

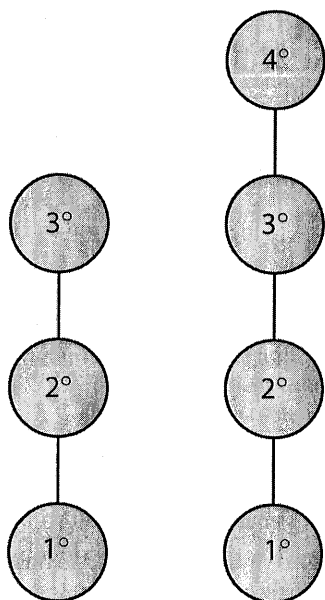
Food-Web Approaches in Restoration Ecology

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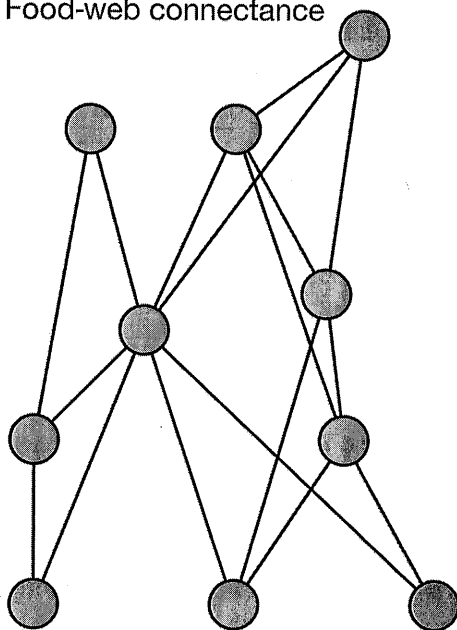
No species exists in a vacuum. Rather, each species is embedded within a network of predator-prey interactions in what Charles Darwin referred to as an “entangled bank” and is now known in the most general sense as a *food web*. In its most basic form, a food web reveals to us something about the feeding relationships in a system. More broadly, food webs represent a way of thinking about an ecological system that considers trophic (consumer-resource) interactions among species or groups of similar species (trophic guilds or trophic levels). Food-web ecology is an ever-changing subdiscipline of ecology, and it is critical to recognize the diversity of approaches to the study of food webs (Paine 1980; Schoener 1989; Pimm 1991; Polis and Winemiller 1996). The term *food-web structure* can have several meanings to food-web ecologists. Food-web structure can refer simply to the number of trophic levels in a food chain (Figure 8.1a) or, alternatively, can represent the degree of complexity in a food-web network (Figure 8.1b). Food-web diagrams may be used to represent the pathways of energy flow through a system (energetic webs, Figure 8.1c) or, alternatively, the dynamically important linkages for regulating trophic structure (functional webs, Figure 8.1d). An alternative meaning of food-web structure refers to the distribution of biomass across different trophic levels, and ultimately how bottom-up and top-down factors regulate the accumulation of biomass across trophic levels (Figure 8.2a–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 have yet to take hold in many applied management endeavors, such as fisheries and wildlife management, conservation biology, and ecological restoration. We argue that food-web ecology has the potential to contribute to ecological restoration by encouraging a more dynamic, interaction-driven view of ecosystems, and it can alert practitioners to the types of trophic interactions that may have bearing on restoration outcomes (Zavaleta et al. 2001). In some situations, adopting 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 recent reintroduction of wolves into Yellowstone Park, Wyoming, USA, has precipitated a cascade of food-web changes that has allowed the recovery of riparian vegetation and associated biota from damaging effects of herbivore overgrazing (Berger et al. 2001; Ripple et al. 2001; Ripple and Beschta 2003), an effect that would not

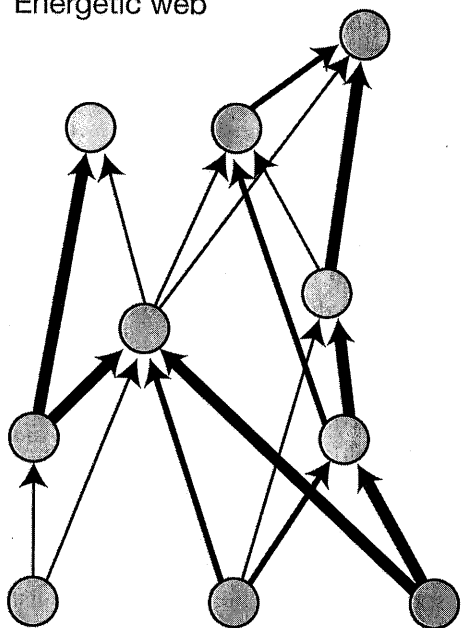
A
Number of trophic levels



B
Food-web connectance



C
Energetic web



D
Interaction web

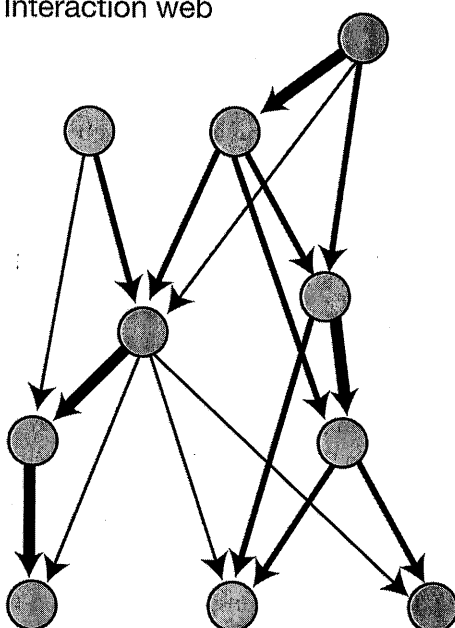
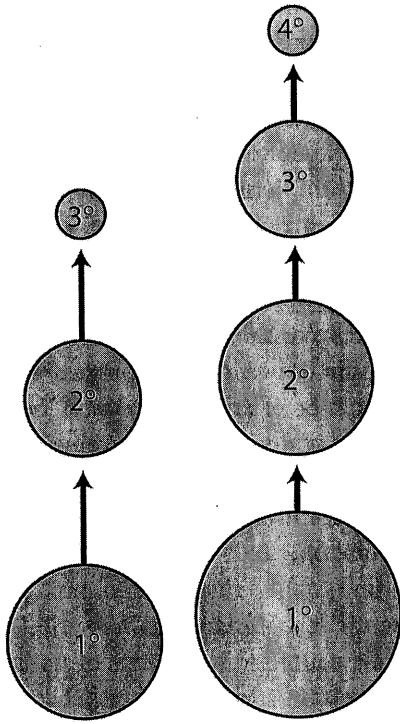


FIGURE 8.1 Different meanings of “trophic structure” used by food-web ecologists: (A) number of trophic levels (three versus four levels); (B) food-web connectance, the pattern of trophic linkages among species in a complex web; (C) energetic web, depicting the pathways of mass or energy flow; and (D) interaction web, showing the dynamically important food-web linkages.

