

Current Normative Concepts in Conservation

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Abstract: *A plethora of normative conservation concepts have recently emerged, most of which are ill-defined: biological diversity, biological integrity, ecological restoration, ecological services, ecological rehabilitation, ecological sustainability, sustainable development, ecosystem health, ecosystem management, adaptive management, and keystone species are salient among them. These normative concepts can be organized and interpreted by reference to two new schools of conservation philosophy, compositionism and functionalism. The former comprehends nature primarily by means of evolutionary ecology and considers Homo sapiens separate from nature. The latter comprehends nature primarily by means of ecosystem ecology and considers Homo sapiens a part of nature. Biological diversity, biological integrity, and ecological restoration belong primarily in the compositionist glossary; the rest belong primarily in the functionalist glossary. The former set are more appropriate norms for reserves, the latter for areas that are humanly inhabited and exploited. In contrast to the older schools of conservation philosophy, preservationism and resourceism, compositionism and functionalism are complementary, not competitive and mutually exclusive. As the historically divergent ecological sciences—evolutionary ecology and ecosystem ecology—are increasingly synthesized, a more unified philosophy of conservation can be envisioned.*

Conceptos Normativos de Conservación en la Actualidad

Resumen: *Una gran cantidad de conceptos normativos en conservación han emergido recientemente, la mayoría de ellos han sido mal definidos: diversidad biológica, integridad biológica, restauración ecológica, servicios ecológicos, rehabilitación ecológica, sustentabilidad ecológica, desarrollo sustentable, salud del ecosistema, manejo de ecosistemas, manejo adaptivo y especies clave sobresalen entre ellos. Estos conceptos normativos pueden ser organizados e interpretados en referencia a dos nuevas escuelas de filosofía de la conservación, composicionalismo y funcionalismo. La primera concibe la naturaleza básicamente mediante la ecología evolutiva y considera a Homo sapiens separado de la naturaleza. La segunda concibe a la naturaleza mediante la ecología de ecosistemas y considera a Homo sapiens como parte de la naturaleza. La diversidad biológica, integridad biológica y la restauración ecológica pertenecen primariamente al glosario composicionalista; el resto pertenecen primariamente al glosario funcionalista. El primer juego de conceptos es más apropiado para normatividad de reservas; el segundo para áreas que son humanamente habitadas y explotadas. En contraste con las escuelas viejas de filosofía de la conservación, preservacionismo y recursoismo, composicionalismo y funcionalismo son complementarias, y no competitivas y mutuamente excluyentes. Al igual que las ciencias ecológicas divergentes—ecología evolutiva y ecología de ecosistemas—son sintetizadas en forma creciente, una filosofía de la conservación más unificada puede ser visualizada.*

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Introduction

With the advent of conservation biology and “clinical ecology”—an even more recently emerged transdiscipline (Rapport 1992)—a plethora of ill-defined normative concepts are now in circulation in the conservation community. The most salient are biological diversity, biological integrity, ecological restoration, ecological services, ecological rehabilitation, ecological sustainability, sustainable development, ecosystem health, ecosystem management, adaptive management, and keystone species. We provide a synopsis, analysis, and schema for organizing them. A normative conservation concept—sometimes called an “umbrella concept” (Noss 1995a)—sets the agenda for conservation efforts. Such a concept is nakedly value-laden. Other important concepts in conservation have recently been advanced: minimum viable population, source-sink dynamics, habitat fragmentation. Although these concepts may also be value-laden, they are less openly so and are more technical and tactical than philosophical and strategic.

The normative terms in conservation discourse are sometimes called “buzzwords” and thus are rhetorically dismissed as ill-defined and lacking in substance (Wicklum & Davies 1995). Some of them, however, are institutionalized in national, international, and multinational policy and law. For example, biological integrity has been mandated for the waters of the United States since 1972 (Ballantine & Guarraia 1977) and for the national parks of Canada (Woodley 1993) and the waters between Canada and the United States (Regier 1992) since 1988. Ecosystem health is mentioned in the *Rio Declaration on Environment and Development* and in other official international conventions (Rapport 1995). Such influential high-level policy documents as *World Conservation Strategy: Living Resource Conservation for Sustainable Development* (World Conservation Union/United Nations Environmental Program/The World Wide Fund for Nature 1980), *Our Common Future* (World Commission on Environment and Development 1987), and *Caring For the Earth: A Strategy for Sustainable Living* (World Conservation Union/United Nations Environmental Program/The World Wide Fund for Nature 1991) promote the concept of sustainable development. Although some scientists remain skeptical (Ludwig et al. 1993), these concepts are at large in the world shaping conservation thought and policy. Further, robust efforts to define them precisely and usefully exist in the literature of applied ecology, conservation biology, and clinical ecology. Because they help shape and articulate conservation policy, conservation efforts will be confused and confounded in the absence of a clear understanding of, and consensus regarding, these normative ideas.

Sometimes one norm is proffered as preeminent, in an attempt to eclipse a need for the others and to focus all conservation efforts on a single, preferred goal. Since its

advent in the 1980s, the *summum bonum* of conservation biology has been biological diversity, or biodiversity for short (Soulé 1985). Alternatively, Angermeier (1994) and Angermeier and Karr (1994) argue that the best norm for conservation biology is biological integrity. Salwasser (1990) has tried to refocus conservation biology even more radically by proposing that sustainability be its principal goal. We suggest that all these current normative concepts in conservation are useful, and the more narrowly and precisely they are interpreted the more useful they will be. Our approach is pluralistic. We recommend the preservation of conceptual diversity in conservation philosophy, by parity of reasoning with arguments for the preservation of both biological and cultural diversity.

Our definitions are stipulative, not descriptive. That is, we do not attempt to survey and catalog the ways these normative terms are used, calculate the most frequent usage, or recommend that as the standard, technical definition of each. Rather, within the limits of their etymologies, lexical definitions, and common usage, we craft interpretations useful to conservation applications. In addition to defining them, we explore an ordering intellectual structure, characterized by two complementary worldviews, in which these normative concepts in conservation are embedded. By means of this structure, the current conceptual thicket of conservation norms can be surveyed and mapped.

