Food Webs at the Landscape Level

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Chapter 24

Subsidy Effects on Managed Ecosystems: Implications for Sustainable Harvest, Conservation, and Control

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THE USE OF SUBSIDY THEORY IN APPLIED CONTEXTS

It is conceivable that somewhere, in an isolated pocket of ancient groundwater deep in the earth's crust, there exists a hydrogen-based food web that has not yet felt the hand of man. Otherwise, it is hard to think of any ecosystem on earth that is not dominated, or strongly perturbed, by humans (Vitousek, Mooney et al. 1997; Kareiva et al. 1993; Crowder et al. 1996). Human effects have become so pervasive that most people in present and future generations will never experience "unmanaged" ecosystems. The effects of the human enterprise, intended or otherwise, have spread over regional or global scales (e.g., Riley and Jefferies, chap. 25 in this volume). To anticipate the consequences, we must better understand how our activities have changed the spatial and temporal scales of natural ecosystems. The study of "ecological subsidies," fluxes of organisms, energy, or materials across ecosystems boundaries, can make key contributions toward this understanding.

Ecological subsidy theory adds an explicit spatial context to the study of food web interactions. As explained by Polis, Anderson, and Holt (1997), it organizes the potentially overwhelming complexities of spatially registered food web ecology into a framework useful for exploring the community- or ecosystem-level consequences of fluxes between habitats. Just as economic subsidies (e.g., funding by the U.S. government of "below-cost" timber sales or interbasin water diversions) distort local economies and ecosystems, so do their ecological counterparts. Ecological subsidies of materials or organisms from distant sources, through arrays of direct and indirect effects, can change the structure and dynamics of local recipient food or interaction webs.

Applying the subsidy framework to food web ecology involves several steps: (1) characterizing the flux, including its variation in space and time; (2) identifying key members and linkages in recipient webs; (3) evaluating the population-level responses of recipient web members that directly intercept fluxes; and (4) analyzing (or predicting) the community- or ecosystem-level consequences emanating from the subsidy's direct and indirect effects on these and other web members. We begin to understand subsidy effects if we can answer the question, how would the web function if the subsidy changed or disappeared?

These steps can be tailored for application to management, in which explicit spatial information is crucial: (1) How did (would) the ecosystem function without human transfers of energy, materials, or organisms between previously isolated habitats? Where and when has land use or resource harvest reduced or stopped cross-habitat flows that were formerly important to ecosystems? Where and when have they distorted ecosystems by accelerating or concentrating flows, such as nutrient fluxes? (2) What are the direct and indirect effects (sometimes corresponding to the intended and unintended consequences) of human alterations of subsidies? (3) How will these consequences play out over years, decades, and centuries and over local, regional, and global scales? (4) How might system trajectories and feedbacks change under various management schemes or with changes in climatic or ecological conditions? Could failure to recognize food web linkages across larger spatial or temporal scales precipitate unpleasant surprises (management disasters)?

The global-scale consequences of human (postindustrial) effects on land cover, nutrient fluxes, and species distributions are reviewed by Riley and Jefferies (chap. 25 in this volume). In this chapter, we will focus on more local processes that mediate the effects of human subsidies on food webs we hope to manage. As Robert Holt (personal communication to MEP) has pointed out, for every subsidy, there is an "anti-subsidy," or "resource shadow": a zone with organisms from which resources of energy, materials, or organisms have been diverted. Human-induced resource shadows include the deserts that have followed water diversion, deforestation, and overgrazing (Reisner 1986, 1990; Southwick 1996; Sauer 1967; Perlin 1991) and the rivers that have suffered losses of huge fish migrations (salmonids, eels) following damming (e.g., National Research Council 1992). While resource diversion clearly influences the diversity and sustainability of both donor and recipient ecosystems, we will focus here on what happens to recipient ecosystems when subsidies from spatially extensive sources are discharged into them. We present several case histories that illustrate how subsidy theory can produce testable hypotheses about spatial food web and ecosystem processes that could inform adaptive management of ecosystems and species. Subsidy theory, by expanding the scope of ecological studies, can also aid in our recognition of how management for one target (e.g., agricultural production) may affect other societal goals (e.g., water quality or species conservation).

EFFECTS OF AGRICULTURAL SUBSIDIES

Agriculture is probably the oldest and most widespread human impact on the earth. Human agriculture appears to have begun around 8500 B.C. in the Fertile Crescent of southwestern Asia and less than a thousand years later in China. By 5500 B.C., it had spread to southwestern Europe, and it was independently initiated in the Americas about 2,000 years later (Diamond 1998). Over the subsequent millennia, agricultural production fueled increases in human populations, and humans, in turn, have intensified agricultural production by diverting and concentrating water, nutrients, and organisms (Matson et al. 1997). Subsidy analyses can help us recognize some of the interactions and controls that act over various spatiotemporal scales to influence the yields, as well as the impacts, of agriculture.

Agricultural food webs are less diverse than natural food webs, and they are often highly managed to maximize the yield of one or a very few species of crops. Nevertheless, they respond to the same direct and indirect processes that influence more natural communities. Cross-habitat fluxes of nutrients, plant competitors (weeds), herbivores, and predators from various spatial sources affect the dynamics of agricultural food webs and the productivity of target crops. Most of the important entities involved move across a variety of scales.

Nutrients

Terrestrial nutrients, particularly nitrogen and phosphorus, are distributed quite heterogeneously at almost all spatial scales, from within a watershed to the entire planet (Huston 1993). Before commercial fertilizers were available, our most fertile crop areas were enriched by allochthonous nutrients deposited by water. Rich floodplain soils were deposited annually by rivers (e.g., in the Nile delta and the "bottomlands" of the Mississippi) before human engineering isolated these rivers from their floodplains. Over a longer but more continuous time, soils from nutrient-rich areas are transported as atmospheric dusts at scales from meters to thousands of kilometers (Jackson 1971; Likens et al. 1990; Chadwick et al. 1999). These dusts transfer nutrients, especially phosphorus, over the entire world, from areas geologically rich in such elements to more depauperate areas. For example, pineapples and sugarcane in Hawaii are fertilized by phosphorus dusts from central Asia (Chadwick et al. 1999). Transfers of windblown iron dust from continents to oceanic phytoplankton may have been greater during glacial times, elevating production of iron-limited phytoplankton, which may have drawn down more CO_2, resulting in a cooler climate. Marine aerosols that contain rare micronutrients, macronutrients, and organic compounds travel, sometimes long distances, inland on continents (J. Noller, personal communication to GAP). The time-integrated contributions of marine aerosols to local soils may be very large, but their effects on plant productivity in agroecosystems and natural systems are poorly known.