A
Bottom-up control



B
Top-down control

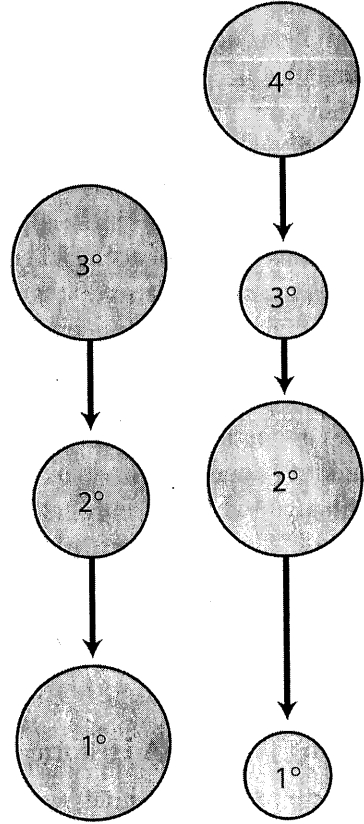


FIGURE 8.2 Bottom-up versus top-down control of the distribution of biomass at different trophic levels. Note that compartment size indicates trophic level biomass: (A) In the case of bottom-up control, primary production is the basis for higher trophic levels. Increasing primary production allows higher 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°).

have been predicted without considering the cascading effects of predator-prey interactions across multiple trophic levels.

Many of the world's ecosystems are highly degraded, and natural recovery processes, particularly in light of the onslaught of biological invasions, are often inadequate to achieve desired goals for ecosystem recovery (Dobson et al. 1997; Hobbs and Harris 2001; D'Antonio and Chambers, this volume). Ecological restoration is undertaken to hasten the recovery of damaged ecosystems, restore ecosystem function, and slow the declines of biodiversity (Jordan III 1987; NRC 1995; Dobson et al. 1997; Young 2000). Restoration in North America has its historical roots in plant community ecology: a perusal of the leading journals in the field such as *Ecological Restoration* and *Restoration Ecology* reveals the botanical nature of the discipline.

As such, succession and community assembly theory have provided the theoretical underpinnings for restoration ecology (Weiher and Keddy 1999; Young 2000; Young et al. 2001). While food-web ecology is often viewed as a subdiscipline of community ecology, community and food-web ecology differ in several significant ways. Community ecologists generally study the factors affecting abundance, species composition, and diversity within a particular trophic guild or group (i.e., the bird community, the plant community) (Drake 1990; Suding and Gross, this volume; Menninger and Palmer, this volume). In contrast, food-web studies consider the energetic and dynamic linkages within a broader spectrum of the ecological community, and the scale of analysis typically spans several trophic levels.

A critical aspect of ecological restoration is the establishment of well-defined restoration targets (Hobbs and Harris 2001). The traditional approach emphasizes *structural* restoration targets, including taxonomic characteristics, such as species richness, or the presence or abundance of indicator species or assemblages. Yet the mere presence of desired taxa or functional groups does not mean that the restored system is functioning as desired, or that the species are performing ecologically relevant roles within the restored system. Thus, a complementary approach considers *functional* targets, which include ecosystem processes, such as primary production, nutrient cycling, and the maintenance of critical food-web linkages (Palmer et al. 1997). 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, more informally, “food-web thinking” might contribute fruitfully 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 on food-web ecology, we recommend the following sources: Schoener (1989); Pimm (1991); Polis and Winemiller (1996); Persson (1999); Post (2002); and Polis et al. (2004).

Among the first published food web studies was Summerhayes and Elton’s description of the food webs of Spitsbergen and Bear Islands (Summerhayes and Elton 1923; Elton 1927). The next major advance in food-web ecology was undoubtedly Lindeman’s (1942) trophic-dynamic study of a small Minnesota lake. Lindeman viewed the lake as a chain of energy transformations—solar energy was “fixed” via photosynthesis, a portion was converted to herbivore biomass, and so on up the food chain. Decreasing production was available at successive trophic levels due to metabolic inefficiencies at each trophic step. In this view, primary production limited higher trophic level production, suggesting “bottom-up” control of the distribution of biomass in food webs (Figure 8.2a). This work provided the operational structure for modern food-web research by introducing the concept of trophic levels as well as 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), an idea that serves as a basis for assessing whether the energetic needs of higher consumers (often the target of restoration efforts) are likely to be met within a restored ecosystem. Lindeman’s ideas also raise the issue of whether variables such as food-chain length could be used as a meaningful restoration endpoint.

Two decades later, a study by Hairston, Smith, and Slobodkin (1960) (now known as HSS) 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 in HSS was predicated on the idea that predators control the abundance of their prey, and that these effects can subsequently cascade down food chains, ultimately impacting primary producer biomass (Figure 8.2b). This radical proposition ran counter to the dominant paradigm of the time: that nutrients and/or environmental factors limited plant communities and biomass, which, in turn, constrained higher trophic levels (compare Figure 8.2a and 8.2b). HSS has since inspired major research efforts directed toward the role of predators and resources as determinants of the abundances of organisms at different trophic levels in a variety of ecosystem types (Oksanen et al. 1981; Fretwell 1987; Power 1992; Hairston and Hairston 1993; Polis and Strong 1996; Polis 1999). 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 biomass. In fact, both processes likely operate concurrently and often interact in complex ways (Denno et al. 2003).

Studies predicated upon simple food-chain models have played an important role in ecology. Not only do such models generate easily testable predictions, but many natural systems appear to exhibit dynamics consistent with simple food-chain structures (Oksanen et al. 1981; Carpenter et al. 1985). Interestingly, many descriptive food-web studies offer the paradoxically different view that food webs are immensely complex—with hundreds of species and trophic links, coupled with rampant complications such as ontogenic diet shifts, omnivory, and intraguild predation (Warren 1989; Hall and Raffaelli 1991; Martinez 1991; Polis 1991). In addition, trophic levels themselves are often heterogeneous, such that the addition of grazers to a system may reduce plant biomass or, alternatively, may cause a compensatory shift toward grazer-tolerant plants (Leibold 1989; Hunter and Price 1992). While simple food-chain models undoubtedly overlook certain trophic linkages and interactions, the critical issue to be resolved is whether these complexities are mere details or, alternatively, when and if these trophic linkages are truly important in driving the dynamics of the system (Power 1992).

