestern United States. The population size of the native humpback chub (*Gila cypha*) has declined precipitously due to multiple factors, including predation by introduced rainbow trout (*Oncorhynchus mykiss*). Stable isotope and dietary studies suggest that suppression of nonnative trout should have a positive effect on native fishes (Whiting et al. 2014). In response, restoration efforts have focused on the removal of rainbow trout and other nonnative fishes, which corresponds with increased survival and recruitment of juvenile native fishes (Coggins et al. 2011).

Although salmonids are common nonnative species, these same trout species are sometimes endangered or extirpated in their native range due to loss of habitat, water quality degradation, exploitation, obstructions to migration, and nonnative species (Gustafson et al. 2007). Not only are trout viewed as "sensitive," but theory indicates that extinction risk increases with body size and trophic level, and that top predators are vulnerable to harvest and habitat degradation (Pimm 1991), making them particularly difficult to recover or reestablish (Neubauer et al. 2013). Indeed, for a species reintroduction to succeed, reintroduced individuals must survive at low population levels, and successfully reproduce in spite of predators, competitors, and pathogens. Although these are the same challenges faced by invasive species, this highlights the need to better understand food web interactions involving nonnative and native species in the context of ecological restoration.

Human alteration of physical processes in ecosystems may also have important food web implications. Restoring or maintaining natural flow regimes is critical for maintaining the integrity of riverine ecosystems (Poff et al. 2010). In Pacific Northwest rivers, human alteration of stream flow patterns has disrupted food web interactions. In response, there has been interest in how linkages between flood disturbance and food chain length in rivers could guide the restoration of riverine food chains (Power et al. 1996), though food web concepts have not been widely applied to stream restoration (Lake et al. 2007). In unregulated streams in the southwestern United States, the natural flooding regime has allowed the continued persistence of native fishes, despite the presence of nonnative predatory fishes (Gido et al. 2013). Similarly, the occurrence of seminatural flow regimes in dammed rivers during high precipitation years resulted in greater dominance of native fishes. Recognition that natural flow regimes promote the persistence of desired native species has been the basis for many large-scale flow releases on the Colorado River and elsewhere around the world (Olden et al. 2014).

Food Web Assembly

Ecological communities are not static entities, but rather are dynamic in composition (chap. 2). Community ecologists have examined whether ecological assembly rules and the order of species introductions govern the composition of ecological communities (chap. 9). Relatively few studies have examined food web assembly involving interacting species across several trophic levels (Thornton 1996), and more generally, a lack of empirical and observational studies has hindered our understanding of food web assembly (Fahimipour and Hein 2014). Simulation models of food web assembly have been equivocal with regard to how food web complexity influences resistance to invasive species (Drake 1990b; Lurgi et al. 2014).

Microcosm studies generally find that changing the sequence of species introduction can produce very different community outcomes (Robinson and Dickerson 1987; Drake 1990a). For example, a species that is competitively dominant under one set of circumstances may be unable to establish given a different assembly scenario (Drake 1990a). Further, mesocosm experiments have found that arrival order can influence the flux of material through different trophic pathways—an important component of ecosystem function. Assembly of grassland food webs was found to be regulated by both spatial conditions and trophic relationships (Harvey and MacDougall 2014). Generalist guild establishment was more dependent on spatial isolation of patches whereas specialists tend to establish in larger patches with more diverse plant communities. Though the applicability of food web assembly to ecosystem restoration efforts remains uncertain, this work suggests that species diversity, food web connectivity, and introduction sequence are likely to be important considerations (for more on assembly theory, see chap. 9).

An example of food web assembly concepts being incorporated into ecological restoration involves lake restoration efforts in Ontario, Canada. Following the successful control of industrial sulfur emissions in the region, lake pH has improved to levels (pH > 5.5–6.0) capable of supporting top predators such as lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieu*). The success of predator reintroduction has been examined in acid-recovering Ontario lakes. Trout recovered rapidly in lakes with few fish species, while in species-rich systems, lake trout were slow or unable to reestablish. This suggested that community attributes or reintroduction order (priority effects) played a role in the recovery of this species. In contrast, reintroduced smallmouth bass established rapidly, regardless of community composition (Snucins and Gunn 2003). Smallmouth bass have well-documented predatory impacts on forage fishes and adverse competitive impacts on lake trout (Vander Zanden et al. 1999). Restoration of fish assemblages in these lakes will require further attention to priority effects and

the order of species reintroductions. In acid-recovering lakes, lake trout should be reintroduced early in the reassembly process (Snucins and Gunn 2003), although such a strategy may limit the subsequent chance of successfully establishing native prey fishes that are vulnerable to lake trout predation.

