Biological Integrity versus Biological Diversity as Policy Directives

Protecting biotic resources

Paul L. Angermeier and James R. Karr

Two phrases—*biological integrity* and *biological diversity*—have joined the lexicon of biologists and natural resource managers during the past two decades. The importance of these phrases is demonstrated by their influence on environmental research, regulatory, and policy agendas. The concepts behind the phrases are central to strategies being developed to sustain global resources (Lubchenco et al. 1991). Unfortunately, the phrases are widely used by the media, citizens, policy makers, and some biologists without adequate attention to the concepts they embody. Precise use of the terms *integrity* and *diversity* can help set and achieve societal goals for sustaining global resources; imprecise or inappropriate use may exacerbate biotic impoverishment—the systematic decline in biological resources (Woodwell 1990).

Although the related concepts of integrity and diversity were developed more or less independently (integrity in the study of aquatic systems, diversity in the study of terrestrial systems), both apply to all biotic systems. The US Clean Water Act and Canada's National Park Act enunciate the explicit goal of protecting biological integrity. No specific legislative mandate exists to protect biological diversity in the United States, but such protection became a central goal of the 1992 Earth Summit and the Global Biodiversity Protocol endorsed by many nations. The focal positions of the two concepts dictate that a clear understanding of their meanings is critical to developing effective resource policy.

Paul L. Angermeier is an assistant unit leader at the National Biological Survey, Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0321. James R. Karr is director of the Institute for Environmental Studies, University of Washington, Seattle, WA 98195.

Resource policy would be most effective if the goal were the protection of biological integrity

Our review of current conceptions of integrity and diversity indicates that resource policy would be most effective if based on the more comprehensive goal of protecting biological integrity. Specific policy shifts related to that goal include a reliance on preventive rather than reactive management and a focus on landscapes rather than populations. We draw heavily from our experience with aquatic systems, but our conclusions apply equally to terrestrial systems.

Aquatic systems are appropriate models for illustrating general ecological consequences of anthropogenic impacts, because research is advanced on ecological impacts in these systems (e.g., Allan and Flecker 1993, Schindler 1990), and rates of extinction and endangerment for aquatic fauna exceed those for terrestrial fauna. Among North American animals, for example, Master (1990) reported that 20% of fishes, 36% of crayfishes, and 55% of mussels were extinct or imperiled, compared with 7% of mammals and birds. Similarly, only 4% of the federally protected aquatic species in the United States with recovery plans have recovered significantly, compared with 20% of protected terrestrial species (Williams and Neves 1992).

Defining biological diversity

The term *biological diversity* (or *biodiversity*) emerged as species extinction rates began to increase dramatically (Myers 1979). The specter of mass extinctions, combined with huge gaps in biological knowledge, has convinced many scientists that a global biological crisis exists (Wilson 1985). Moreover, because biological diversity provides important aesthetic, cultural, ecological, scientific, and utilitarian benefits to human society, the crisis is everyone's concern (Ehrlich and Wilson 1991).

One of the first formal definitions of biological diversity termed it "the variety and variability among living organisms and the ecological complexes in which they occur" (OTA 1987, p. 3). In addition, because "items are organized at many [biological] levels," biodiversity "encompasses different ecosystems, species, genes, and their relative abundance" (OTA 1987, p. 3). Other thorough discussions of biodiversity confirm that multiple organizational levels (e.g., genes, species, and ecosystems) are fundamental to the concept (Noss 1990, OTA 1987, Reid and Miller 1989), thereby distinguishing it from the much simpler concept of species diversity.

Table 1. Levels of organization in three hierarchies used to characterize biological diversity. These hierarchies are linked at the species-genome-population levels (see text for details) but not precisely at any other levels.

Taxonomic	Genetic	Ecological
Biota	Genome	Biosphere
Kingdom	Chromosome set	Biome
Division/Phylum	Chromosome	Landscape
Class	Gene	Ecosystem/Community
Order	Allele	Population
Family		
Genus		
Species		

Hierarchies

Organizational hierarchies are useful tools for understanding complex biological phenomena. Several distinct hierarchies—taxonomic, genetic, and ecological (Table 1)—are relevant to biological diversity. We follow Reid and Miller (1989) in referring to biotic units at any level within a hierarchy as elements. Thus, species and classes are taxonomic elements, genes and chromosomes are genetic elements, and populations and biomes are ecological elements. Levels are nested within each hierarchy: a phylum comprises classes, a chromosome comprises genes, and a landscape comprises communities. The hierarchies in Table 1 are linked at the species-genome-population levels; any population of organisms has a taxonomic identity (species), which is characterized by a distinct genome. However, taxa may share genetic elements, and ecological elements may share taxa.