The commercial fertilizers used today are imported from natural accumulations (e.g., seabird guano from oceanic nesting islands; phosphate mines), collected from concentrations of livestock, or derived by industrial nitrogen fixation using petrochemicals whose elements were assembled by ancient plant communities. Many problems and threats have arisen from the massive introduction of synthetic nitrogen fertilizers into groundwater, surface water, and terrestrial and marine ecosystems (Carpenter, Caraco et al. 1998; Paerl 1985; Howarth, Billen et al. 1996; Vitousek, Aber et al. 1997; Riley and Jefferies, chap. 25 in this volume). The dead zone in the Gulf of Mexico, apparently a result of nutrient export from U.S. agriculture in the Mississippi basin, is one notorious example (Rabalais et al. 1996). Scientists have also raised concern over the effects of atmospheric deposition of anthropogenic nitrogen on plant composition and productivity worldwide (e.g., Vitousek 1994; Vitousek, Aber et al. 1997; Paerl 1985; see Riley and Jefferies, chap. 25 in this volume).

Pests

Pests in agroecosystems also move among patches (of different plant species) and habitats. Many herbivores on crops are generalists that thrive on several species of host plants. Japanese beetles, Oriental and Mediterranean fruit flies, and the corn earworm (*Helicoverpa (Heliothis) zea*, economically the most harmful pest in North America) each infect many crop species. Microbial plant pathogens often move among hosts as spores blown over short and long distances from conspecific and heterospecific populations (Walker 1969; Roberts and Boothroyd 1972). Stages of some heteroecious rust fungi must move among different host species to develop; cedar-apple rust, for example, alternates between apples and eastern red cedar. Farmers decrease "take" by these agricultural competitors by manipulating the vegetation surrounding their fields to avoid combinations favorable to pests.

Some populations of agricultural pests move great distances. Probably most infamous are the migratory locusts (acridid grasshoppers) that destroy thousands of square kilometers of croplands annually. The corn earworm is another well-known migratory pest. Pollen tracer studies identified southern Florida, the Bahamas, Cuba, the Yucatán Peninsula, and northern Central America as potential source areas 1,515 km from capture sites in Oklahoma and Texas (Lingren et al. 1994). Biologists deduced that dispersing moths would have to fly over water for 72 hours or have very limited diurnal resting periods on seaweed (*Sargassum* spp.), ships, oil platforms, or the sea surface. Pair et al. (1991) used ecological and meteorological evidence and ground-based radar to identify irrigated corn grown in the Lower Rio Grande Valley of Texas and northeastern Mexico as the source of the migrant fall armyworm, *Spodoptera frugiperda*, which subsequently infested crops in Texas, Missouri, and Iowa, up to 1,900 km away. Individual corn earworms that infest the central to northern midsection of the United States come each year from a 200,000 ha area in northern Mexico (McCracken et al. 1996). Pupae do not overwinter north of mid-Texas, and populations hopscotch their way across America each year over several generations, wafting and flying up to 400 km in 9 hours. The corn earworm and fall armyworm do not overwinter in temperate areas. These and similar studies are revealing how weather systems, habitat modification, and biology underlie long-distance migrations of pests from defined source areas to crops in remote areas (Westbrook and Isard 1999). Vertebrate pests (starlings in North America, cockatoos and mice in Australia, and hippos, elephants, and quela and weaver birds in Africa) also move among habitats and sometimes cause crop damage.

Biological Enemies

Enemies of crop pests also move among patches (of plant species) and habitats. For example, swifts, swallows, martins, and bluebirds often either migrate varying distances or live in non-crop habitats adjacent to agricultural fields. Many arthropod predators have populations that live on prey from both crop and non-crop plants. In an apparent competition interaction, prey that are not crop pests may increase predator populations to levels capable of suppressing pests. For example, in a California vineyard (Napa), predatory two-spotted mites move from Johnson grass to relatively less productive grapevines; this steady influx allows higher populations of these mites to suppress an important in situ pest prey, the Willamette mite, to lower densities in the grapevines than if Johnson grass were absent (Flaherty 1969). Spiders of several varieties reside in ground detritus but move daily to row crops to feed on herbivores, significantly increasing crop yield (Riechert and Bishop 1990). Movements by predators and parasitoids are important to the population dynamics of crop pests (McCauley et al. 2000; Murdoch and Briggs 1996).

Parasitoid wasps are a key element in biological pest control. They require two distinct resources: host arthropods (insects or spiders) for their developing larvae and flowering plants to provide adult wasps with nectar and pollen for energy and egg production. Control of pest species by wasps appears to be more successful when the wasps have access to flowering plants that surround crops (Jervis et al. 1993). Polis et al. (1998) recognized the importance of adult resources during our work on spider dynamics on islands in the Gulf of California. Most years are exceptionally dry (<20 mm of rain), and in those years, spider wasps (Pompilidae) are basically absent as a mortality factor, even though spider populations may be very dense. In wet (El Niño) years, however, the biomass of annual flowering plants increases by two orders of magnitude. Under these conditions, adult wasps had sufficient nectar and pollen resources to depress spider populations by an average of 90% or more on twenty-one different islands. These results suggest that resource subsidies provided to adults may increase the effect of larval parasitoids in agricultural habitats as well.

Knowledge of the spatial ecology of agricultural food webs has been used for centuries in traditional farming practices to enhance yields. For example, appropriate plant combinations in polycultures are used to nurture beneficial birds and arthropods. Traditional shade-grown coffee and cacao cultivation uses polycultures with overstory and understory plants that are important habitats for migratory and resident birds, which consume pests (Greenberg and Ortiz 1994). Hedgerows along field edges or other plants between crop rows (e.g., Johnson grass and grapes) are used to harbor natural enemies. Farmers also provide structures for predator habitats (e.g., ground detritus for spiders; bird boxes for martins). Trap crops (Scholte 2000; Barbercheck and Warrick 1997; Buntin 1998; Luther et al. 1996) or trap habitats adjacent to harvested crops are used to lure pests to sites where they can be easily destroyed (e.g., pest ant species can be concentrated and burned under hay bales, where they attempt to nest; P. Ward, personal communication). Manipulating habitat structure to influence organisms at trophic positions above and below pests can reduce crop damage without the toxic consequences of pesticides (Matson et al. 1997).