New Food Web Tools and Ecological Restoration

A common goal in restoration ecology is to reestablish impaired or lost functionality in ecosystems. Species are essential building blocks of communities, and reestablishing their interactions is critical to restoring function to degraded ecosystems (Gray et al. 2014). Restoration of food web interactions is a potential restoration goal that incorporates aspects of ecosystem structure and function and is starting to be used as a restoration monitoring tool (Wozniak et al. 2006; Kovalenko et al. 2013). Thus, in addition to monitoring for the presence or absence of species, identifying what critical interactions need to be restored and whether this has occurred is increasingly recognized in restoration ecology. Unfortunately, identifying species interactions is challenging, especially in species-rich communities, or when organisms have cryptic life stages (e.g., parasites). As a result, indirect approaches to elucidating trophic interactions are becoming widespread and can provide insights on the nature, diversity, and strength of interactions among species (Traugott et al. 2013).

Use of stable isotope techniques to infer trophic flows in food webs is widespread (Peterson and Fry 1987). Ratios of stable isotopes ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) vary predictably from resource to consumer tissues. Differences in plant $\delta^{13}\text{C}$ are preserved in consumer tissues, such that $\delta^{13}\text{C}$ is an indicator of the sources of carbon in food webs. In contrast, protein biosynthesis and catabolism tend to excrete the lighter N isotope, resulting in a 3%–4‰ enrichment of $\delta^{15}\text{N}$ from prey to predator. Nitrogen isotopes are used to infer trophic position of consumers (Vander Zanden and Rasmussen 2001).

Stable isotopes provide a powerful tool for monitoring and evaluating food web linkages, greatly facilitating the incorporation of food web approaches into restoration ecology (Wozniak et al. 2006; Kovalenko et al. 2013; Howe and Simenstad 2015). For example, Gratton and Denno (2006) used stable isotopes to monitor arthropod food webs in New Jersey salt marshes that had been restored to *Spartina* following the extirpation of invasive *Phragmites*. The trophic position of most consumers including the top predatory spiders were indistinguishable from those in reference *Spartina* habitats with no history of *Phragmites* invasion (fig. 11-4), indicating that trophic interactions among arthropod consumers had been largely reestablished in restored habitats in less than five years. Stable isotope data suggested that consumers used resources primarily from the habitat where they