Compositionism and Functionalism

Although the current normative concepts in conservation can be delineated and sorted out in many different ways, they can be most generally and insightfully ordered by association with two new (in comparison with twentieth-century resourceism and preservationism [Callicott 1990]) schools of conservation thought that have clearly taken shape. These schools are characterized by an inclination toward one or the other of two different approaches to ecology, clearly distinguished by Hutchinson (1978), Hagen (1989), and Bocking (1994), and by a difference of opinion about the correct answer to an age-old philosophical question: What is the human place in nature? (Fig. 1).

Compositionists perceive the world through the lens of evolutionary ecology, an essentially entity-oriented, biological approach to ecology that begins with organisms aggregated into populations. These evolving populations interact, most often autecologically and agonistically, in biotic communities (Whittaker & Woodwell 1972). *Functionalists* perceive the world through the lens of ecosystem ecology, an essentially process-oriented, thermodynamical approach to ecology that begins with solar energy coursing through a physical system that includes but is not limited to the biota (Odum 1968). From the functionalist perspective, organisms are regarded as moments in interlocked processes of energy transfers and

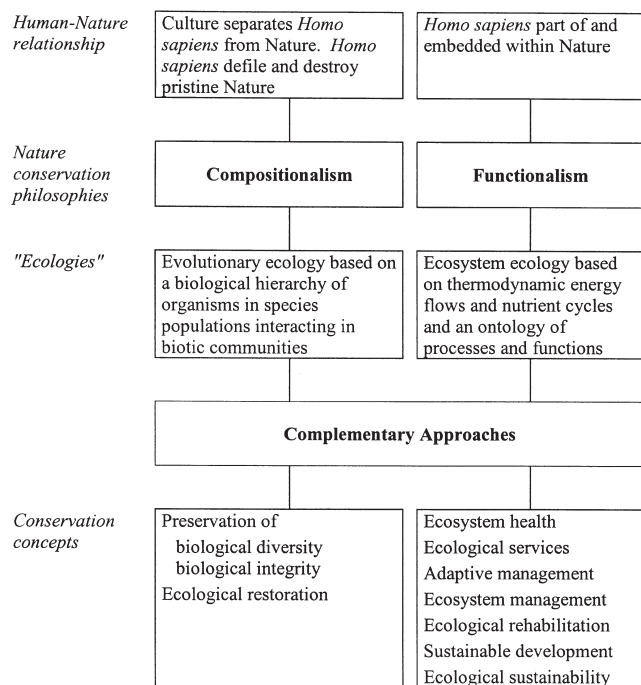


Figure 1. Associations between conservation philosophies, human-nature relationships, "ecologies," and conservation concepts.

nutrient cycles, quite indifferently, in the classic formulations of ecosystem ecology, to specific taxonomic identity (Lindeman 1942; Likens et al. 1970).

Functionalists tend to think that people are a part of nature and that *Homo sapiens* is no less natural than any other species. Functionalism's humanity-nature doctrine is based on the Darwinian interpretation of *Homo sapiens* as a precocious primate—a naked ape—differing in degree but not in essence from other species (Darwin 1871, 1872). This view of the human place in nature is elegantly articulated by Leopold (1949): "It is a century now since Darwin gave us the first glimpse of the origin of species. We know now what was unknown to all the preceding caravan of generations: that men are only fellow-voyagers with other creatures in the odyssey of evolution."

Compositionists tend to think that people are a case apart from nature. Classically, what distinguishes people from nature is the biblical image of God or its ancient Greek philosophical equivalent, divine rationality. Compositionists do not dispute the Darwinian claim that *Homo sapiens* is an evolved species, kin to all the rest. Rather, *Homo sapiens'* acquisition of culture has propelled the species out of nature's ambit (Rolston 1991) because culture uniquely enables *Homo sapiens* to adapt to various environmental conditions many orders of magnitude faster than can other species, which generally are limited in their adaptive responses to the relatively slow process, spread over many generations, of genetic mutation and natural selection (Dobzhansky 1963). If one thinks that way about

the humanity-nature relationship, one will be inclined to think that any human modification of nature is unnatural.

The connection between a compositionalist view of the humanity-nature relationship and evolutionary ecology is tenuous and contingent, not logically necessary. On evolutionarily significant scales of time, *Homo sapiens* is a latecomer, a new species in comparison with any other of comparable size. The rapid temporal and wide spatial scales of human activity often greatly alter the composition of biotic communities. From a Dobzhanskyan evolutionary point of view, *Homo sapiens* thus appears to be a destructive force of change external to the biota because—albeit an evolved species—*Homo sapiens* employs a unique means, culture, of adapting to its environments and altering its environments to suit itself.

The connection between a functionalist view of the humanity-nature relationship and ecosystem ecology is also tenuous and contingent, not logically necessary. Functionalism is more abstract than compositionism, hence human dissipative structures do not stand out so sharply from others of comparable size and distribution. Early research in ecosystem ecology often focused on environments affected by people, some of which surrounded major nuclear facilities, and was also often violently experimental (Golley 1993). Changes in the biota that people routinely impose do not always affect the ecological processes that compose ecosystems. When human changes in the biota do not adversely alter ecosystem functions, people may appear to live in harmony with nature even though they are significantly altering the composition of biotic communities.

We sharply distinguish compositionism and functionalism only for expository purposes; they in fact constitute two ends of a continuum. Some conservationists may sometimes exemplify one or the other extreme. For example, according to Allen and Hoekstra (1993), conservation "is almost never the preservation of a primeval condition, but rather means maintaining the critical functions of the primeval system." Soule (1996) pointedly disagrees: "What is wrong with simply maintaining or restoring ecological processes? It is this: the processes . . . are generic. They can be performed by weedy species." Our experience suggests, however, that most conservationists lie somewhere toward the middle of the compositionism-functionalism continuum, moving back and forth in emphasis depending on circumstances. In this respect, our characterization of the compositionalist and the functionalist schools of conservation thought is analogous to a political scientist's characterization of the Democratic and Republican political parties in the United States. Although some politicians may exemplify the party stereotype, most lie somewhere between the extremes of the left-right political continuum and move back and forth in emphasis depending on the circumstances and issues. Biological diversity, biological integrity, and ecological restoration are more at home in the compositionalist glossary.

Ecosystem health, ecological services, adaptive management, ecosystem management, ecological rehabilitation, sustainable development, and ecological sustainability are more at home in the functionalist glossary.