Specifying levels within hierarchies and elements within levels may be arbitrary. For example, ecologists may add an ecological level for guilds, or taxonomists may debate the number of families within an order. Because each level and element contributes to biotic variety and value, all are appropriate targets of conservation. To focus assessment or conservation on a single hierarchy or level (e.g., species) is to arbitrarily ignore most biodiversity.

Spatiotemporal scale is not precisely defined by hierarchical level. Ecological elements are typically defined by spatial extent (e.g., a pond community or a desert landscape), yet most levels can correctly encompass a wide range of spatial scales (Allen and Hoekstra 1992). The dynamics of oak populations in a savannah landscape or of fungus populations in a stream-channel landscape, for example, may operate at vastly different spatial scales. The appropriateness of a spatiotemporal scale for studying a given element depends on the organisms and questions at issue (Levin 1992).

At ecological levels of organization above population (see Table 1), spatiotemporal bounds are often arbitrary, integration is often loose, and composition may be dynamic. However, these elements are not random assemblages, and they can be defined on the basis of ecological attributes and societal benefits. For example, the biota of the Chesapeake Bay basin is a legitimate element of biodiversity because it has objectively definable boundaries and confers societal benefits (e.g., fisheries) that would not exist if the component populations had not coevolved.

We do not distinguish community and ecosystem as different hierarchical levels but rather as complementary ways of viewing the same system (Karr 1994, King 1993). Community perspectives are grounded in evolutionary biology and focus on the 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. Either perspective can be applied at any level in the ecological hierarchy.

Misconceptions

Because biological diversity is more comprehensive than species diversity, one must specify clearly the biological hierarchy and organizational level at issue in any discussion. In estimating biodiversity in a study area (e.g., a pond or continent), a researcher might count all the taxonomic elements present, all the genetic elements present, or all the ecological elements present. Even in the unlikely event that all the elements present are known, no accepted calculus permits integration of counts of elements across levels within a hierarchy (e.g., phyla and species) or across hierarchies (e.g., species and genes). Arguably, no such calculus should be sought.

Furthermore, the number of elements at different organizational levels need not be correlated. For example, there are more than twice as many marine phyla as terrestrial phyla, but fewer marine species (Ray and Grassle 1991). Similarly, Hoover and Parker (1991) found that species diversity and community diversity of overstory plants were inversely correlated among several Georgia landscapes. In neither example is it unequivocal which system has more biodiversity.

Failure to conceptually integrate the multiple aspects of biodiversity results in narrowly conceived comparisons. For example, Vane-Wright et al. (1991) measured biodiversity with an index of taxonomic diversity based on cladistics, which assesses distinctness of taxa. Similarly, Mares (1992) used a comparison of mammal diversity (at several taxonomic levels) among South American biomes to infer that biodiversity is greater in drylands than in lowland Amazon forest. These analyses are valuable, but they cannot be interpreted as comprehensive (or even representative) assessments of overall biodiversity because genetic and ecological hierarchies were ignored.

A common misuse of the term *biodiversity* makes it synonymous with *species diversity* (Redford and Sanderson 1992), a usage that trivializes the broader meaning of biodiversity and promotes misconceptions of conservation issues. Palmer (1992) takes this misconception to the extreme by depicting biodiversity loss as nothing more than species extinction. This incomplete view fails to recognize that elimination of extensive areas of old growth forest, dramatic declines in hundreds of genetically distinct salmonid stocks in the Pacific Northwest (Nehlsen et al. 1991), and the loss of chemically distinct populations from different portions of a species range (Eisner 1992) represent significant losses of biodiversity, regardless of whether any species become extinct. Other misuses of the term stem from inclusion of human-generated elements in assessments of an area's biodiversity (Angermeier 1994).

Table 2. Elements, processes, and potential indicators of biological integrity for five levels of organization within three biological hierarchies. Assessing the integrity of a given area should incorporate indicators from multiple levels.