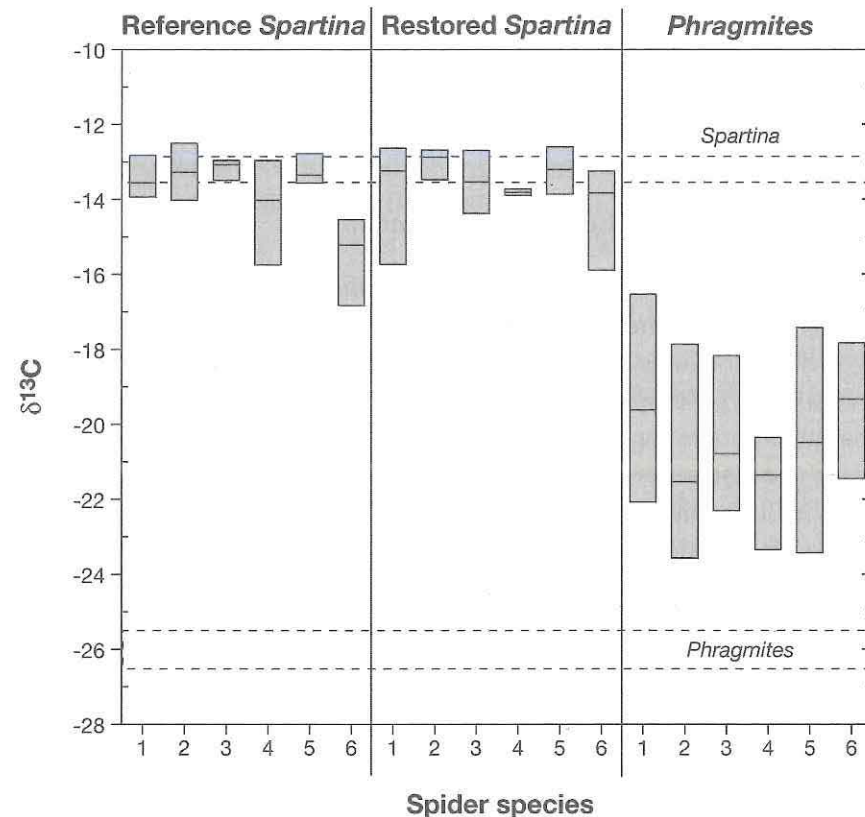


Figure 11-4. $\delta^{13}\text{C}$ stable isotope box-plot (median and interquartile range) of dominant spider predators from reference *Spartina*, restored *Spartina*, and *Phragmites*-dominated habitats within the Alloway Creek Watershed Restoration site (Salem County, New Jersey, US). Dotted lines indicate the ranges of the basal resources (*Phragmites* or *Spartina*) in each habitat. Spiders in restored habitats are feeding on *Spartina*-based resources (herbivores and other predators) and are indistinguishable from the same species found in reference habitats while *Phragmites*-collected spiders are feeding on non-*Phragmites* based resources, likely detritivores. Spider species are (1) *Tetragnatha* sp.; (2) *Pachygnatha*; (3) *Grammonota trivittata*; (4) *Hentzia* sp.; (5) *Clubiona* sp.; (6) *Pardosa* sp. Based on Gratton and Denno (2006).

were collected, and that as habitats were restored, predators integrated into local food webs.

Stable isotopes have been used to assess the restoration of southern California salt marshes (Kwak and Zedler 1997). Marsh-derived algae and vascular plants, particularly *Spartina*, are important energy sources for invertebrates and fish (Kwak and Zedler 1997; Desmond et al. 2000), supporting the idea that these habitats should be managed as a single ecosystem. Mitigation and restoration projects in southern California coastal areas have focused either on the creation of basin or

channel habitat for fishes, or alternatively, the creation of coastal salt marshes as habitat for endangered birds. Although both are valid restoration targets, restoration of habitat for fishes and endangered birds may have erroneously been viewed as a competing objective (Kwak and Zedler 1997). Considering the food web linkages between these two habitats, restoration might more productively focus on the creation of integrated channel-tidal salt marsh systems to accomplish both restoration objectives.

Food web approaches are also valuable for assessing the restoration potential of freshwater ecosystems. Vander Zanden et al. (2003) characterized historical food web changes in Lake Tahoe (California, US) using stable isotope analysis of contemporary and preserved museum specimens. The introduction of nonnative freshwater shrimp (*Mysis relicta*) and lake trout disrupted pelagic food web structure. These two nonnatives are thought to limit the restoration potential of native Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*) in Lake Tahoe. Food webs in two nearby headwater lakes are relatively intact despite some nonnative species introductions, and stable isotopes indicate that food webs in these lakes resemble that of Lake Tahoe prior to nonnative species introductions (Vander Zanden et al. 2003). These relatively unaltered lakes are ideal candidates for Lahontan cutthroat trout reintroduction, and provide an opportunity to examine whether historical food web niches are regained when species are reestablished (Vander Zanden et al. 2003). The above studies demonstrate the value of stable isotopes as a tool for documenting how food webs have been altered, identifying energy sources for key species, and assessing food web recovery as systems move along restoration trajectories. Newer approaches such as compound-specific stable isotope analysis appear to be more accurate and robust to assumptions for inferring trophic position and hold great promise in the analysis of food web structure (Chikaraishi et al. 2009).

The molecular revolution has made DNA-based techniques more available to ecologists for reconstructing the diets of consumers (Pompanon et al. 2012; Clare 2014). By amplifying genes that are common to a range of potential prey, for example, insects prey for bats (Clare et al. 2011), and comparing sequences to existing DNA libraries of known species, it is possible to reconstruct the presence or absence of particular species within the diet of a consumer. These approaches are becoming more widespread and provide insights into the feeding associations of insects on plants (García-Robledo et al. 2013), predators on prey (Piñol et al. 2014), parasites on hosts (Hreck et al. 2011), and pollinator visitation of flowers (Keller et al. 2015). In general, molecular-based approaches tend to identify many more species interactions than were previously recognized, forcing us to fundamentally reconsider how food webs are structured (Wirta et al. 2014). One key limitation of these approaches is that they tend to reveal the presence-absence

of interactions. This makes it challenging to understand the relative importance of food web links, though semiquantitative methods (e.g., the proportion of individuals that feed on a particular diet item) can be used to infer the energetic importance of food web links (Clare 2014). Despite some limitations, the novel insights provided by molecular methods can complement traditional approaches and provide a more complete picture of food web.