The Compositionalist Glossary

Biological diversity is the variety of life at every hierarchical level and spatial scale of biological organization: genes within populations, populations within species, species within communities, communities within landscapes, landscapes within biomes, biomes within the biosphere (Wilson 1992). Because of widespread concern about the currently acute species-extinction crisis, preserving biodiversity is popularly understood to mean preserving species (Wilson 1988). But a species can be preserved in a zoo or lab or even as germ plasm in seed banks or cryopreserves. To make the concept more comprehensive, the hierarchical levels of biological organization both below and above the species level were soon included in the concept of biodiversity (Noss 1990a). To make it maximally comprehensive, Noss and Cooperrider (1994) define *biodiversity* so broadly that it refers not only to this tall hierarchy of biological entities—from genes to landscapes—but also to “ecological and evolutionary processes.” The leading champions of biodiversity advocate making the preservationist legacy of national parks and other roadless areas the starting point of much-expanded “big, fierce wilderness” reserves—not for recreational, aesthetic, or spiritual enjoyment by human pilgrims, but as habitat for evolutionarily viable nonhuman species populations (Noss 1990c; Foreman 1995; Grumbine 1996).

Biological integrity is native species populations in their historic variety and numbers naturally interacting in naturally structured biotic communities (Angermeier & Karr 1994). As the principal goal toward which conservation efforts should aim, biodiversity has been challenged by Angermeier (1994) and Angermeier and Karr (1994), who argue that biological integrity ought to be the principal normative concept in conservation because biodiversity may be artificially increased by introducing exotic species into vacant or underexploited niches, thereby violating the integrity of a biotic community. Champions of biodiversity, therefore, sometimes simply limit the concept, ad hoc, to “native biodiversity, not diversity per se” (Noss & Cooperrider 1994).

Noss (1995b) and Noss and Cooperrider (1994) defend such a limitation on the biodiversity norm, arguing that although local species diversity may be increased by introducing exotics, the same introductions may decrease both landscape diversity (by making biotic communities more alike) and global species diversity (through the competitive exclusion of sensitive native and endemic species by hardy cosmopolitan species). Clear Lake in California is a case in point. In the past it had 12 native fish species;

it is now home to 23 (Moyle 1989). Thus its fish fauna is nearly twice as diverse as in its historic condition. The cultural introduction of 16 species has made Clear Lake a more diverse aquatic community than it formerly was, but it is now similar to many other aquatic communities and 5 of its native fishes were extirpated, of which 2 are now globally extinct (Moyle 1989). According to Noss (1995b), “the global scale is the most critical scale for evaluating these kinds of changes.” Of course, it must be remembered that sometimes the introduction—whether cultural or natural, intentional or unintentional—of an exotic species can dramatically decrease biodiversity at every scale (Coblentz 1990). A few such cultural introductions are infamous: the sea lamprey and the alewife in the upper Great Lakes (unintentional), the brown tree snake on Guam (unintentional), and the Nile Perch in Lake Victoria (intentional).

For reasons too technical to review here, Angermeier and Karr (1994) argue further that, although natural processes are many and complex, they are not plausibly characterized as aspects of biodiversity. Most historic efforts to conserve biodiversity have in fact targeted species diversity, the “fine-filter” approach, and community diversity, the “coarse-filter” approach (Noss 1990b). And processes as such are not the more population-oriented, technically defined targets of recent legally mandated biodiversity conservation: evolutionarily significant units (Waples 1995). In general, according to one leading compositionalist, “the processes of ecosystems are universal, but the species are not. The processes, including photosynthesis, nutrient transport, fixation of nitrogen, the water cycle, the decomposition of organic matter by invertebrates and microorganisms, the sequence of seasonal events . . . and disturbances by fire and floods occur in nearly every terrestrial or aquatic ecosystem on Earth. They are generic” (Soulé 1996). Hence Angermeier and Karr (1994) can plausibly insist that “diversity [conventionally, at least] describes only the elements” of the biota and that biological integrity more inclusively comprises ecological processes. For this reason, perhaps, other authors have preferred the term *ecological integrity* (Woodley et al. 1993; Westra & Lemons 1995). We follow Angermeier and Karr (1994) and stipulate that the concept of biodiversity is limited to elements, whereas biological integrity comprises both biological components and ecological processes. The preservation of biological integrity is, accordingly, the most comprehensive as well as the most rigorous of current norms in conservation.

Ecological restoration is the process of returning, as nearly as possible, a biotic community to a condition of biological integrity (Society for Ecological Restoration 1997). According to Angermeier and Karr (1994), “the goal of ecological restoration is to produce a self-sustaining system as similar as possible to the native biota.” So understood, the concept of ecological restoration seems to involve the extreme compositionalist assumption that

anthropogenic disturbances are essentially different from equally severe nonanthropogenic disturbance. Angermeier and Karr (1994) are quite explicit: "variation in elements attributable to natural processes does not represent a variation in integrity, but variation caused by humans does." Thus, if a biotic community is disturbed by some natural force, such as a lightning-caused fire or a hurricane, its integrity will not have been compromised even if its composition is radically altered. Should a biotic community be humanly disturbed, however, by logging or strip mining, resulting in the loss of native species or the invasion of exotic species, its integrity may be more or less completely restored by getting rid of the exotic and reintroducing the native species populations.

The naturalness criterion, central to the concepts of biological integrity and ecological restoration, is fraught with problems (Hunter 1996). As Angermeier and Karr (1994) admit, "because of the pervasive effects of human actions, it is often difficult to characterize naturally evolved conditions." According to Pickett and Ostfeld (1995), "landscapes that have not experienced important human influences have been the exception for hundreds if not thousands of years." Anderson (1991) proposes that, in the absence of absolute naturalness, degrees of naturalness should be assessed quantitatively across a continuum. One measure is the extent to which a biotic community would change if humans were removed: the less change, the more natural. A second measure is the amount of cultural effort—energy and other inputs—required to maintain an artificial assemblage: the less cultural effort, the more natural. A third measure is more questionable: the more the post-settlement assemblage of an area resembles the pre-settlement assemblage, not only in species composition but in the relative abundances of species populations, the more natural. Such a measure would have no meaning in areas of the world where "settlement"—recent colonization by *Homo sapiens* of European ancestry and cultural habits—did not occur.