Agricultural Intensification

Traditional methods of pest control using local knowledge of the variation in weather, soils, plants, and animals are less and less practiced, however, as human population pressure drives the increasing industrialization of agriculture (Lal 1987). With agricultural intensification (Matson et al. 1997), the temporal scales of repeated extraction of crops or livestock from cultivated areas are shortening, while the spatial scales over which we are redirecting flows of nutrients and agricultural products are increasing.

Large-scale manipulation of the earth for agriculture is not a twentieth-century phenomenon. Massive irrigation projects have repeatedly subsidized crops and ultimately salinized soils, starting in Mesopotamia from 2400 to 1700 B.C. (Perlin 1991) and continuing to this day in the arid western United States and many other places (Reisner 1986; Southwick 1996). Globalization and intensification of agriculture on the modern scale, however, would not have been possible without industrial nitrogen fixation. The invention of the Haber-Bosch process for ammonia synthesis just before World War I, and its proliferation for global fertilizer production following World War II, released human agriculture from its previous nitrogen limitation and permitted the quadrupling of the human population during the twentieth century (Smil 1997). These changes have had obvious consequences.

In the next section, we discuss some of the more local effects of nutrient subsidies resulting from land use changes, including agriculture within a watershed, on the food web and water quality of a midwestern U.S. reservoir. In the following section, we discuss how regional nutrient subsidies from North American agriculture affect a wetland maintained for wildlife conservation in the arid Southwest. In both of these examples, enough has been learned about specific nutrient vectors and controls over the spatial dynamics of the subsidy to guide management responses.

WATERSHED MANAGEMENT: RESERVOIRS IN EASTERN NORTH AMERICA

Export of nutrients from terrestrial landscapes to aquatic ecosystems stimulates aquatic primary production and can modify food web structure in lakes, streams, and coastal environments (Carpenter, Caraco et al. 1998; Smith 1998). Watershed-scale transport of nutrients enhances the production and biomass of algae and vascular plants and sometimes alters the species composition of plant assemblages, which can then further alter food web structure. A well-known example is the shift toward cyanobacteria (blue-green algae) in fresh waters when anthropogenic increases in phosphorus inputs render nitrogen relatively more limiting (Smith 1998). Because cyanobacteria are less edible than other algae, shifts in the herbivore assemblage from generalist feeders (e.g., *Daphnia*) toward more specialized feeders (e.g., copepods and rotifers) may occur. Fish assemblages may also shift in response to increased nutrient inputs (e.g., Bachmann et al. 1996). Increased algal "blooms" and associated symptoms of eutrophication generally reduce water quality in a variety of ways, including the formation of surface scums of algae, depletion of deep-water oxygen and subsequent loss of fish habitat, and shifts toward fish species less desirable to humans. Eutrophication remains the most prevalent environmental problem facing fresh waters in terms of the number of lakes or the total length of rivers affected (Carpenter, Caraco et al. 1998).

Linkages among Watersheds and Reservoir Food Webs

Watersheds also export large quantities of nutrients in particulate form—for example, as nutrients attached to soil or sediment particles. These particulate-bound nutrients are generally much less available to primary producers than are dissolved nutrients. However, particulate inputs may subsidize aquatic food webs by providing a food source for certain key species. Reservoirs of eastern North America provide an excellent system for examining the consequences of these subsidies for several reasons (see Vanni and Headworth, chap. 4 in this volume). First, reservoirs have large watersheds (compared with natural lakes) because they are impounded rivers. (In contrast, most glacial lakes have small stream inflows or lack stream inflows altogether.) Therefore, reservoirs often receive large quantities of sediment and nutrients from their watersheds (Thornton 1990). Second, many reservoirs are constructed in agricultural areas; since these landscapes are often subject to high rates of soil erosion, reservoirs in agricultural areas are particularly likely to receive massive amounts of sediments and particulate nutrients (Renwick 1996; Vanni et al. 2001). Third, omnivorous gizzard shad (*Dorosoma cepedianum*) often dominate the fish assemblages of reservoirs of eastern North America (Stein et al. 1995; see Vanni and Headworth, chap. 4 in this volume). In reservoirs, postlarval gizzard shad often feed mainly on sediments (Mundahl and Wissing 1987; Yako et al. 1996; Schaus et al. 2002). By consuming sediment-bound nutrients and excreting nutrients in dissolved inorganic form into the water column, gizzard shad transport considerable quantities of dissolved inorganic nutrients (phosphate and ammonium), which increase phytoplankton biomass and nutrient standing stocks (Schaus et al. 1997; Schaus and Vanni 2000; Vanni and Headworth, chap. 4 in this volume).

Gizzard shad abundance is probably limited by subsidies from watersheds. These fish are more abundant in productive (eutrophic and hypereutrophic) lakes and reservoirs than in unproductive systems. Water quality in reservoirs is subject to positive feedback between watersheds and gizzard shad activities (Vanni and Headworth, chap. 4 in this volume). As land cover is converted from forest to agriculture, the export of both particulate and dissolved nutrients to reservoirs increases. Several "subsidy pathways" may then interact to affect reservoir food webs and degrade water quality (fig. 24.1). Suppression of large zooplankton species by high gizzard shad biomass (adult shad consume some zooplankton, and shad larvae are obligate phytoplanktivores that may exploitatively outcompete zooplankton) may also result in low rates of herbivory, further contributing to high algal biomass. In short, watershed degradation (increased nutrient and sediment export) leads to increased algal production and gizzard shad biomass; increased gizzard shad biomass further stimulates algal production.

At least three factors, however, can break this positive feedback loop and regulate shad biomass. First, gizzard shad growth rates are density-dependent and tend to be lower in highly productive habitats where shad are extremely abundant (e.g., DiCenzo et al. 1996). This factor could reduce reproductive output. Second, gizzard shad exhibit variable year-class strengths. Survival of young-of-the-year (YOY) shad varies considerably among years, in part due to events occurring at the larval stage, when gizzard shad are obligate planktivores. Third, relatively severe winters, when prolonged ice cover can lead to long periods of anoxia, depress shad populations, particularly in highly productive systems in which bacterial respiration rates are high. These factors probably interact to regulate gizzard shad abundance over interannual scales (Schaus et al. 2002).