To understand food-web dynamics, it is critical to distinguish between direct and indirect food-web effects (Abrams et al. 1996). An example of a direct effect is that an increase in species A reduces the density of species B due to predation. An indirect effect implies a change in the density of species B in response to a change in species A, but through interactions with a third species. The three trophic level interaction proposed in HSS (Figure 8.2b) described above is a simple indirect effect (changes in predators affect plant biomass through impacts on herbivores). In the rocky intertidal zone, Robert Paine’s (1966) seminal food-web experiments demonstrated that predation by the Ochre sea star (*Pisaster ochraceus*) upon 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 (Figure 8.3a). Paine labeled *Pisaster* a “keystone species” due to its role in structuring the community. The implication here was that all species are not equally important, and that a few species play central roles in structuring the system (Power et al. 1996c; Lawton 2000). Apparent competition is another type of indirect interaction, whereby two prey species share a common predator, and predation rates on a focal prey species are *increased* due to the presence of the alternative prey (Figure 8.3b) (Holt

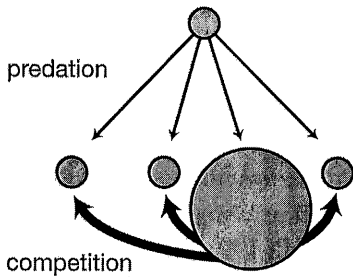
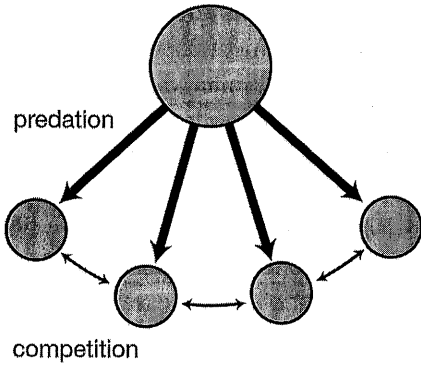
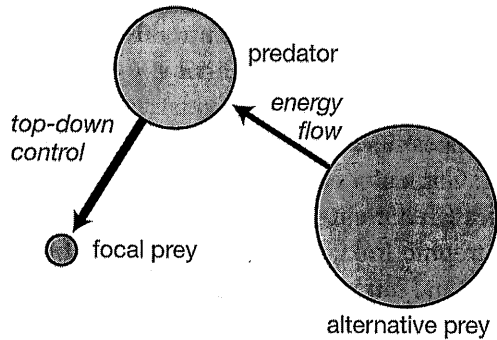
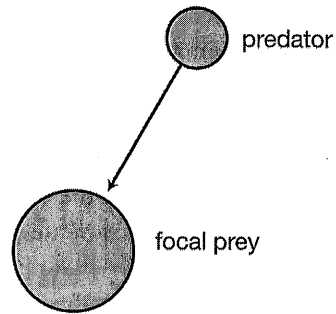
A
Predator-mediated competition**B**
Apparent competition

FIGURE 8.3 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.

1977; Holt and Lawton 1994). If the vulnerability of the two prey differs, consumption of a less vulnerable, abundant prey can have the effect of augmenting the predator population, subsequently increasing predation rates on the more vulnerable prey (Holt 1977; Holt and Lawton 1994).

Application of Food-Web Theory to Restoration Ecology

Restoration ecology has historically been based on a succession-driven, bottom-up view of ecosystems, and current paradigms in ecological restoration do not generally incorporate a food-web perspective. Even if restoration targets do not specifically involve the reestablishment of trophic linkages per se, there may be value in food-web approaches, since the dy-

TABLE 8.1

Areas of food-web research and applications to restoration ecology discussed in this chapter.	
Section	Key references
<i>Food-chain approaches</i>	
Ecosystem role of predators	Pace et al. 1999; Soulé and Terborgh 1999
Trophic cascades in lakes	Carpenter et al. 1985
Trophic control in salt marshes	Silliman and Bertness 2002
Mesopredator release	Crooks and Soulé 1999
Trophic control in Yellowstone NP	Beschta 2003
<i>Complex Interactions</i>	
Apparent competition in Guam	Savidge 1987
Complex interactions in Channel Islands	Roemer et al. 2003
Landscape context in Hudson Bay	Jeffries et al. 2004
<i>Invasions and reintroductions</i>	
Trout introductions and restoration	Knapp et al. 2000
Natural flow regimes	Poff et al. 1997
<i>Food-web assembly</i>	
Food-web assembly in recovering lakes	Gunn and Mills 1998
<i>Applications of stable isotopes</i>	
Recovery of salt marsh food webs	Kwak and Zedler 1997
Long-term food-web change in Lake Tahoe	Vander Zanden et al. 2003

namics of any species or community depend critically on interactions among prey and predators (Pimm 1991). For example, identifying keystone species may be of concern in restoration, since they play a critical role in determining community and ecosystem structure (Mills et al. 1993; Power et al. 1996c). Table 8.1 lists the major areas of food-web research examined in this chapter, with potential applications to restoration ecology.

Food-Chain Approaches

There is growing evidence that top predators can have impacts that cascade to lower trophic levels (Pace et al. 1999). In aquatic systems, the decline of top predators (Post et al. 2002) can have cascading effects on lower trophic levels (Carpenter et al. 2001). Similarly, predation is now recognized as a key process in the maintenance of biodiversity and ecosystem function in terrestrial systems (Soulé and Terborgh 1999). Terrestrial conservation biologists and limnologists are recognizing the importance of predation in structuring ecosystems and are focusing efforts on restoring or maintaining predation as a component of ecological restoration efforts. Below, we present several examples where an ecosystem was viewed through the lens of a simple food-chain model, with important implications for ecological restoration.