Compositionalists tend either to ignore the historical presence of *Homo sapiens* in the Americas or to treat such peoples as wildlife. According to Martin (1973), however, 31 genera of large North American mammals were rendered extinct 11,000–12,000 years ago by spear-wielding *Homo sapiens* who immigrated by land from west to east. If the overkill hypothesis is correct, the degree of deviation from the natural condition of the Americas was greater (determined by a generalization of Anderson's third measure) after colonization by the Siberian big-game hunters than after colonization by European agriculturists and industrialists. Had European *Homo sapiens* been the first of their species to invade the Western Hemisphere, the biota they encountered would have been much different. Martin (1973) also suggests, however, that after the extinctions in the Western Hemisphere 10,000 years ago, new ecological equilibria were eventually established among the remaining spe-

cies, including *Homo sapiens*. In Mesoamerica and parts of the Neotropics, large human populations practicing intensive agriculture arose prior to European conquest (Denevan 1992; Whitmore & Turner 1992). Hence those regions then had a low degree of naturalness by Anderson's second measure. In the Nearctic, however, the human population was smaller and more dispersed, and horticulture was patchy and most of it shifting (Denevan 1992; Doolittle 1992). The new ecological equilibria that evolved in the Nearctic after the great New World extinctions, at the Pleistocene-Holocene boundary, among the surviving species populations could thus incorporate such disturbances as shifting horticulture, cultural fire, and cultural predation. Hence those disturbances can be regarded as "natural" for compositionalist conservation purposes.

The native-exotic (indigenous-nonindigenous) species notion is no less problematic than the natural habitat notion (Westman 1990). Should horses, for example, be regarded as indigenous or nonindigenous in the Americas? *Equus* evolved in the Nearctic but was extirpated in the Western Hemisphere approximately 10,000 years ago (Simpson 1956). The genus reappeared in the Western Hemisphere approximately 500 years ago. The reintroduction of the horse to the Americas was cultural, but its extinction may also have been (Martin 1973). From the extreme compositionalist point of view, represented by Angermeier and Karr (1994), if it were extirpated by natural causes (e.g., sudden climate change), *Equus* would be an invasive exotic; but if it were extirpated by cultural predation, it would be a restored native. No less than extinctions, invasions also occur without as well as with human assistance (Elton 1958). A recent immigrant that arrived by a natural process of dispersion is an exotic, but a long-established naturally dispersed immigrant is a native (Westman 1990). Both naturally and culturally introduced species that are well established but not long established are sometimes referred to as "naturalized species" (Tanner et al. 1980; Westman 1990). But by what temporal metric are the concepts of "recent" and "long established" to be quantified? Soulé (1990) implicitly assumes a geologic metric: "lions, cheetahlike cats, camels, elephants, horses, saiga antelope, yaks, and spectacled bears are native taxa to North America that disappeared very recently. The reintroduction of these large mammals . . . represents the restoration to the Nearctic of the great paleomammalian megafauna."

What past biotic community composition and structure that existed in a given area should be selected as the target for restoration efforts? The answer to this question is by no means obvious (Higgs 1997). Soulé's suggestion that, in respect to the Nearctic, the biota at the Pleistocene-Holocene boundary should be the target is entirely consistent with the compositionalist ideal of integrity, a biotic community composition and structure unsullied by human activities. The continental spatial scale and the

geologic-evolutionary temporal scale assumed by Soulé (1990) seem inappropriate, however, relative to *ecological* restoration. Shouldn't ecological restoration be geared spatially to ecological regions, landscapes, and patches and temporally to such ecological processes as succession and disturbance regimes (Pickett & White 1985)? After the great extinction of the paleomammalian megafauna, relatively stable ecological interactions between the surviving native and naturalized species—*Homo sapiens* among them—were established in the Americas. Dynamic assemblages persisted for centuries in various successional stages, disturbed periodically by wind, flood, and natural and cultural fire; they gradually changed in composition through occasional additions and subtractions of species and moved north and south in response to fluctuations in climate (Botkin 1990). Such Holocene assemblages seem to be more appropriate, albeit moving (and therefore somewhat arbitrary), targets for ecological restoration than assemblages that existed prior to initial invasion by *Homo sapiens*.

Noss (1990b) notes that "the terms 'exotic' and 'native' are relative, scale-dependent (temporally and spatially), and about as ambiguous as any in our conservation lexicon (except perhaps 'natural')." So, to what range of scales are these terms appropriately related? Temporal scales calibrated in centuries, not millennia, might also be used to define the difference between native and exotic species. Thus, even if *Equus* were a victim of cultural overkill 10,000 years ago in the Nearctic, the horse was an exotic—*pace* Soulé (1990)—when reintroduced 500 years ago. The American biota had by then thoroughly reorganized itself. Whether or not by now the horse and other nonindigenous species have become naturalized might be determined by an additional ecological criterion: To what extent is the species in question a good citizen of its new biotic community? Does it displace or adversely affect its native and naturalized neighbors? Perhaps only long-established *and* well-behaved species should qualify as naturalized; otherwise, they should remain in the noxious exotic category for purposes of compositionalist conservation practice.

The Functionalist Glossary

Ecosystem health is the occurrence of normal ecosystem processes and functions (Costanza et al. 1992). Biotic communities are composed of species populations. Ecosystems are composed of linked ecological processes, such as primary production of biomass, nutrient recruitment, retention, and cycling and of disturbance regimes (O'Neill et al. 1986; Allen & Hoekstra 1992). We concur with Angermeier and Karr (1994) that one should "not distinguish community and ecosystem as different hierarchical levels but rather as complementary ways of viewing the same system. . . . Community perspectives are

grounded in evolutionary biology and focus on dynamics of organism distribution and abundance; ecosystem perspectives are grounded in thermodynamics and focus on the dynamics of energy and materials through and around organisms." Ecosystems are healthy when the linked ecological processes that compose them occur normally—that is, as they occurred historically (Costanza et al. 1992). According to Leopold (1941), a science of ecosystem health would "determine the ecological parameters within which land may be humanly occupied without making it dysfunctional." Ecosystem health, like organismic health, can alternatively be defined as the absence of its opposite, ecosystem disease (or "ecosystem distress syndrome"), which is indicated by, among other things, leaching of nutrients in terrestrial ecosystems and loading of nutrients in aquatic ecosystems, reduction in primary productivity in terrestrial ecosystems and increase in primary productivity in aquatic ecosystems, increased amplitude of oscillations in the species populations in the organic sector of ecosystems, and reduction in the size and longevity of organisms at the apex of the trophic pyramids of ecosystems (Leopold 1941; Rapport 1995). Further, ecosystem health, like organismic health, is characterized by "counteractive capacity," the capacity to absorb external perturbations and rapidly resume normal activities after being substantially assaulted (Rapport 1995).