Interactions of Cross-Habitat Subsidies and Water Quality Management

The potential interactions of nutrient subsidies have several implications for water quality management in ecosystems containing gizzard shad.

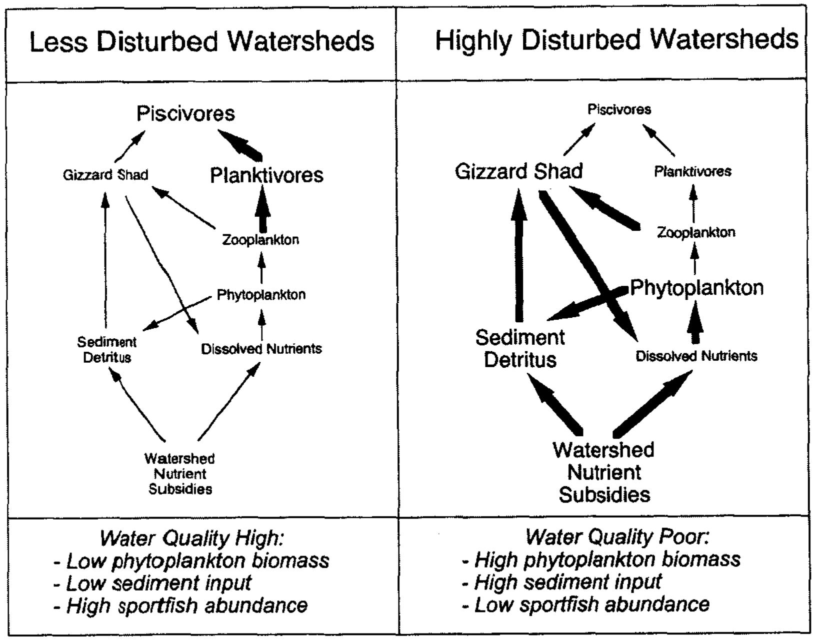

Figure 24.1 Proposed linkages between watersheds and reservoir food webs in reservoirs of eastern North America. The relative sizes of the arrows indicate the relative difference in a particular flux rate between the less disturbed and highly disturbed watersheds. Similarly, the relative font size labeling the system compartments represents the relative difference in biomass between the watershed types. In less disturbed watersheds, subsidies from the watershed are lower and gizzard shad are scarce. This allows planktivores (e.g., bluegill sunfish) to thrive; piscivores (many of which are sportfish) are abundant because they feed on these planktivores. In highly disturbed watersheds, subsidies of dissolved and particulate nutrients from watersheds are more substantial. These inputs stimulate phytoplankton productivity and also provide detrital resources for gizzard shad. Shad biomass therefore increases, leading to increased nutrient transport by shad. This transport leads to further increases in phytoplankton biomass. Gizzard shad larvae are obligate planktivores and may exploitatively outcompete zooplankton, leading to declines in planktivores. Shad also are not as vulnerable to piscivores as are other planktivores, and hence piscivores are less abundant in highly disturbed watersheds.

Improved watershed practices, particularly in agriculture, may yield relatively large water quality benefits—perhaps greater than those in systems lacking gizzard shad. Agriculturally derived nutrient inputs can be lowered by reduced fertilizer use, reduced soil erosion via improved tillage practices, and protection of riparian zones to reduce the movement of nutrients from land to water. Practices that lower inputs of both particulate and dissolved nutrients are likely to have the greatest effects, as they will reduce direct nutrient subsidies to phytoplankton (i.e., dissolved nutrient inputs) as well as food subsidies to gizzard shad. Furthermore, integrated management of fisheries and watersheds is likely to lead to the greatest water quality benefits. For example, gizzard shad biomass might be lowered directly through enhancement of piscivorous fish populations in conjunction with reductions of watershed-derived nutrient subsidies. These two management practices should act synergistically to improve water quality.

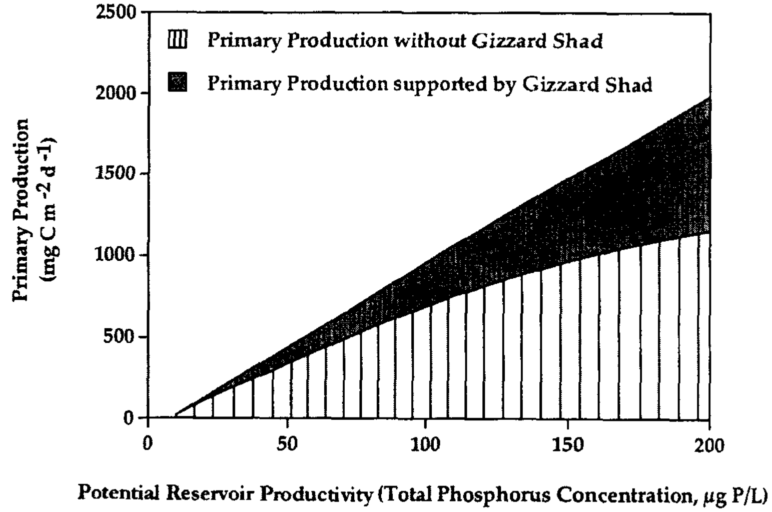

Figure 24.2 Predicted phytoplankton primary production in reservoirs with and without nutrients transported by gizzard shad. The open area represents predicted primary production without the nutrient transport process, and the shaded area represents additional primary production supported by nutrient transport by gizzard shad. The top line therefore represents total primary production supported by shad and all other sources. (Adapted from Vanni and Headworth, chap. 4 in this volume.)

If either gizzard shad populations or watershed-derived nutrient inputs are reduced, the model of Vanni and Headworth (chap. 4 in this volume) suggests that the greatest improvements in water quality may be achieved in the most highly productive reservoirs. This is because, according to this model, nutrient transport by gizzard shad sustains a greater proportion of phytoplankton primary productivity in highly productive systems than in unproductive systems (fig. 24.2). If shad biomass increases more than linearly with potential reservoir productivity, then reducing watershed-derived nutrient inputs should also have greater proportional effects on water quality in highly productive reservoirs (Vanni and Headworth, chap. 4 in this volume). Thus, relatively small improvements in watershed practices could lead to both direct improvement in water quality through a reduced supply of dissolved nutrients and indirect improvement via reduced gizzard shad biomass. Potentially synergistic measures such as these need to be better integrated into management efforts.