Areas of Research Need and Opportunity

While the field of ecological restoration builds on key areas of ecological theory such as community succession, population biology, and alternative stable states, other areas, including food web ecology, are only now being integrated into ecological restoration (Memmott 2009; Montoya et al. 2012). In this chapter, we have discussed how consideration and understanding of food webs can contribute to ecological restoration. Here, we identify some of the challenges and opportunities likely to be encountered in the application of food web ecology to ecological restoration.

Food Web Experiments and Adaptive Management

In some ecosystems, predation is critical in structuring ecosystems, while in other ecosystems habitat and resource availability drive ecosystem dynamics. How can we identify ecosystems in which predation and top-down forces are important for structuring the food web? Experimental manipulations of consumers and resources can be used to examine this, though in many systems the necessary manipulations are not practical or feasible. Observational studies and a “natural history” understanding of a system can provide some basis for identifying what factors are responsible for structuring a food web, though important food web interactions may simply not be apparent without experimentation. In the absence of experimentation, there remains a need to understand whether ecosystems are dominated by top-down (predation) or bottom-up (productivity) forces, how these factors interact, and the role of indirect and other complex food web interactions. The above issues are difficult to resolve because ecological restoration projects are typically carried out at the ecosystem level, while much of ecology is based on small-scale, highly replicated experiments. Can we scale up from small-scale experiments to the management and restoration of real ecosystems? Small-scale experiments suffer from “cage-effects,” whereby the results are artifacts of experimental conditions. Findings cannot be generalized or “scaled up” to real ecosystems. Small-scale approaches are also likely to fail to capture relevant food web processes such as cross-habitat linkages, complex trophic interactions, and the

role of mobile predators. One obvious alternative is to conduct large-scale, whole-ecosystem manipulations (Carpenter et al. 1995). Restoration projects provide unique opportunities for whole-ecosystem experiments within an adaptive management, “learning-by-doing,” framework (Holl et al. 2003). Such experiments speed the accumulation of knowledge about food webs and the response of ecosystems to management actions, and hasten the application of ecological knowledge to restoration (Donlan et al. 2002). In addition, ecological restoration can improve basic understanding of food webs and inspire new directions in food web theory with more direct relevance to ecosystem management (Palmer et al. 1997).

The Backdrop of Nonnative Species and Global Change

Although the restoration potential of many ecosystems may be high, accelerating species invasions may severely limit prospects for achieving restoration goals (Donlan et al. 2003). Combined with global climate change, it is certain that existing food webs will be torn apart, and new food webs will be reassembled (Lawton 2000). The “rules of engagement” in food webs and ecosystems will change, yielding completely new outcomes and interactions. Restoring ecosystems within the context of the shifting backdrop of climate change and nonnative species seriously confounds the task at hand, necessitating a more complete incorporation of food web, landscape, and ecosystem perspectives. Restoration ecology draws increasingly from the field of invasion biology, and is demanding improved methods for controlling undesirable nonnative species. Perhaps a more critical challenge will be to find ways to manage ecosystems so as to maintain native species and ecosystem services in the face of invasive species. In some cases, reliance on nonnative species may be crucial for promoting restoration of ecosystem services and energy flows to higher trophic levels, and food web approaches will figure prominently into assessing the value and viability of such efforts (Schlaepfer et al. 2011).

Closing Remarks

The study of food webs is a long-standing and rapidly expanding subfield of ecology with the goal of understanding and predicting multispecies interactions. Though ecologists recognize the interconnectedness of species in ecosystems, new tools and new paradigms are allowing advances in our understanding of food web interactions, particularly the role of predation and indirect effects in structuring ecosystems. Restoration of food web interactions may not necessarily follow restoration of the plant community or physical habitat features (i.e., the “field of dreams” paradigm—that is, “build it, and they will come” [Palmer et al. 1997]). While restoration of habitat is critical, it is not guaranteed that the desired consumer taxa

will recolonize and food webs will assemble as expected. Invasive species can be a barrier to achieving restoration goals. We present several examples in which food web interactions affect ecosystem attributes, with important implications for ecological restoration. Viewing restoration at the whole-ecosystem level and incorporating a food web perspective can contribute in a real way to ecological restoration efforts. We offer that further advances will derive from restorationists incorporating "food web thinking" into restoration projects, and treating restoration projects as ecosystem experiments (see also chap. 13). Food web ecology has demonstrated the value of more holistic approaches for understanding species and ecosystems, lessons that will undoubtedly contribute toward efforts to restore ecosystems.

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