The importance of simple food-chain interactions in ecosystem restoration has been most thoroughly described for aquatic ecosystems. Human-induced eutrophication caused by excess nutrient loading is a critical environmental problem affecting lakes, resulting in algal blooms, oxygen depletion, loss of aquatic vegetation, and declines in water quality (Carpenter et al. 1998). While nutrient reductions are an obvious approach for improving water quality,

food-web manipulations can also play an important role. The trophic cascade hypothesis (Carpenter et al. 1985) 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. This recognition of the role of predators in lake ecosystems has led to the use of biomanipulation, particularly the stocking of piscivorous (fish eating) fishes as a lake restoration tool (Shapiro et al. 1975; Jeppesen et al. 1997; Hansson et al. 1998). North-temperate lakes generally function as four trophic level systems comprised of phytoplankton, zooplankton, planktivorous fish, and piscivorous fish (Carpenter et al. 1985). A common goal of biomanipulation is to alter the food web to increase zooplankton grazing, thus reducing the accumulation of algal biomass. Reduction of planktivore biomass “releases” zooplankton from predation, allowing larger and more abundant zooplankton. Reducing planktivore biomass can be achieved by protecting or augmenting populations of piscivorous fishes (Horppila et al. 1998). An important impact of humans on lakes has been the reduction or elimination of piscivore populations due to overfishing and habitat alteration (Post et al. 2002). This decline of piscivores has likely amplified eutrophication effects as a result of changing food-web interactions.

In contrast with lakes, where it is recognized that nutrients and food-web interactions both play a role in determining plant biomass and productivity, predation in Atlantic Coast salt marshes has traditionally been assumed to be unimportant in regulating marsh plant (*Spartina*, cordgrass) productivity. This view has been challenged recently, as work in mid-Atlantic U.S. marshes has demonstrated an important role of periwinkle (*Littoraria*) herbivory in regulating *Spartina* production and biomass (Silliman and Zieman 2001; Silliman and Bertness 2002). This suggests that efforts to restore salt marsh communities may benefit from not only the traditional approach of restoring the system’s hydrology and improving abiotic conditions for growth (i.e., nutrient enhancements), but may also be hastened by efforts to manipulate food-web interactions. For example, a temporary reduction of *Littoraria* abundances at restoration sites would benefit *Spartina* growth due to reduced grazing and scarring. Based on simple food-chain concepts, augmenting or protecting populations of blue crabs, a major predator of *Littoraria*, would also be expected to benefit *Spartina* restoration efforts (Silliman and Bertness 2002).

Similar patterns of relatively simple food-chain dynamics have been revealed in terrestrial systems. For example, the rapid suburban development in coastal canyons of southern California has left little remaining habitat, and what remains is highly fragmented. 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 coyotes support large numbers of small carnivores (raccoon, grey fox, striped skunk, opossum, domestic cat), which are effective predators on birds and other small vertebrates. An increase in abundance of these mesopredators following the extirpation of coyotes in habitat patches is the likely explanation for the recent avifauna decline in these habitat fragments. Based on this work, efforts to restore the avifauna would not be expected to respond to restoration efforts aimed at improving bird habitat; managing bird predators would perhaps be a more productive approach.

In a similar way, ecologists have recently elucidated the central role of top predators in structuring terrestrial food web in the Rocky Mountains of the western United States. Ripar-

ian ecosystems in the Greater Yellowstone Ecosystem (and much of the western United States) have undergone declines over the past century (Ripple et al. 2001; Ripple and Beschta 2003). An important aspect of this decline has been the unexplained recruitment failure of riparian trees such as native cottonwoods and aspens. While a number of possible explanations have been examined, evidence is emerging that food-web interactions play an important role in maintaining riparian vegetation structure (Beschta 2003). More specifically, wolves were extirpated from Yellowstone in the 1920s, which coincided with riparian tree recruitment failure. Reintroduction of wolves in the mid-1990s has altered the foraging behavior of elk (Ripple et al. 2001; Ripple and Beschta 2003); where elk are vulnerable to wolf predation, woody plants are now recovering from past unimpeded browsing by herbivores. Emerging evidence suggests that the regeneration of riparian vegetation associated with wolf reintroductions may have far-reaching positive effects on the broader riparian ecosystems. There is an expectation of long-term benefits to avifaunal communities by improving bird nesting habitat (Berger et al. 2001). Benefits are also expected for aquatic ecosystems, including stabilization of stream banks, strengthened linkages between riparian and riverine habitats, and moderation of water temperatures (Osborne and Kovacic 1993).

Complex Interactions

The above examples illustrate how simple food chains can be useful models for guiding ecological restoration efforts. Yet chain-like interactions may not accurately describe many systems, which are often considerably more complex. Here, we illustrate the value of recognizing food-web complexity, predator-mediated competition, and apparent competition in a restoration context. In addition to food webs being complex, energy and nutrients also move across habitat boundaries and may have important dynamic implications (Polis et al. 2004). Top-down control can be dampened or reinforced by energy “subsidies” from outside the focal habitat, which can cascade to lower trophic levels (Nakano et al. 1999; Polis 1999; Nakano and Murakami 2001). Recognition of landscape context and cross-habitat linkages represents an important conceptual shift in food-web ecology of the past decade (Polis et al. 2004) with potential implications for ecological restoration.

An example of apparent competition in natural systems is the introduction of the exotic 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, thereby preventing avifaunal recovery.

Studies on islands provide strong evidence for the importance of food-web interactions when conducting ecosystem-level restoration. The eight California Channel Islands off the coast of southern California have been the subject of intensive restoration efforts during recent years. During much of the nineteenth and twentieth centuries, Santa Cruz Island supported exotic 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 exotic herbivores, European fennel (*Foeniculum vulgare*) rapidly be-

came 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 a series of direct and indirect interactions among a mix of native and exotic 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 (*Urocyon littoralis*) and the island spotted skunk (*Spilogale gracilis amphiala*). Introduction of feral pigs in the mid-nineteenth century expanded the prey resource base, ultimately allowing the island to be colonized by golden eagles (*Acquila chrysaetos*) from the mainland. Golden eagles have since become significant fox predators, with the result that the endemic island fox has declined dramatically (Roemer et al. 2002). In turn, skunk populations have increased due to competitive release from their main competitor, the island fox. As with the fennel-pig interactions described above, recognizing these more complex food-web interactions will be a central part of developing a restoration strategy for these island ecosystems. These examples demonstrate the potential role of indirect food-web interactions in determining ecosystem response to restoration. Simple food-chain models would not have predicted the observed changes, thus underscoring the importance of being familiar with the other types of food-web interactions.

Because islands are isolated ecosystems, they are free from the heavy influence of landscape context that can complicate restoration at mainland sites. In addition, islands are conducive for 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 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 broader landscape context. Nutrients and consumers may be imported or exported from the wetland via a connecting stream, 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 restorationists 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; Nakano and Murakami 2001).

A dramatic example in which the dynamics of distinct habitats are linked by mobile consumers is that of lesser snow geese, which migrate between arctic breeding grounds in Canada and wintering grounds in the central United States (Jefferies 2000; Jefferies et al. 2004). Intensification of agricultural activities and fertilizer use in the central United States during the past century has shifted snow goose wintering grounds from coastal marshes to agricultural areas. In effect, this has subsidized snow goose populations, allowing a 5% annual increase in snow goose population size. 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. The local impacts of this 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 declines in bird and insect communities have also 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 closely linked trophically, and it highlights the need to better understand landscape-level food-web linkages (Polis et al. 2004).