In another model, Carpenter, Ludwig, and Brock (1999) predicted that recycling of nutrients from sediments and lack of flushing could make lakes vulnerable to irreversible degradation. A more optimistic prediction for reservoirs may be in order because of the potential for flushing excess nutrients from reservoirs through outflow rivers. This mitigation, however, may simply transfer eutrophication problems to downstream water bodies (Rabalais et al. 1996; Riley and Jefferies, chap. 25 in this volume).

Potential Barriers to Water Quality Management

Even though the interactions of nutrient subsidies described above may facilitate management for water quality, there are a number of potential barriers to improving water quality in reservoirs dominated by gizzard shad. For example, reductions in gizzard shad populations via enhanced piscivory may not be feasible, as it appears that native piscivores (such as largemouth bass) are not likely to control gizzard shad populations (Stein et al. 1995). For example, in highly productive Ohio reservoirs, gizzard shad hatch earlier than other fish, and juveniles can switch to feeding on sediments once they develop a gizzard (which occurs when they are just a few months old). This developmental pattern results in relatively rapid growth of YOY gizzard shad, rendering them less vulnerable to YOY bass. Bass recruitment (and ultimately, population size) is greatly affected by success in the first year of life; thus, bass populations may not reach the densities necessary for regulation of gizzard shad populations (Stein et al. 1995, 1996). Introductions of exotic piscivores, such as striped bass or saugeye, may be more effective in controlling YOY gizzard shad, and hence overall gizzard shad biomass (Stein et al. 1996). Of course, introductions of exotic species are risky "experiments." Nevertheless, introductions of exotic piscivores are carried out all the time by state agencies, and these introductions may offer opportunities to test some predictions of food web theory (Stein et al. 1996).

Gizzard shad are virtually the only abundant fish in North American reservoirs that rely on sediment detritus. Therefore, reductions in watershed-derived sediment might effectively reduce gizzard shad populations. Efforts to control soil erosion in watersheds would also increase water clarity, an additional benefit. One effective means of reducing soil erosion is to reduce the extent to which croplands are tilled (conservation tillage) or eliminate tillage entirely (no-till methods). However, reduced tillage frequency may lead to increased export of dissolved phosphorus from croplands to water (Logan 1990; Gaynor and Findlay 1995) by at least two mechanisms (Logan 1990). First, P bound to sediments from conservation tillage fields tends to be more labile than P bound to sediments from conventional tillage fields because the former sediments tend to be higher in clay and organic matter. Second, the surface application of P fertilizer to the relatively undisturbed soils of conservation tillage fields can lead to a greater buildup of labile P at the soil surface than in the more frequently disturbed (tilled) fields of conventional agriculture. Because conservation tillage usually results in reduced export of particulate-bound P but sometimes results in increased export of dissolved P, the net effect of conservation tillage on total P export will depend on the relative contributions of dissolved versus particulate P export from a given watershed. Nevertheless, increased export of dissolved P under conservation tillage could increase algal biomass in recipient aquatic systems, particularly if light intensity penetration increases along with decreased sediment loading. Other strategies of reducing nutrient inputs from watersheds, such as reducing fertilizer use or protecting riparian habitats, therefore must be explored (Gaynor and Findlay 1995).

Carbon Sequestration in Reservoirs

Recent evidence suggests that exports of matter and nutrients from watersheds to aquatic systems and food web interactions within aquatic systems have implications for the global carbon cycle and hence global climate change. Based on recent data, Dean and Gorham (1998) concluded that 3 times as much organic carbon is buried annually in the sediments of freshwater ecosystems (lakes, reservoirs, and peatlands) as in the sediments of all of the world's oceans, even though freshwater ecosystems constitute less than 2% of the earth's surface. About half of all C buried in freshwater sediments is buried in reservoirs (Dean and Gorham 1998). Two mechanisms account for these high rates of burial in freshwater sediments. First, the rate at which materials are transported from land to water, expressed per unit surface area (of water), is much higher in fresh waters. This difference arises simply because freshwater systems are in closer contact with land than is the average ocean locale. This is analogous to the situation on oceanic islands, where inputs of ocean-derived detritus are greater (per unit island area) on small islands than on large islands (Polis and Hurd 1994). Second, because freshwater ecosystems are much shallower than the oceans, a much greater proportion of organic carbon becomes buried in sediments before being respired to CO_2. In the ocean, a much larger proportion of carbon is respired as organic matter sinks. Thus, freshwater systems may effectively trap considerable amounts of carbon. Reservoirs, having large watersheds, may play a critical role in storing carbon.

Food web structure and nutrient fluxes influence how much carbon is stored in lake sediments. Schindler et al. (1997) showed that the level of nutrient enrichment and food web structure affects whether lakes are net sources or sinks with respect to atmospheric CO_2. When lakes are fertilized or when herbivory is low (i.e., when planktivorous fish are abundant and large herbivores scarce), phytoplankton biomass is relatively high. High rates of photosynthesis draw CO_2 from the atmosphere into the lake water. Under these conditions, lakes are net sinks for carbon, presumably because much of the organic carbon is ultimately buried in sediments. When lakes have low nutrient inputs or when large grazers are abundant, phytoplankton biomass and photosynthetic rates are low. Under these conditions, respiration exceeds photosynthesis, and more CO_2 is released to the atmosphere than is drawn in.

Evidence strongly suggests that most lakes are net heterotrophic systems (i.e., respiration exceeds photosynthesis) because they are subsidized by organic carbon inputs from watersheds (Cole et al. 2000; Caraco and Cole, chap. 20 in this volume). This is almost certainly the case in most reservoirs, where allochthonous inputs of organic carbon are large. Indeed, it has been argued that reservoir fish production could not be sustained by in situ photosynthetic production (Adams et al. 1983). On the other hand, the high rates of organic carbon burial in reservoir sediments could cause reservoirs to be net carbon sinks. Food web interactions in reservoirs probably mediate the extent to which these ecosystems are net carbon sinks or sources. In Ohio reservoirs, phytoplankton abundance is much higher when sediment-feeding gizzard shad are abundant than when shad are scarce. This pattern has been demonstrated by enclosure experiments (Schaus and Vanni 2000) as well as whole-lake observations (M. J. Vanni et al., unpublished data). Thus gizzard shad abundance may be positively correlated with the net flux of carbon from the atmosphere to lake water, and ultimately with the rate at which autochthonously produced carbon is buried in sediments. On the other hand, sediment-feeding fish often resuspend sediments. Once resuspended, carbon may be exported via outflow streams or may be respired by bacteria. In other words, bioturbation of sediments by gizzard shad may decrease the rates at which organic carbon (including that from watershed-derived sources) is permanently buried in sediments. Thus it is clear that in reservoirs, watershed inputs and gizzard shad have the potential to affect net carbon flux, and that these factors may interact in complex ways. To determine whether reservoirs, or any other habitats, are net sources or sinks for carbon, we need to consider cross-habitat fluxes among their watersheds, the atmosphere, the water column, and the bed sediments and how these fluxes are mediated by food web processes.