Ecological services are the often vital and economically valuable functions of healthy ecosystems (Costanza et al. 1997). Normally functioning ecosystems not only harbor economically valuable organic natural resources but also provide economically valuable ecological services for free. Among such services are soil building and stabilization, water retention and purification, nitrogen fixation, and crop pollination. The economic value of ecological services is difficult to estimate, but it is likely quite substantial (Costanza et al. 1997; Daily 1997). Organic natural resources are often taxonomically determinate—teak, for instance—whereas ecological services are often less so. For example, all plants—native or exotic, cultivated or wild—remove carbon dioxide from and emit oxygen to the atmosphere. Hence many of the most fundamental ecological services may be rendered by healthy ecosystems, the organic elements of which are far removed from the compositionalist ideal of biological integrity (Westman 1990).

Adaptive management is treating management goals and techniques as hypotheses that are confirmed or falsified by success or failure (Walters 1986). Ecosystems are devilishly complex and wonderfully idiosyncratic. No universal rules or principles exist to guide their deliberate manipulation or management (Shrader-Frechette & McCoy 1993) within the ecological parameters of healthy function indicated by Leopold (1941) and specified by Rapport (1995). Many ecologists (e.g., Paine 1969, 1995; Holling 1992; Walker 1992) believe that in ecosystems a few spe-

cies are “drivers” and most others “passengers.” That is, a few species are “strong interactors” and thus are critically important to the maintenance of various ecosystem processes, whereas the others are redundant and thus potential candidates for replacement by economically more attractive species. But it is difficult to be certain, *a priori*, which are which. The deliberate manipulation or management of ecosystems, therefore, will almost certainly involve some untoward surprises. Adaptive management assumes that such surprises will occur as a matter of course (Holling 1978). It treats management goals and techniques as a scientist treats hypotheses (Walters 1986). If expected results are obtained from experimental management, then goals and techniques are confirmed. But if expected results are not obtained, then either or both must be revised. And in the process, especially from the “falsification” process, something new is learned and uncertainty is proportionately reduced, thus making subsequent management decisions more determinate (Lee 1993).

Ecosystem management is managing for ecosystem health with commodity extraction as an ancillary goal (Grumbine 1997). The ecosystem management norm was institutionalized in a 1992 policy directive for the U.S. Forest Service (memorandum to regional foresters and station directors from D. F. Robertson, chief: ecosystem management of the national forests and grasslands) and was featured in an interagency federal report written in response to the old-growth forest controversy in the Pacific Northwest (Forest Ecosystem Management Assessment Team 1993). In a synthetic review of the ecosystem management literature, Grumbine (1994) defined ecosystem management in compositionalist terms of biological integrity. Stanley (1995), however, points out that biological integrity is not the goal of ecosystem management as envisioned by the U.S. Forest Service (and other agencies that have publicly embraced this norm) and argues that ecosystem management is therefore just traditional forestry (and other forms of resource management) repackaged. We suggest a functionalist middle path: managing ecosystems with the primary goal of maintaining their health and relegating commodity extraction to a subordinate goal. In a subsequent discussion, Grumbine (1997) appears to have shifted from a compositionalist to a functionalist interpretation: ecosystem management protects “sources—the ecosystems that produce resources. . . . Traditional resource management has been concerned primarily with producing goods and services for humans. [Ecosystem management] is also concerned with this, but only if production can be maintained with ecosystems remaining healthy.” Exploration of the scientific basis for ecosystem management has begun under the auspices of the Ecological Society of America (Christensen et al. 1996).

Sustainable development is meeting “the needs of the present without compromising the ability of future generations to meet their own needs” (World Commission on Environment and Development 1987). This term be-

came globally current with the 1987 Brundtland Report, and since then various constituencies have tried to define it self-servingly: some would like us to think it means sustaining renewable resources, others sustaining development or even sustaining economic growth (Lélé & Norgaard 1996). The Brundtland Report definition provides, moreover, no means of distinguishing genuine needs from superfluous wants. Worse still, the substitutability axiom of neoclassical economics allows this definition to be interpreted antithetically to nature conservation. When a given natural resource becomes scarce, its price increases, which encourages entrepreneurs to find or invent a cheaper substitute (Barnett & Morse 1963). According to this way of thinking, then, there are no irreplaceable natural resources, and the needs (and wants) of the present can be met by rapidly exploiting current organic natural resources to commercial—if not to biological—extinction and bequeathing a legacy of wealth and technology and a culture of business and inventiveness to future generations by means of which they can meet their own needs and wants (Callicott & Mumford 1997). The substitutability axiom in neoclassical economics is technological optimism by another name, an optimism we do not endorse and that appears risky at best and cavalier at worst.

Ecological sustainability is meeting human needs without compromising the health of ecosystems (Callicott & Mumford 1997). A more conservation-friendly take on *sustainable development* can be fashioned in tandem with the concepts of ecological sustainability and ecosystem health. In the modern past, any proposed development project has in theory been judged by an economic criterion. To be sound, its monetary benefits must exceed its costs. For a proposed development project to be deemed sustainable, it should meet an analogous ecologic criterion. It should be ecologically sustainable as well as economically sound. An ecologically sustainable development project does not compromise ecosystem health. Amazonian hydroelectric impoundments, such as the Tucuruí dam in Brazil, that flood and destroy many square miles of rainforest may be economically sound—although that too is questionable—but they are certainly not ecologically sustainable (Lutzenberger 1996). Agroforestry projects in the same region, however, that carefully increase the frequency of economically exploitable plant species—such as rubber or Brazil nut trees—in standing forests without altering the forests’ structure are both economically sound and ecologically sustainable (Peters et al. 1989). Counterbalancing the business-as-usual economic interpretation, the Ecological Society of America has weighed in with a major impetus to base sustainable development on sound science (Lubchenco et al. 1991).