Invasions and Reintroductions

Biological invasions are of global concern because of mounting economic and ecological costs (Lodge and Shrader-Frechette 2003). Exotic species can pose major barriers to achieving restoration goals, which are often focused on native species and communities (D'Antonio and Chambers, this volume). Yet with accumulating numbers of exotics, eradication may not be compatible with restoration goals due to food-web interactions involving native and exotic species (Box 8.1). In addition, exotics are not always considered harmful (Ewel and Putz 2004). In the Laurentian Great Lakes, exotics have adversely affected native biodiversity, though food chains comprising exotic species now support valuable sport fisheries, and the native predators in these systems are now partially reliant on exotic prey (Kitchell et al. 2000). Indeed, non-native species are sometimes used for achieving desired restoration goals and providing ecosystem functions (Ewel and Putz 2004). This does not negate the adverse impacts that exotic species have had on global biodiversity (Wilcove et al. 1998), and reliance on exotics warrants thoughtful consideration of costs, benefits, and other constraints to restoration. 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, "disturbed" systems, the very sites that require restoration, are more likely to be invasible (Mack et al. 2000), and invasive species may themselves be an agent of disturbance that can promote further invasions, leading to what has been termed an invasion "meltdown" (Ricciardi and MacIsaac 2000). There are also many cases where exotics prevent the reestablishment of desired native species (Simberloff 1990; Vitousek 1990), whose recovery is often a primary goal of ecological restoration (Bowles and Whelan 1994).

Several trout species (brown trout, brook trout, lake trout, rainbow trout) have been widely introduced throughout the world. These species have generally been viewed as "desirable" exotics since they provide valuable recreational fisheries. Yet as the broader ecosystem and food-web consequences of these introductions have been documented, this perspective is shifting toward a more cautious view of trout introductions (Flecker and Townsend 1994; Knapp et al. 2000; Schindler et al. 2000). A notable example of food-web interactions involving exotic trout and native species in a restoration context can be seen in the

Box 8.1

Complex Food Webs and Management of Exotic Species

Conventional wisdom suggests that undesired exotics should be controlled during restoration. But this may not always be the preferred course of action (Ewel and Putz 2004), and the ever-increasing numbers of invaders makes removal decisions more complex. What happens when a desired native animal species comes to depend on an exotic plant for feeding or nesting habitat (Zavaleta et al. 2001)? This was the case in the southwestern United States, where declines in native riparian vegetation forced the endangered Southwestern willow flycatcher (*Empidonax traillii extimus*) to rely on exotic salt cedar *Tamarix* for habitat. Removal of *Tamarix*, in the absence of concurrent efforts to restore native vegetation, would likely adversely affect this endangered species, underscoring the need for thoughtful consideration of secondary effects of invasive species removal.

Another concern is the growing number of systems with several exotics interacting at different trophic levels. Again, food-web interactions may be such that exotic species control may have unexpected consequences for desired native species. Although there are many scenarios, Smith and Quin (1996) reported that declines of Australian island-dwelling mammals were most severe on islands containing both exotic predators (cats, foxes) and prey (rabbits, mice). To explain this pattern, they proposed a "hyperpredation" hypothesis, in which exotic predator populations were maintained at artificially high levels due to consumption of exotic prey, thereby increasing predation rates on native prey species. This process is analogous to apparent competition—in that alternative prey leads to increased predation rates on native species (Courchamp et al. 2000; Courchamp et al. 2003), and highlights the diversity of trophic interactions that can occur where food webs comprise a mix of exotic and native species. In this example, modeling results of Courchamp et al. (1999) indicate that simultaneous control of exotic predators and prey would be the best strategy for conserving native island vertebrate species.

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Colorado River below Glen Canyon Dam (Stevens et al. 2001). The population size of the native humpback chub (*Gila cypha*) has declined precipitously in the last decade (GCMRC 2003). In response, restoration has focused on the removal of rainbow trout (*Oncorhynchus mykiss*) to examine whether trout predation on juvenile chub is limiting their recovery (Marsh and Douglas 1997).

While trout are common exotic species, populations of these same trout species are often extirpated in their native range due to loss of habitat, water quality degradation, exploitation, obstructions to migration, and exotics (Donald and Alger 1993; Gunn et al. 2004). 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 habitat fragmentation and degradation (Pimm 1991). This suggests that top predators would be particularly difficult to reestablish (Lawton 2000). Indeed, for a reintroduction to succeed, reintroduced individuals must survive at low population levels and successfully reproduce in spite of predators, competitors, and pathogens. While these are the same challenges faced by invasive species, this highlights the need to better understand food-web interactions involving exotic and native species in the context of ecological restoration.

While biological invasions are an important aspect of global environmental change, and of great importance to ecological restoration (Vitousek et al. 1996), 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. 1997; Richter et al. 1997). In Pacific Northwest rivers, human alteration of stream flow patterns has disrupted food-web interactions (Power et al. 1996a; Wootton et al. 1996). 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. 1996b; Marks et al. 2000). In unregulated streams in the southwestern United States, the natural flooding regime has allowed the continued persistence of native fishes despite the presence of exotic predatory fishes (Meffe 1984). Similarly, the occurrence of seminatural flow regimes in dammed rivers during high precipitation years resulted in greater dominance of natives fishes (Probst and Gido 2004). Recognition that natural flow regimes promote the persistence of desired native species has been the basis for experimental flow releases on the Colorado River aimed at rebuilding aquatic habitats that were lost following dam construction (Valdez et al. 2001).

Food-Web Assembly

Ecological communities are not static entities but rather are dynamic in their composition, typically accumulating species through time following disturbances. Community ecologists have examined whether simple rules and the order of species introductions govern the composition of ecological communities. These ideas comprise what are known as the study of ecological assembly rules, which have played a central role in community ecology (Diamond 1975; Weiher and Keddy 1999). It is important to note that “communities” studied by community ecologists are most often a single trophic group (i.e., “the plant community” or “the bird community”) (Drake 1990). Few studies have examined ecological assembly involving interacting species across several trophic levels. One approach to examine ecological assembly has been to assemble food webs in small containers or laboratory beakers. These microcosm food-web studies generally find that changing the sequence of species introduction during food-web assembly can produce very different community outcomes (Robinson and Dickerson 1987; Drake 1990). For example, a species that is competitively dominant under one set of circumstances may be unable to establish given a different assembly scenario (Drake 1990, 1991). Simulation models of food-web assembly generally predict that species-

rich, complex food webs better resist invaders and their disruptive impacts (Post and Pimm 1983; Robinson and Dickerson 1987; Drake 1991). These studies also indicate that food webs with more links per species are more resistant to invasions (Robinson and Valentine 1979; Post and Pimm 1983). Though the applicability of microcosm studies and simulation models to real ecosystems is uncertain, this work suggests that species diversity, food-web connectivity, and introduction sequence may be important considerations in ecological restoration.