WETLANDS AFFECTED BY REGIONAL AGRICULTURAL SUBSIDIES TO GEESE

Certain wetlands derive nutrients from spatial scales vastly greater than their local watershed through inputs mediated by the continental migrations of agriculturally subsidized geese. Along the marshes bordering Hudson Bay, tens of thousands of lesser snow geese arrive each summer to hatch and rear their goslings and graze on local graminoids (Jefferies et al., chap. 18 in this volume). Over recent years, populations of these geese have increased dramatically due to subsidies from grain fields in their wintering grounds in the United States and decreased human hunting. The increasingly crowded summering geese have had to switch from nondestructive clipping of aboveground graminoid leaves to destructive grubbing of the perennating roots and rhizomes. As a result, once productive marshes along Hudson Bay are being converted to mudflats, which are unlikely at these high latitudes to support much secondary invertebrate production. This conversion may be long-term, as it is stabilized by feedbacks such as salinization following graminoid extirpation (Jefferies et al., chap. 18 in this volume).

Wetlands in the southwestern United States that are wintering grounds for geese and other waterfowl are also being damaged by agricultural subsidies (Post et al. 1998). Wetlands in the arid Southwest have been largely lost to development and water diversion for human use. Flocks of lesser snow geese and Ross's geese winter on the small remnant wetlands that are managed for waterfowl production. Up to 40,000 geese winter in the Bosque del Apache National Wildlife Refuge along the middle Rio Grande Valley in central New Mexico, making up about 50% of the bird biomass on these wetlands, which also support sandhill cranes and ducks (Post et al. 1998). Using bioenergetics modeling calibrated with feeding, movement, and roosting observations, Post and colleagues estimated that geese translocated enough nutrients from local corn and alfalfa crops into these wetlands to account for 40% and 75% of the annual nitrogen and phosphorus inputs into their study area during one winter season.

These nutrient subsidies may have at least four consequences for the small areas of remaining wetlands. First, arriving goose populations (subsidized by agricultural production elsewhere before arriving on their wintering grounds) feed on marsh vegetation (such as bulrushes, *Scirpus pungens*), deplete it, and damage its regenerative potential. The damage may be direct, from overgrazing, as well as indirect, as goose-imported nutrients encourage the growth of periphyton and phytoplankton that shade submerged macrophyte leaves (Moss 1990). Second, after geese deplete the marsh vegetation, they expand their foraging area to graze local crops, which they can also damage (again, this effect may be intensified by subsidies from more remote agriculture). Third, geese translocate nutrients from croplands into the marsh, degrading wetland water quality and elevating nutrients to levels that support blooms of blue-green algae. Blue-greens may attain densities that are toxic to waterfowl and other animals. Finally, this eutrophication of wetlands enhances the probability of outbreaks of contagious avian cholera and type C botulism, which threaten other waterfowl of conservation concern, specifically the sandhill cranes (see Post et al. 1998 and references therein).

Post and colleagues studied these subsidy mechanisms and flow paths in sufficient detail to provide useful information to managers. First, they identified the vector organisms and the spatial and temporal scales of the fluxes. Geese (and not ducks, which fed within the wetlands, or cranes, which sometimes foraged outside wetlands for prolonged periods but farther afield) were largely responsible for importing nutrients from local agricultural fields into the wetlands. The amount of nutrients geese loaded into the wetlands was influenced by the weather. When wind speeds rose above a certain (temperature-dependent) threshold, geese tended to loaf at midday on a field, recycling some of their acquired nutrients locally. Under lower wind speeds and warmer temperatures, they returned midday to loaf and excrete on the wetlands. Loading also depended on whether geese fed on corn or alfalfa. Alfalfa had a higher gut passage rate, so a larger proportion of the nutrients in ingested biomass was excreted on agricultural fields. Alfalfa also, however, had a lower energy content than corn, so geese had to eat 8–9 times more biomass to meet their energy needs. Consequently, managers could reduce nutrient inputs to wetlands by planting only corn in areas foraged by geese. Of course, the most effective remedies for goose-induced eutrophication would be to flush more water through the wetland units where the geese rest, to reduce goose densities by hunting or harassment to overcome their colonial roosting habits (90% of the geese roost on 10% of the wetlands), or to expand available wetland habitat. Habitat expansion and increased flushing would require more water, an increasingly limiting resource in the arid western United States (Reisner 1986, 1990; Gleick 1998; Power et al. 1997) and wherever human diversions and groundwater mining have altered food webs and ecosystems (Riley and Jefferies, chap. 25 in this volume; Kindler 1998).

SUBSIDIES AND CONSERVATION BIOLOGY

Food web connections across habitats affect focal species for conservation biology, whether these are endangered species themselves or key interactors that influence the fates of endangered species and their ecosystems.

Many key and endangered species forage in multiple adjacent habitats or migrate among distant habitats. Moose (Belovsky 1981), hippopotamuses (Naiman and Rogers 1997), eagles, and salmon (Spencer et al. 1991) use a mix of marine, freshwater, and terrestrial habitats. Consumers that depend on spatially and temporally variable resources (fruit, nectar, insects, forbs) must be highly mobile to track those resources, sometimes over intercontinental scales (Levey and Stiles 1992). Within a region, most birds and large herbivores and carnivores obtain foods from a mosaic of habitats. For example, Serengeti ungulates must migrate in order to acquire the proper mix of required elements (e.g., Na, P, Ca) from plants that grow in several different places (McNaughton 1990). Across regions, endangered migratory songbirds, water birds, and raptors, land and marine mammals, and some insects migrate long distances to feed in quite distinct habitats. Songbirds are vulnerable to changes in resource and habitat availability in either their northern (summer) or southern (winter) habitats.