Ecological rehabilitation is the process of returning, as nearly as possible, an ecosystem to a state of health (Michigan Department of Natural Resources 1994). The Laurentian Great Lakes afford an example of a set of large-scale

aquatic ecosystems that were ravaged by industrial and municipal pollution, shoreline destruction, over-fishing, and invasion by exotic species. By the mid-twentieth century, Lakes Ontario, Erie, Huron, and Michigan were ecological disaster zones (Francis et al. 1979; Tanner et al. 1980; Bocking 1997). One way to rehabilitate them would be to restore, as nearly as possible, the native biotic communities. Meffe (1995) defines ecological rehabilitation as incomplete restoration: "A partial movement along the trajectory from degraded to the original state is termed 'rehabilitation.'" This is essentially a compositionalist definition of *ecological rehabilitation*. What Meffe (1995) means by "original state" is probably the same thing that Anderson means by a "pre-settlement" biotic community. Meffe's discussion of rehabilitating the Great Lakes is confined to the restoration of genetically diverse native species populations, and he recommends strongly against the introduction of any more exotic species. In viewing *Homo sapiens* as a part of the biota and considering ecosystem processes ecologically more enduring and fundamental than transient species populations, functionalists define ecological rehabilitation in terms of ecosystem health, thus more sharply distinguishing it from ecological restoration defined in terms of biological integrity.

Lake Michigan, for example, reached its nadir in the 1960s, having virtually become an alewife-lamprey "fishery" (Bocking 1997). In tandem with efforts to eradicate sea lamprey, nonnative salmonids (coho, chinook, and Atlantic salmon, steelhead, and brown trout) were deliberately introduced (Francis et al. 1979). The ostensible goal was to create a sport fishery (Tody & Tanner 1966), but the managers responsible did not treat Lake Michigan as merely a big tank into which game fish might be put to be taken immediately by anglers. Care was taken to rehabilitate the fishery by selecting appropriate alewife predators, with the goal of reestablishing "a normal predator-prey balance of fish species" (Tanner et al. 1980). Maintaining such a balance by means of continuous stocking was considered acceptable and, due to the spectacular success and popularity of the sport fishery, more salmonids were stocked than the alewife forage base could sustain (Kitchell & Crowder 1986). The decline of alewife in Lake Michigan permitted an expansion of remnant populations of the extant native planktivorous coregonin species populations, which were not exploited by the exotic piscivores (Kitchell & Crowder 1986). Thus, ironically, ecological rehabilitation by use of exotic species accidentally contributed to the restoration of some elements of Lake Michigan's "original" biotic community. This illustrates an interesting complementary and dialectical relationship between different conservation goals, functionalist rehabilitation and compositionalist restoration.

Presently, the reliance in the Great Lakes on the "put-grow-take" management approach has been acknowledged to have created "aquatic communities that are structurally and functionally volatile and that exhibit rapid

changes in species number and abundance" (Great Lakes Fishery Commission 1992) and an "ecosystem [that] appears to be highly unstable and vulnerable to further invasion" (Christensen et al. 1996). The current goal is to create new self-sustaining and self-reproducing biotic communities in the most degraded lakes, necessarily relying on a mix of native and naturalized species (Michigan Department of Natural Resources 1994). Irreversible events—such as the global extinction of four native coregonin species; the loss of genetically distinct stocks of lake trout; and the introduction of the sea lamprey, the alewife, the rainbow smelt, and the zebra mussel—preclude bringing all the Great Lakes back to a condition of biological integrity (Great Lakes Fishery Commission 1992; Michigan Department of Natural Resources 1994). Hence, management of the most massively degraded Great Lakes must by default aim for ecosystem health, not biological integrity, through ecological rehabilitation, not restoration. Any deliberate future introduction of exotic species for purposes of rehabilitation should be contemplated with great caution, however, especially in connected ecosystems such as those of the Great Lakes. For the less severely degraded Great Lakes, such as Lake Superior, refraining from deliberately introducing any more exotic species and shooting for biological integrity through ecological restoration is a feasible management goal.

The "normal" criterion of ecosystem function central to the concept of ecosystem health and its associated concepts seems to be vitiated by conundrums similar to those bedeviling the "natural" criterion central to the concept of biological integrity and its associated concepts. If "normal" ecosystem function is understood to mean ecological processes occurring as they have occurred historically, then what historic moment should be selected as the benchmark? Ecosystem processes and functions certainly change over time—for example, a lake undergoes nutrient-cycle changes as it passes from an oligotrophic to a eutrophic state (Hutchinson & Wolack 1940) or a forest goes through bioenergetic phase changes from early succession to old growth (Odum 1969)—but they do not typically change as rapidly as species populations fluctuate in their associated biotic communities (Schindler 1990). Primary production, trophic structure, nutrient retention, hydrology, and rates of erosion (in terrestrial ecosystems) are more constant in normally functioning ecosystems than are the elements (species populations) in natural biotic communities (Soulé 1996).

Moreover, the notion of normal ecosystem function does not exclude human influence by definition, as does the notion of natural assemblages. Healthy ecosystems may therefore include and incorporate human inhabitation, economic exploitation, and cultural maintenance (Leopold 1941). Rapport (1992) even builds human preferences for particular economically valued species, whether native or exotic, and for particular ecological

amenities and services into the concept of ecosystem health. Holling (1992) notes that different ecosystemic “stability domains,” any of which might be characterized as normal, may be associated with different biotic communities. Climate change or changes in disturbance regimes may “flip” an ecosystem “into a qualitatively different stable state”—such as the flip from mixed-grass-and-tree savannas to shrub-dominated semideserts in the southwest United States following fire suppression and livestock grazing (Leopold 1924; Holling 1992; Whitford 1995). Because mixed-grass-and-tree savannas are, from a subjective, human point of view, preferable to shrub-dominated semideserts, some domains of ecological attraction may be regarded as healthier than others, although from an objective, scientific point of view both may be functioning normally: producing biomass; recruiting, retaining, and cycling nutrients; holding soil; modulating the flow of water; and so on.