One example of food-web assembly concepts being incorporated into ecological restoration involves lake restoration efforts in the region of Sudbury, Ontario (Gunn 1995). Following the successful control of industrial sulfur emissions in the region, lake pH has improved to levels ($\text{pH} > 5.5\text{--}6.0$) capable of supporting top predators such as lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieu*). The success of predator reintroduction has recently been examined in these acid-recovering Ontario lakes (Gunn and Mills 1998; Snucins and Gunn 2003). Lake trout, the native top predator, recovered (i.e., recruited successfully in the absence of stocking) rapidly in lakes with few fish species, while in species-rich systems lake trout were slow or even unable to reestablish. This suggests that community attributes or reintroduction order (priority effects) may play 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 (Whittier and Kincaid 1999; Findlay et al. 2000) and adverse competitive impacts on lake trout (Vander Zanden et al. 1999), though the strength of smallmouth bass–lake trout interactions is mediated by the presence of pelagic forage fishes (Vander Zanden et al. 2004). Restoration of native community assemblages in these lakes will require further attention to priority effects and the order of species reintroductions (Evans and Olver 1995; Gunn and Mills 1998; Snucins and Gunn 2003). In acid-recovering lakes, lake trout should be reintroduced as early as possible 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. These lakes should also be protected from unauthorized introductions of rock bass and smallmouth bass, at least until self-sustaining lake trout populations establish. Lake trout are a critical component of shield lake ecosystems—not only do they provide an important fishery, but they are also an important indicator of ecosystem integrity (Gunn et al. 2004). An understanding of food-web interactions in these systems suggests that species introductions should be controlled *during* the restoration process, at least until desired components of the community have established. Yet in other cases, desired native species may come to depend on exotics in various ways (Kitchell et al. 2000; Zavaleta et al. 2001), such that the broader food-web and ecosystem consequences of exotic species removals also need to be carefully considered (Zavaleta et al. 2001).

Application of Stable Isotopes to Restoration

Restoration efforts have traditionally targeted individual species, guilds, or communities, though there is increasing interest in restoration of ecosystem-level processes such as natural flow regimes in rivers (Poff et al. 1997), or fire regimes in terrestrial systems (Baker and Shineman 2004). Restoration of food-web interactions has also been discussed as a potential restoration goal that incorporates aspects of ecosystem function (Palmer et al. 1997), although the idea has not often been applied in restoration projects. The key reason has been

that monitoring food webs is not a trivial task: food webs are complex, and trophic interactions are highly variable in space and time. Stable isotope techniques are used increasingly to infer the movement of energy in food webs (Peterson and Fry 1987; Dawson et al. 2002). Ratios of stable isotopes ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$, expressed as δ notation relative to a known standard), vary predictably from resource to consumer tissues. For example, plants with C_4 photosynthetic pathways are enriched in ^{13}C relative to C_3 plants. These differences in plant $\delta^{13}\text{C}$ are preserved in consumer tissues, such that $\delta^{13}\text{C}$ is an indicator of the ultimate 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 have therefore been used to infer trophic position of consumers in complex food webs (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. For example, Gratton and Denno (unpublished) used stable isotopes to monitor arthropod food webs in New Jersey salt marshes that have been restored to *Spartina* following the extirpation of exotic *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 (Figure 8.4) indicating that trophic interactions among arthropod consumers had been largely reestablished in restored habitats in less than five years. In the same marshes, Currin et al. (2003) used stable isotopes to show that benthic microalgae and *Spartina*-derived organic matter were a significant component of the diet of mummichogs, *Fundulus heteroclitus*, in *Spartina*-dominated marshes. Reliance on these resources was much lower in *Phragmites*-invaded areas. Energy sources for fish in restored marshes were intermediate between *Phragmites* and *Spartina* marshes. Thus, stable isotopes were useful in delineating resources use by consumers in degraded (invaded), restored, and reference habitats. In the case of arthropods, the isotope data suggests that consumers utilized resources derived primarily from the habitat in which they were collected and as habitats were restored, predators integrated into the local food webs.

Stable isotopes have also been used to assess the restoration of southern California salt marshes (Kwak and Zedler 1997). Recent work indicates that marsh-derived algae and vascular plants, particularly *Spartina*, are important energy sources for invertebrates and fish (Kwak and Zedler 1997; Desmond et al. 2000; West and Zedler 2000; Madon et al. 2001), 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 (i.e., light-footed clapper rail [*Rallus longirostris levipes*] and Belding's savannah sparrow [*Passerculus sandwichensis beldingi*]). While both are valid restoration targets, restoration of habitat for fishes and endangered birds may have erroneously been viewed as competing objectives (Kwak and Zedler 1997). In light of recent research documenting the importance of linkages between these two habitats (Desmond et al. 2000; West and Zedler 2000; Madon et al. 2001), future restoration efforts should focus on the creation of integrated channel-tidal salt marsh systems, which is expected to simultaneously accomplish both restoration objectives.

Food-web approaches are also valuable for assessing long-term changes and the restoration potential of ecosystems. Lake Tahoe has undergone substantial change during the past