Many key and endangered species use resources that arrive from more than one habitat. These include species living in habitat edges (such as riparian and coastal ecotones; see below) and species that use migratory foods. For example, approximately fifty species of terrestrial predatory and scavenging vertebrates in Alaska receive much of their annual energy budget by eating anadromous salmon (Willson et al. 1998 and chap. 19 in this volume). The orange roughy, an important commercial fish, lives on deep seamounts, areas of very low light and in situ productivity. These fish eat prey carried to them by currents and vertical migrations; their population biomass was once an order of magnitude higher than that of deep-sea fish populations that do not receive allochthonous prey. Nevertheless, their overexploited populations are now plummeting (Koslow 1997).

Enemies of key or endangered species are frequently subsidized by foods produced in other habitats. This problem worsens as habitats become more fragmented and edge-to-area ratios increase. For example, nest parasitism by cowbirds from nonforested habitats can greatly depress forest birds in fragmented forests because the smaller a forest fragment, the greater the proportion of that fragment that lies along a nonforested edge (Ambuell and Temple 1983; Wilcove et al. 1986; Andrén and Anglestam 1988). In a similar manner, subsidized domestic cats threaten English songbird populations and ground-dwelling birds in northern California.

Mobile animals can damage ecosystem structure and function. Concentrations of domestic herbivores (e.g., cattle, sheep, goats) denude vegetation worldwide around water holes, riparian areas, corrals, and feeding stations. These effects should be considered when aid agencies sink wells to ameliorate the effects of drought in developing countries. An unpleasant management surprise resulted from spatially rearranging water subsidies in Kruger National Park, South Africa (Starfield and Bleloch 1986). When game managers dug water holes in northern parts of the park to support the local endangered roan antelope, zebras were attracted to areas formerly too dry to support them. Lions followed the zebras, but wiped out the roan antelope instead. Wildlife modelers deduced this by noting that the roan antelope had good adult body weight but poor juvenile survival, indicating that its population declined because of apparent competition (sensu Holt 1977) rather than exploitative competition with zebras. Apparent competition may also affect a species' conservation status in natural circumstances. Nomadic herds of ungulates traveling through the Serengeti track rainfall to forage in relatively productive habitats (Sinclair and Norton-Griffiths 1979; Senft et al. 1987). Such migratory prey (e.g., wildebeest) are thought to allow resident lions to increase to the point at which they depress resident species (e.g., warthogs, impala; Schaller 1972). Subsidized lions are a key factor limiting endangered cheetah populations (Caro 1987). Heavy poaching of mobile Cape buffalo outside the Serengeti lowered buffalo numbers in the game park, causing lions to decrease substantially and resulting in increases in several alternative prey species (A. R. E. Sinclair, personal communication to GAP).

Trophic interconnections among habitats carry important implications for conservation efforts, which are usually directed at target species or circumscribed habitats. Most obviously, conservation may require the preservation or management of more than just focal species and their habitats. Allochthonous inputs may affect the success and abundance of a species directly (as food) or indirectly (via food web effects). Migrations to and inputs from external habitats can affect local community dynamics and ecosystem function. The loss of allochthonous resources could threaten species and whole communities. An excellent example of a non-trophic but crucial allochthonous resource is the shifting sands needed to preserve the Coachella fringe-toed lizard and several endemic beetle species in the Coachella Valley of California (Turner et al. 1984; Beatley 1992; Barrows 1997). To preserve the unstable habitats that gave these rare species an edge over competitors that could exclude them in more stable habitats, The Nature Conservancy of California and other planners had to protect not only the lizard's immediate habitat, but also the source areas generating the sands and the landscape corridors that convey sands to the dunes actually inhabited by the lizard.

Overall, it is critical to understand that species success, community structure, and ecosystem function are often strongly connected to the dynamics of other habitats. Adequate conservation plans ideally should include all habitats influencing the dynamics of the target species and ecosystems.

CONSERVATION AT THE LAND-SEA INTERFACE

We now explore how the sea influences, both positively and negatively, conservation on islands and along the coastal ecotone. These habitats are home to many of the world's endangered and endemic species. Diverse terrestrial animals using marine resources attain high densities on coasts and small islands worldwide (Polis et al., chap. 14 in this volume). For example, many island endemics depend on foods associated with seabirds (e.g., the tuatara of New Zealand; Daugherty et al. 1990). Many large vertebrates flourish along coasts, including large birds of many types (e.g., eagles and large vultures) and mammalian carnivores (e.g., many canids and felids) (Rose and Polis 1998). These diverse species eat intertidal foods, marine carrion, and foods from colonies of marine birds and mammals. For example, photographs from the early 1900s show groups of the now endangered California condor foraging on whale carcasses stranded along southern California beaches. For all these creatures, input from the ocean is key to the success and numbers not only of coastal populations, but also possibly of inland populations via source-sink dynamics.

Humans have changed many aspects of marine ecosystems. Most notably, overfishing and pollution have decreased the productivity and species diversity of coastal and open ocean communities. Such changes must exert profound influences on the quality and quantity of input to islands and thus to island communities. For example, decreased fish populations depress the abundance of seabirds, a dominant group that structures entire communities on islands worldwide (Hutchinson 1950; Polis et al., chap. 14, and Anderson and Polis, chap. 6 in this volume). Decreases in the abundance of marine fish and mammals also lower the numbers of carnivorous and scavenging vertebrates that forage on marine carrion along the coast (Rose and Polis 1988) and on anadromous fish along river shorelines (e.g., Willson et al., chap. 19 in this volume, Ben-David, Bowyer et al. 1998; Wipfli 1997).

Humans have also damaged island communities by introducing exotic animals (Atkinson 1994), either deliberately (e.g., grazing sheep, goats, rabbits, and cattle; omnivorous pigs and boars; and predatory domestic cats, mongooses, and foxes) or inadvertently (several species of rats). The results have usually been catastrophic for native biota. It is not as well recognized, however, that foods from the sea have magnified the harmful effects of introduced species. Scattered reports document that most of these invasive mammals use marine foods (either shore material or seabirds). These subsidized exotics then depress populations of local endemic species, sometimes to the point of extinction. In many cases, invasive species have largely extirpated native endemics but still occur at high numbers, maintained by shore, intertidal, and seabird resources. Such subsidized populations place continuous pressure on those few natives that have escaped the initial depredation and thwart attempts to reintroduce and restore native populations.