Hierarchy	Elements	Processes	Indicators
Taxonomic	Species	Range expansion or contraction	Range size
		Extinction	Number of populations
		Evolution	Isolating mechanisms
Genetic	Gene	Mutation	Number of alleles
		Recombination	Degree of linkage
		Selection	Inbreeding or outbreeding depression
Ecological	Population	Abundance fluctuation	Age or size structure
		Colonization or extinction	Dispersal behavior
		Evolution	Gene flow
	Assemblage	Competitive exclusion	Number of species
		Predation or parasitism	Species evenness
		Energy flow	Number of trophic links
		Nutrient cycling	Element redundancy
	Landscape	Disturbance	Fragmentation
		Succession	Number of communities
		Soil formation	Persistence

Defining biological integrity

Biological integrity refers to a system's wholeness, including presence of all appropriate elements and occurrence of all processes at appropriate rates. Whereas diversity is a collective property of system elements, integrity is a synthetic property of the system. Unlike diversity, which can be expressed simply as the number of kinds of items, integrity refers to conditions under little or no influence from human actions; a biota with high integrity reflects natural evolutionary and biogeographic processes.

The concept of biological integrity has played its largest policy role in the management of water resources where it first appeared in the 1972 reauthorization of the Water Pollution Control Act (now Clean Water Act; CWA). The primary charge of the 1972 CWA and subsequent amendments was to "restore and maintain the chemical, physical, and biological integrity of the Nation's waters." This mandate has been the foundation for state and federal water-quality programs over the past two decades. Although implementation often has been ill-focused (Karr 1991), the concept of integrity is the primary directive for water policy in the United States.

The most influential definition of biological integrity was proposed by Frey (1975) and later applied by Karr and Dudley (1981). It defined the concept as "the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region" (Karr and Dudley, p. 56). Various forms of this definition now provide the basis for biotic assessment of surface waters by the US Environmental Protection Agency (EPA 1990) and numerous states (EPA 1991a).

Two important distinctions between integrity and diversity emerge from this definition. First, system integrity is reflected in both the biotic elements and the processes that generate and maintain those elements, whereas diversity describes only the elements. Again, following Reid and Miller (1989), we use processes to refer to a broad range of evolutionary, genetic, and ecological processes (Table 2). Integrity depends on processes occurring over many spatiotemporal scales, including cellular processes giving rise to genetic elements and ecosystem processes regulating the flow of energy and materials.

Although some authors (e.g., Noss 1990) explicitly include processes as components of diversity, we contend that processes are more appropriately considered as components of integrity. Process diversity is unlikely to provide an intuitive basis for distinguishing the biodiversity of different areas because areas vary in process rates rather than process occurrence. All areas support the processes of meiosis, speciation, disturbance, and predation, but rates vary dramatically. Moreover, changes in process rates cannot be interpreted as changes in diversity unless the number of participating elements also changes. For example, an increased rate of landscape disturbance need not produce more or fewer component communities and populations. Although processes clearly are essential to generate and maintain elements, their inclusion as components of biodiversity adds ambiguity without utility.

The second distinction between integrity and diversity is that only integrity is directly associated with evolutionary context. By definition, naturally evolved assemblages possess integrity but random assemblages do not. Adding exotic species or genes from distant populations may increase local diversity but it reduces integrity.

Most uses of the integrity concept focus on the community level of organization, but we suggest that integrity also applies to most other hierarchical levels in Table 1. Integrity of any biotic system can be assessed on the basis of attributes of elements and processes important to its genetic or ecological organization (see Table 2). However, the concept may not apply to taxa above the species level, because most taxonomic levels are artifacts of classification rather than functional biotic entities.

Because systems are hierarchical, an element is generated and maintained (in part) by processes occurring at organizational levels above and below its own level (O'Neill et al. 1989). For example, the integrity of a woodland community may depend on colonization dynamics of component populations as well as landscape-level disturbance dynamics. Thus, assessment of biological integrity should account for the influence of processes at multiple organizational levels and multiple spatiotemporal scales.

Selecting benchmarks

The ability to recognize objectively and assess changes in integrity is critical for the concept's use in policy. The first hurdle in recognizing change in integrity is the selection of a benchmark state against which other states can be compared. Ecologists recognize that biological systems are not strictly deterministic but may develop (i.e., be organized) along multiple pathways as a result of different initial conditions, conditions in neighboring systems, and the sequence of influential events (Pickett et al. 1992). For example, marine intertidal communities are influenced by predation, disturbance, competition, physiological tolerances, and colonization from offshore. The relative importance of each process and the relative abundances of species at a given site depend on coastal circulation (Roughgarden et al. 1988). Variation in elements attributable to natural processes does not represent a variation in integrity, but variation caused by humans does.