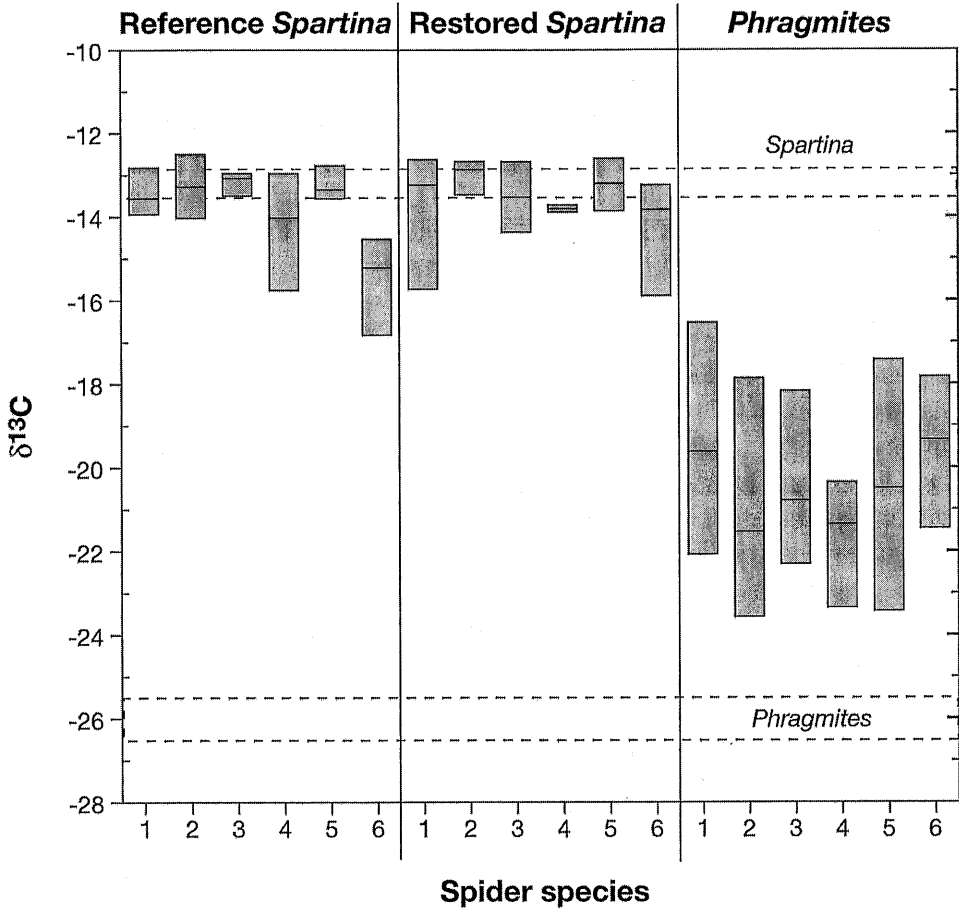


FIGURE 8.4 $\delta^{13}\text{C}$ stable isotope box-plot (median and interquartile range) of dominant spider predators from reference *Spartina*, restored *Spartina*, and *Phragmites*-dominated habitats within the Alloway Creek Watershed Restoration site (Salem County, New Jersey, USA). Dotted lines 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. From Gratton and Denno, unpublished.

century, including eutrophication, exotic introductions, and extirpation of the native top predator, Lahontan cutthroat trout (LCT; *Onorhynchus clarki henshawi*) (Jassby et al. 2001). Vander Zanden (2003) used stable isotopes to characterize historical food-web changes in Lake Tahoe based on analysis of contemporary and preserved museum specimens. The introduction of exotic freshwater shrimp (*Mysis relicta*) and lake trout have substantially disrupted the pelagic food-web structure of Lake Tahoe (Figure 8.5). These two exotics are extremely abundant and both have strong impacts on other species in the pelagic zone of Lake Tahoe. For these reasons, it is likely that these food-web alterations may limit the restoration potential of LCT in Lake Tahoe. Interestingly, native food webs in two Tahoe