Domestic cats (*Felis catus*) and various rats are notorious for causing extinctions on islands. Subsidized by seabirds, they also eat insular terrestrial species (Williams 1978; Burger 1985; Atkinson 1994). Cats on Ascension Island exterminated five species of seabirds, originally present in thousands of breeding pairs. Norway rats (*Rattus norvegicus*) on South Georgia Island restrict the breeding areas and numbers of seven seabird species by eating their eggs and chicks. Worldwide declines of small and medium-sized seabirds are attributed to predation on adults, chicks, and eggs by introduced rats and cats on nesting islands (Atkinson 1985; Stapp 2002; McChesney and Tershy 1998; Hobson et al. 1999; and many others). Cats have strong effects even on non-bird islands. For example, on islands on the Pacific side of Baja California, cats have greatly depressed native reptiles and small mammals (D. Croll, personal communication). These cats still occur in large numbers, but only along the shore, where they prey on and scavenge marine foods.

Regurgitated scraps and corpses of seabirds may be important food sources for mice and rats (e.g., Rowe-Rowe and Crafford 1992), supporting high densities of both native and introduced rodents on some islands with seabird colonies (e.g., Rowe-Rowe and Crafford 1992; Efford et al. 1988). These omnivorous and opportunistic rodents subsequently eat and threaten local populations of other native fauna (e.g., lizards [Cree et al. 1995; Towns 1991] and arthropods [Palmer and Pons 1996; Rowe-Rowe et al. 1989; Bremner et al. 1984]) and flora (Ryan et al. 1989) to an extent not possible if seabirds were absent. For example, kiore (a native New Zealand rat) accidentally introduced to offshore islands have greatly reduced populations of seabirds, endemic arthropods, lizards, and tuatara in New Zealand (Daugherty et al. 1990).

Even large herbivores such as cattle, sheep, and deer can maintain populations above the carrying capacity supported by terrestrial plant productivity by foraging on intertidal algae. Red deer feed on algae and then damage the terrestrial plant community by heavy grazing on Scottish islands (Clutton-Brock et al. 1983). On Auckland Island, introduced cattle survived on algae after removing almost all native land plants. Pigs on Auckland Island take eggs, young, and adults of burrow-nesting birds while also competing with insular herbivores (Atkinson 1994). The interplay among marine subsidies, introduced exotics, and declining native endemic and endangered species merits further investigation.

CONTROL OR LACK THEREOF: SUBSIDIES AND INFECTIOUS DISEASE

Humans have suppressed or eliminated most of the large species that threaten us. We may have accomplished this long ago: higher percentages of dangerous animals (mammoths, rhinos, bears) are prevalent in the earliest known cave paintings (e.g., in Chauvet, dated at 32,000 B.P.) than in more recent cave art painted 12,000–20,000 years B.P. (Jean Clottes, cited in Balter 1999). We have been less successful in controlling our smaller enemies, and may lose ground in this effort as the human population grows denser and more globally mixed. Zoonotic infections (yellow fever, typhus, Chagas' disease, hantavirus) increase with contact between humans and nonhuman hosts. Outbreaks can occur when and where human agriculture subsidizes rodent host populations and concentrates them near human dwellings (e.g., Lassa and Ebola fevers; Garrett 1994). In other cases, we rearrange the environment in ways that facilitate the contact. Felling tropical trees brings *Hemagoggus speggazini*, a canopy-dwelling mosquito that vectors yellow fever, into contact with humans (Southwick 1996). Air travel provides fossil fuel subsidies to pathogens, increasing contact among infected and susceptible human hosts. Infectious disease agents can now spread and explode in a world where the most distant major cities are only 16 hours apart.

Our subsidies to pigs, cattle, chickens, Atlantic salmon, and other livestock, concentrated for industrial meat production, have polluted ecosystems over regional scales. Nitrogenous wastes from pig factories enter coastal rivers, estuaries, lagoons, and shallow coastal waters off the southeastern United States by two paths: continuously by ammonia volatilization and precipitation (Paerl 1985) and episodically, when sewage spills occur (Mallin et al. 1999). The resulting eutrophication of the habitats that once sustained valuable shellfish and finfish populations will be difficult to reverse. When phytoplankton blooms triggered by these nutrient additions sink, they create anaerobic conditions in bed sediments, which mobilize nutrients. These nutrients are then easily stirred by wind or currents back into the water column in shallow estuaries and offshore lagoons, stimulating subsequent phytoplankton blooms (Paerl 1985). These blooms lower the oxygen content of the water and often are dominated by harmful algae, including *Pfeisteria piscicida*. Increasingly frequent blooms and outbreaks off the southeastern United States have caused repeated, large-scale fish kills and human as well as environmental health problems (Burkholder et al. 1997).

Another threat to human health from industrial meat production is the use of antibiotics in highly crowded factory farms and their counterparts in aquaculture. About half of the antibiotics used annually in the United States are used "subtherapeutically" in animal feeds (American Society of Microbiology 1995). The profligate use of antibiotics for meat production selects for strains of drug-resistant bacteria (e.g., antibiotic-resistant *Salmonella* traced to pigs in Denmark; Hwang 2000), reducing our arsenal of antibiotics at a time when we are particularly likely to need them.

CONCLUSIONS

As the natural world falls ever more under human domination, we distort both local ecosystems and the flows among them at regional and global scales. The subsidy framework developed by Gary Polis and his colleagues can help organize our attempts to understand, predict, and manage the consequences. This framework requires first that the landscape positions of the sources and flow paths of fluxes that influence local ecosystems be identified. Failure to do this has precluded efforts to protect species and ecosystem services (e.g., by not distinguishing source from sink populations or by failing to recognize flow paths of enemies or crucial resources). The subsidy framework also requires expanded scales of study, as local short-term studies will not uncover causal linkages and feedbacks acting

over large spatial or temporal scales. With models based on assumptions about key processes and interactions in both source and recipient habitats, we can ask how chains of consequences set in motion when we intensify or curtail ecosystem fluxes will play out over years, decades, and centuries and over local, regional, and global spatial scales. We can also ask how the system would change under various management schemes or under foreseeable changes in the environment.

These approaches could help us recognize when management for one target (e.g., agricultural production) affects other values or goals (e.g., species conservation, water quality, or human health). Understanding these interconnections and the large spatial scales over which the human enterprise distorts them is vital, not only for predicting and evaluating the consequences of our actions, but also for educating the public and marshaling the political will to change destructive practices and policies.