The species populations that function in ecological processes may be interchangeable, provided they are adapted to similar environmental gradients. The preservation of biological integrity via wilderness designation and the maintenance of ecosystem health in humanly inhabited and economically exploited landscapes are, for Leopold (1941), in a complementary and dialectical relationship: “a science of land health needs, first of all, a base-datum of normality, a picture of how healthy land maintains itself. . . . We have two available norms. One is found where land physiology remains normal despite centuries of human occupation. . . . The other and most perfect norm is wilderness.” We need to preserve the integrity of representative biotic communities, Leopold argues, not only for its own sake but as a benchmark of normality so that we can assess the health of the ecosystems that we inhabit and the organic sectors of which we deliberately modify.

Linking Species and Ecosystems in Conservation

We have taken advantage of the relative wealth of current conservation norms to try to gainfully employ them all. In the interest of sharper delineation of these concepts, we offer narrow interpretations and therefore more precision in their application. Our dichotomous organizational structure, compositionism and functionalism, is not intended to be rigid. Adaptive management, for example, might be just as useful to a compositionalist trying to maintain the biological integrity of the Arctic National Wildlife Refuge as to a functionalist trying to rehabilitate Lake Michigan. In the opinion of some notable conservationists, the functionalist concept of ecosystem health, defined in terms of the occurrence of normal ecosystem processes, can be specified only by reference to natural areas in terms of which the compositionalist concept of biological integrity is understood. And, according

to Rapport (1995), one indicator of ecosystem health is biological diversity. We have, furthermore, disavowed conceptual power politics as exemplified by Angermeier and Karr (1994) and Salwasser (1990) in the “battle of buzzwords,” as Noss (1995a) characterizes it, whereby partisans of a single normative concept try to make it cannibalize or vanquish all the rest. And we have tried assiduously to avoid conflating two concepts, as ecosystem health and biological integrity are often conflated, for example by Norton (1995). The concept of a keystone species has emerged at the fusion point of evolutionary and ecosystem ecology. Although arguably less normative and more technical, less strategic and more tactical, than the ones so far discussed, it is the focus of a more synthesized approach to conservation than those characterizing compositionism and functionalism.

O'Neill et al. (1986) provide an arresting image of the oneness of the real world but the duality of the ecological interpretation of it:

[I]magine the natural world . . . hidden from view behind a pair of opaque screens joined along one edge and set at approximately right angles to each other. . . . When we stand in front of the screen labeled “population-community” . . . the questions which arise concern the relationship between the biotic entities and the hierarchical rules that structure assemblages. If we look at the screen labeled “process-functional” . . . the relevant questions involve the rates at which the processes occur and the . . . functions. In any particular circumstance, what is seen on one screen may be difficult or impossible to explain in terms of what one sees on the other screen, yet the same object underlies both observation sets.

The goal of evolutionary ecologists is to explain and predict the behavior of individual organisms and populations. They believe that because natural selection acts exclusively on individuals, as Williams (1966) persuasively argued, the trophic structure of biotic communities can be accounted for by the exclusive application of evolutionary theory. A thorough account of the trophic structure of a biotic community includes the component species populations, their relative numbers, and kinds of interaction. It is these components that evolve, in part through interaction with one another, and therefore it is these components and their interactions, that evolutionary ecology tries to explain and, ideally, to predict.

Dobzhansky (1973) insisted that “Nothing in biology makes sense except in the light of evolution.” Applying Dobzhansky’s dictum to conservation, Meffe (1995) asserts that “We cannot effectively understand and deal with any conservation problem without an evolutionary perspective as the central mode of thought.” Ecosystem ecologists, however, seem to disagree: “Ecosystems do depend on evolved entities for some of their functions, [but] evolution is only tenuously connected to ecosystems” (Allen & Hoekstra 1992). Few attempts have been made to integrate evolution into ecosystem theory (Holt

1995). According to Allen and Hoekstra (1992), "The ecosystem is . . . a parallel development that is highly structured like strictly living systems, but with a different cause than natural selection." Ecosystem ecologists are more interested in the architecture of trophic structures than in the specific building blocks of those structures, and more in how the assembled components perform than in the components themselves (Grimm 1995). Their goal is to model and predict the behavior of ecosystems as units. Hence, ecosystem models often submerge individual species into process-oriented modules and so do not generally specify components shaped by evolution. Recalcitrant problems within each of these two paradigm approaches to ecology have recently led to an effort to synthesize them (Vitousek 1990; Holling 1992; Schultz & Mooney 1993; Jones & Lawton 1995; Polis & Winemiller 1996).

A *keystone species* is "a species whose impact on its community is large, and disproportionately large relative to its abundance" (Power et al. 1996). Ecosystem ecologists have found that efforts to model and predict some ecosystem functions are sometimes thwarted because in fact species sometimes matter. Particular species may alter structural features of food webs, which subsequently modify the rates at which ecosystem processes occur (Power et al. 1996). Some species, that is, seem to operate as keystones. If a keystone species is removed, large changes in community structure and, eventually, ecosystem function ensue. Some keystone species operate as "ecosystem engineers," which, according to Lawton and Jones (1995), are "organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials." Some, such as trees, corals, and kelps, create habitat simply by growing. Others transform the physical structure of an environment by their behaviors: beavers, for example, alter the hydrology of the ecosystems in which they reside. In studies of the effects of fish removals on lacustrine ecosystems, whether and how the effects propagate through the food web seems to depend on the presence of particular species of zooplankton (large *Daphnia* spp., for example), not just on the biomass in the zooplankton "box" (Carpenter & Kitchell 1993).