Regier (1993) contends that states other than those evolved naturally can provide benchmarks for integrity. Although unnatural states may be desirable for aesthetic, utilitarian, or other reasons, they cannot provide an objective basis for assessing biological integrity. Human-induced changes in biotic systems frequently are more rapid and severe than those occurring naturally. Thus, functional and evolutionary limits of the native biota provide objective bases for selecting appropriate integrity benchmarks (Pickett et al. 1992). For example, when forest harvest rates exceed regeneration rates, integrity is reduced, resulting in loss of late-successional communities. When a river is dammed, integrity is reduced, resulting in declines of populations adapted to the natural hydrological regime.

Evolutionary history should provide the primary basis for assessing biological integrity. Even the value of many artificial, human-generated elements (e.g., agricultural landscapes) depends on naturally evolved elements and processes, such as nitrogen-fixing bacteria and soil formation. Sadly, because of the pervasive effects of human actions, it is often difficult to characterize naturally evolved conditions. Because abilities to reconstruct historic scenarios of biotic conditions are likely to become even more impaired in the future, such efforts should proceed with the best information currently available.

Primacy of integrity

Use of integrity as the primary management goal avoids the pitfalls of assuming that greater diversity or productivity is preferred. Knowledge of the couplings between biotic elements and processes is based largely on observations of stressed ecosystems. Experimental studies of whole lakes exposed to nutrient enrichment and acidification indicate that species composition responds more quickly and recovers more slowly than processes such as primary production, respiration, and nutrient cycling (Schindler 1990).

In a review of aquatic ecosystem and mesocosm responses to stress, Howarth (1991) found numerous examples of shifts in biotic elements that were unaccompanied by changes in process rates, but process changes were always accompanied by shifts in elements. These patterns are consistent with observations and predictions from forest ecosystems (Odum 1985) and support the hypothesis that ecological processes are buffered from perturbation by redundancy among elements (Bormann 1985). For example, multiple interchangeable elements (e.g., species) may drive a single process (e.g., nutrient cycle). Of course, given enough stress or element loss, any process can be impaired. As stress on system organization accumulates, nonlinear and threshold responses may result (see cases in Woodwell 1990).

Many changes in diversity can be evaluated objectively only on the basis of changes in integrity. For example, artificial nutrient enrichment of a naturally oligotrophic ecosystem may increase local species diversity yet eliminate a unique community. Such a change may be interpreted as either a gain or loss in diversity, but integrity is clearly reduced because of the shift away from native conditions. Human impacts in the Apalachicola River basin of the southeastern United States reduced freshwater flow into the estuary, resulting in elevated salinity and fish species diversity but loss of productivity and nursery function (Livingston 1991). Management for biological integrity would dictate maintenance of lower species diversity and higher productivity by restoring the original salinity dynamics.

Integrity goals also allow for natural fluctuation in element composition. Loss of a particular element (e.g., species) or replacement by a regionally appropriate one need not indicate a loss of integrity unless the processes associated with the element's maintenance become impaired. For example, natural metapopulation dynamics often include local, temporary extinctions balanced by recolonizations via dispersal (Hanski and Gilpin 1991). Such losses of populations do not indicate losses of integrity unless rates of extinction, dispersal, or recolonization are altered, as might occur in an artificially fragmented landscape.

The inadequacy of diversity as a policy directive is perhaps clearest in the evaluation of situations where humans add elements such as transferred genes, exotic species, or agri-

Table 3. Representatives of five classes of factors that organize ecological systems and provide a framework for assessing ecological integrity. Some factors are especially applicable in aquatic (A) or terrestrial (T) systems.

Class	Factors	
Physiochemical conditions	Temperature pH Insolation Nutrients	Salinity Precipitation (T) Oxygen (A) Contaminants
Trophic base	Energy source Productivity Food particle size	Energy content of food Spatial distribution of food Energy transfer efficiency
Habitat structure	Spatial complexity Cover and refugia Topography (T) Soil composition (T) Vegetation height (T)	Vegetation form (T) Basin and channel form (A) Substrate composition (A) Water depth (A) Current velocity (A)
Temporal variation	Diurnal Seasonal Annual	Predictability Weather (T) Flow regime (A)
Biotic interactions	Competition Parasitism Predation	Disease Mutualism Coevolution

cultural landscapes to natural systems (artificial biological diversity; Angermeier 1994). Artificial elements reduce integrity through widely documented effects on native elements and processes (Karr et al. 1986, Taylor et al. 1984, Vitousek 1990) and should be excluded from evaluations of biodiversity (Angermeier 1994).