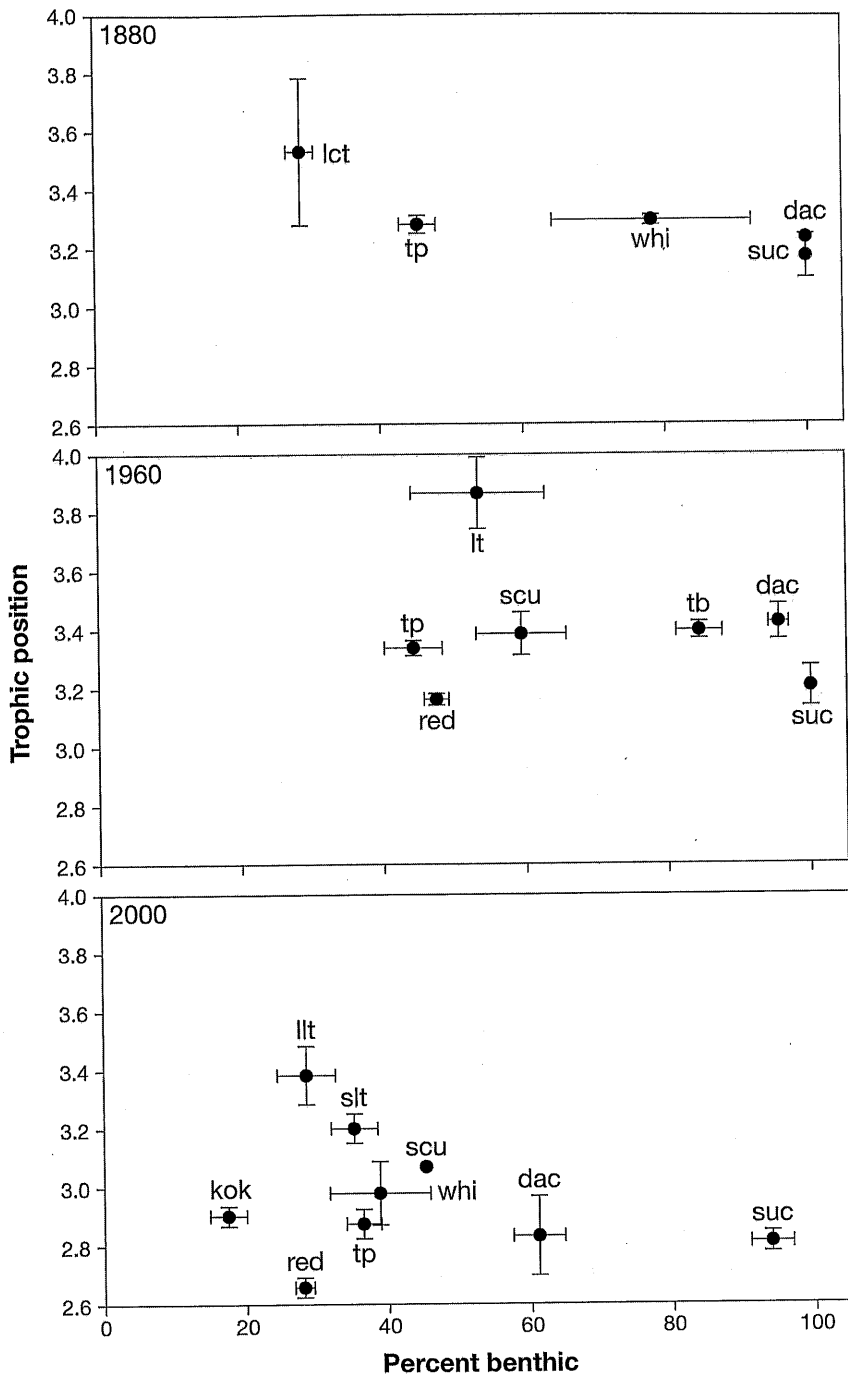


FIGURE 8.5 Food-web structure of Lake Tahoe based on stable isotope analysis of present-day and historical, museum-archived tissue samples. Food webs are presented for several time periods: 1880s, 1960s, 2000s. Species represented are lct = Lahontan cutthroat trout; tp = tui chub (pelagic morph); whi = mountain whitefish; suc = Tahoe sucker; dac = Lahontan speckled dace; scu = Paiute sculpin; red = Lahontan reidside shiner; tb = tui chub (benthic morph); kok = kokanee salmon; lt = lake trout (all individuals); llt = large lake trout (>58 cm); slt = small lake trout (<58 cm). The trend is toward increased pelagic production, and replacement of native Lahontan cutthroat trout with lake trout. Based on Vander Zanden et al. (2003).

basin headwater lakes (Cascade Lake and Fallen Leaf Lake) are still relatively intact despite some non-native introductions, and stable isotopes indicate that food webs in these lakes resemble that of Lake Tahoe prior to exotic introductions (Vander Zanden et al. 2003, unpublished data). These smaller and relatively unaltered systems are ideal candidates for “experimenting” with native LCT reintroductions, and the U.S. Fish and Wildlife Service has been reintroducing LCT into Fallen Leaf Lake since 2002. Ongoing studies are assessing the impact of lake trout predation on LCT in Fallen Leaf Lake during this experimental reintroduction, so that knowledge gained can be meaningfully applied to the restoration of LCT in other systems. The food-web component of this work also provides an opportunity to examine whether historical food-web niches are regained when formerly extirpated species are reestablished (Vander Zanden et al. 2003).

The above studies demonstrate the potential value of stable isotopes as a tool not only for documenting how food webs have been altered relative to reference conditions, but also for identifying important energy sources for restoration target organisms and assessing food-web recovery as systems move along restoration trajectories. Monitoring schemes that only consider presence/absence or abundance of species may overlook important food-web interactions as well as other important functional attributes of recovering ecosystems.

Areas of Research Need and Opportunity

Linkages between basic ecological research and restoration practice are weak, potentially hindering further advancements in both fields (Palmer et al. 1997; Hobbs and Harris 2001). “Bridging the gap,” or perhaps “blurring the lines” between basic ecology and on-the-ground restoration represents a major challenge to both researchers and practitioners (Hobbs and Harris 2001). The good news is that restoration ecology has demonstrated that the degradation of ecosystems is often reversible, and there is ample evidence that restoration can be effective in nudging ecosystems toward a desired state (Dobson et al. 1997; Young 2000; Young et al. 2001). As a result, ecological restoration will play a growing role in global efforts to manage ecosystems to maximize ecosystem services and support biodiversity (Dobson et al. 1997). In this section, we have discussed how an understanding of food-web interactions can contribute to ecological restoration. Below, we identify some of the challenges and opportunities likely to be encountered in the application of food-web ecology to ecological restoration.

Food-Web Interactions and Adaptive Management

In some ecosystems, food-web interactions are critical in structuring ecosystems, while in other ecosystems, habitat and bottom-up factors likely 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 (Carpenter and

Kitchell 1993; Silliman and Zieman 2001; Silliman and Bertness 2002). In the absence of experimentation, there remains a need to understand whether ecosystems are dominated by top-down (predation) or bottom-up (habitat and productivity) forces, how these dual forces 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 whole-ecosystem level, while much of modern ecology is based on small-scale, but highly replicated, experiments. Can we scale up from small-scale experiments to the management and restoration of real ecosystems? Microcosm and small-scale experiments suffer from “cage-effects,” whereby the results are simply an artifact of the artificial conditions of the experimental manipulation. Such 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 (Polis et al. 2004), complex trophic interactions (Carpenter 1996; Roemer et al. 2002), and the role of mobile predators (Soulé and Terborgh 1999). The obvious alternative is to conduct large-scale, whole-ecosystem manipulations (Carpenter et al. 1995; Zedler 2001). Restoration projects provide unique opportunities for whole-ecosystem experiments within an adaptive management, “learning-by-doing,” framework (Zedler 2001; 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 (Walters 1986; Donlan et al. 2002). In addition, ecological restoration has great potential to 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 Exotics and Global Change

While the restoration potential of many ecosystems may be high, we have less optimism about restoration in light of accelerating species invasions, which 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 re-assembled (Root and Schneider 1993). The “rules of engagement” in ecosystems will change, yielding completely new outcomes and interactions (Lawton 2000). Restoring ecosystems within the context of the shifting backdrop of climate change and exotics seriously confounds the task at hand, necessitating a more complete incorporation of food-web, landscape, and ecosystem perspectives (D’Antonio and Chambers, this volume). Restoration ecology will draw increasingly from the field of invasion biology, and it will demand improved methods for controlling undesirable exotics. Perhaps a more critical challenge will be to find ways to manage ecosystems so as to maintain native biodiversity and ecosystem services in the face of invasive exotics (Kitchell et al. 2000; Rosenzweig 2003). In some cases, reliance on non-native species may be crucial for promoting restoration of energy flows and higher trophic levels, and food-web approaches will figure prominently into assessing the value and viability of such efforts (Kitchell et al. 2000; Ewel and Putz 2004). Sustaining native biodiversity will undoubtedly require intensive ecosystem management, which will be carried out by researcher-managers working at the interface of basic and applied ecology (Rosenzweig 2003).

Summary

The study of food webs represents a rapidly expanding subfield of ecology with the goal of understanding and predicting multispecies interactions. Though ecologists have long recognized 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. We have suggested that 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. The field of dreams approach may be sufficient in some systems, while inadequate in others. In addition, nuisance exotic species can be a barrier to achieving restoration goals. We presented several examples in which food-web interactions affect attributes of the ecosystem in important ways, with important and often poorly appreciated implications for restoration. Viewing restoration at the whole-ecosystem level and incorporating a food-web perspective can contribute in a real way to ecological restoration efforts (Soulé and Terborgh 1999; Roemer et al. 2002; Donlan et al. 2003). We offered that further advances will derive from restorationists incorporating “food-web thinking” into restoration projects and treating their efforts as ecosystem experiments. 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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