Evolutionary ecologists seeking to understand the dynamics of populations and communities have found that the foraging behavior or life histories of the species of interest sometimes depend on ecosystem characteristics as well as on interactions with other species populations. For example, Hugie and Dill (1994) found, by means of game theoretic models, that simple autecological predictions of habitat selection by fish species had to be altered to take into account disturbance regimes that altered the outcome of species interactions, as well as the behaviors of competitors, prey, and predators. Further, the role particular species play in the structure of biotic communities and the functioning of ecosystems—especially whether or not they are a keystone species—can vary from place

to place and time to time, depending on the physical conditions of the habitat as well as the presence of other organisms (Holling & Meffe 1996). This has been dubbed "context dependency" (Menge et al. 1994; Power et al. 1996) and suggests that food-web structure and the physical environment can alter the outcome of the interactions among species populations. Going straight to the heart of evolutionary concerns, Holling (1992) explains why the body sizes of birds and mammals, irrespective of trophic niche, are "clumped" and discontinuous. Ecological processes occur at discrete, discontinuous temporal scales, which create discrete, discontinuous scales in ecological space—the landscape, the patch, the micro-habitat. The body sizes of animals are an adaptation to one or another of these spatial scales as their home range. Thus community ecologists must fuse the previously disparate ecosystem and evolutionary approaches to ecology in order to predict accurately the impact of particular species introduced into particular food webs or to predict the outcome of human "development projects" at various spatial scales on the architecture of a community and hence on its biota. Such predictive power is especially important for ecosystem management and ecological rehabilitation.

For purposes of conservation, therefore, neither the evolutionary nor the ecosystem orientation by itself is adequate. Of course, depending upon management objectives—the preservation or restoration of biodiversity and biological integrity, or the maintenance or rehabilitation of ecosystem health—an approach biased toward either community structure and particular species, on the one hand, or ecosystem process and function, irrespective of species identity, on the other, may be emphasized. But no matter what the management objectives, conservation efforts must draw upon both ecosystem and evolutionary ecology. Perhaps the synthesis already underway in food-web research (Jones & Lawton 1995; Polis & Winemiller 1996) will lead the way to a fusion of these formerly disparate perspectives in ecology. The theoretical complementarity of evolutionary ecology and ecosystem ecology suggests a corresponding complementarity in application. If the two historically disparate approaches to ecology become fused, as present trends suggest, into a single, synthesized approach, then that would suggest a corresponding unity in application (Fig. 2).

Conclusion

The compositionalist emphasis on the preservation of biodiversity or biological integrity and on ecologically restoring areas that have been adversely but not irredeemably affected by commercial fishing, industrial forestry, or agriculture is appropriate for actual and potential designated wilderness areas, wildlife refuges, national and state parks, world heritage sites, the core areas of international biosphere reserves, and the like, as Hunter (1996) sug-

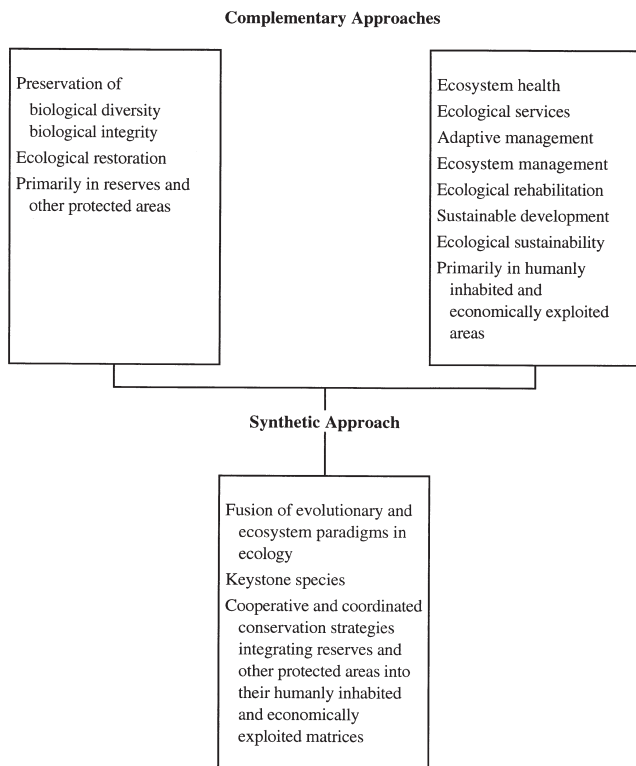


Figure 2. Complementary and synthetic approaches to conservation.

gests. Originally set aside for other reasons, national parks and wilderness areas are, accordingly, being redefined as biodiversity reservoirs, the primary function of which is to provide living room for interacting and mutually dependent non-human species populations (Noss 1990c; Foreman 1995; Grumbine 1996). Thus reconceived, they might be expanded and multiplied to realize the goal of preserving biodiversity and biological integrity. Such is the compositionalist ideal. It deanthropocentrizes and ecologizes the classic preservationist program. Areas of great species richness, endemism, or unusual assemblages that are challenged by growing human populations and development face the greatest risk of biological impoverishment (Dobson et al. 1997). In selecting areas for establishing new biodiversity reserves, the presence of high biodiversity, endemic species, and unique biotic communities should therefore warrant particular consideration.

The functionalist emphasis on ecosystem health, ecological services, ecological rehabilitation, adaptive management, ecosystem management, ecological sustainability, and sustainable development is a philosophy of conservation more suited for the proportionately much greater part of the world that is inhabited and economically exploited by humans. The really innovative idea in contemporary conservation is the functionalist ideal, which conceives of human economies as embedded in the larger

and more enduring economy of nature. Its goal is to adapt human economies to ecological exigencies, thus achieving a mutually sustaining relationship between human cultures and the ecosystems in which they are situated and on which they depend.

Pleas for a synthesis of the compositionalist and functionalist conservation camps are being expressed (Meine 1992; Vandermeer & Perfecto 1997). The fusion we envision will likely emerge from the need to unify the two traditional approaches to ecology if either the compositionalist or the functionalist ideals are to be realized. The preservation of islands of biological diversity and integrity and ecological restoration necessarily occurs at present in a humanly inhabited and economically exploited matrix. Hence the success of nature preservation and restoration necessarily depends on ecologically rehabilitating and maintaining the health of these matrices. And that, circling back, will require the preservation of biological-diversity-and-integrity reserves, if Leopold (1941) is right, as databases of normal ecosystem function. Such reserves are also important to the health of surrounding matrices as a source of recruitment. According to Naeem (1998) "local extinction [extirpation] within functional groups is inevitable and frequent, but reservoirs of species from adjacent ecosystems generally ensure that functional group or ecosystem failure, if it occurs, is likely to be transient." Thus the maintenance of ecosystem health in humanly inhabited and economically exploited areas depends upon the existence of proximate reservoirs of biodiversity. Therefore neither of these approaches to conservation can effectively proceed in isolation from the other.

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