Some (e.g., Palmer 1992) argue that artificial elements are components of biodiversity and therefore appropriate targets of biological conservation. We reject this argument for several reasons. First, culturally or technologically derived elements rarely perform life-support services as effectively as native elements (Ehrlich and Mooney 1983). Second, technology applied on massive spatial scales erodes biological integrity, ultimately leading to biotic impoverishment. And, third, including artificial diversity in conceptions of biodiversity wrongly legitimizes management strategies that erode native diversity.

Conceivably, through genetic engineering, species introduction, landscape modification, and other technologies, we could manufacture a biota with more elements, and thus more diversity, than the naturally evolved one, even to the exclusion of native elements. In contrast, the normative postulates of conservation biology (Soule 1985) were intended to protect products and processes of biogeography and evolution. Thus, current definitions of biodiversity should incorporate explicit native criteria.

In sum, biological integrity encompasses element composition (measured as number of items) and process performance (measured as rates) over multiple levels of organization; it is assessed in comparison with naturally evolved conditions within a given region. Biological integrity is thus generally defined as a system's ability to generate and maintain adaptive biotic elements through natural evolutionary processes. Current loss of biological diversity is tragic, but loss of biological integrity includes loss of diversity and breakdown in the processes necessary to generate future diversity.

Ecological indicators

To assess biological integrity, one should be familiar with regional organizing processes and elements, including how they are influenced by human actions. A conceptual organization with five classes of interacting factors—physicochemical conditions, trophic base, habitat structure, temporal variation, and biotic interactions (Table 3)—has been useful in selecting ecological indicators to assess (Karr 1991, Karr et al. 1986) and tactics to restore (Gore 1985) integrity in aquatic systems.

Biological integrity can be assessed through diagnostic attributes or indicators, which ideally are sensitive to a range of stresses, able to distinguish stress-induced variation from natural variation, relevant to societal concerns, and easy to measure and interpret. Several authors (e.g., Karr 1991, Noss 1990, and Schaeffer et al. 1988) offer extensive lists of potential indicators of ecological integrity (also see Table 2); others have listed indicators of genetic integrity (Lande and Barrowclough 1987, Noss 1990). In practice, elements are used more frequently than processes as indicators of integrity because elements are typically more sensitive to degradation, more fully understood, and less expensive to monitor. Thus, biodiversity is an important indicator of biological integrity.

The complexity of biotic systems dictates that integrity assessments should incorporate a variety of indicators (including elements and processes) from multiple organizational levels and spatiotemporal scales. The index of biotic integrity (IBI) represents a successful approach for incorporating information from multiple indicators into a single numerical index (Karr 1991, Karr et al. 1986). Conditions observed in the system being assessed are compared to region-specific expectations for an undegraded system, (i.e., the reference condition).

The original IBI incorporated numerical criteria on species composition and diversity, trophic composition, population density, tolerance to human impacts, and individual health to assess integrity of lotic fish communities. The IBI has been used successfully in more than 20 states of the United States and in Canada, France, India, Poland, and Venezuela. Similar protocols (some using aquatic invertebrates) also have been developed for reservoirs, lakes, and estuaries (Deegan et al. 1993, EPA 1991b, Ohio EPA 1988). Efforts to apply such assessment approaches in terrestrial systems have lagged behind those in aquatic systems, but they can succeed if defensible criteria for appropriate indicators are developed.

Ecological restoration

The goal of ecological restoration is to produce a self-sustaining system as similar as possible to the native biota. But biological, socioeconomic, or technological constraints may limit our ability to attain that goal despite the best intentions. For example, past extinctions of many Great Lakes fish stocks prevent restoring integrity to those ecosystems even if exotic species and toxic chemicals could be removed. Similarly, as rangeland degradation progresses, the costs and time for restoration become increasingly prohibitive (Milton et al. 1994). Thus, restoration goals must be based on social and political constraints as well as biological potential. Once a goal (benchmark state) is selected, however, assessing restoration success is analogous to assessing integrity under other circumstances, which includes identifying organizing processes and selecting appropriate indicators.

Restoration methods usually mimic recovery from natural perturbations and reflect important organizational processes. Common approaches for aquatic systems include manipulating water quality, habitat structure, hydrology, riparian/watershed vegetation, and (less frequently) animal populations (Gore 1985, Osborne et al. 1993). Restoration of terrestrial systems typically focuses on establishing native vegetation and manipulating succession.

To maximize effectiveness, restoration efforts should employ and encourage natural ecological processes rather than technological fixes and should incorporate spatiotemporal scales large enough to maintain the full range of habitats necessary for the biota to persist under the expected disturbance regime. Failure to recognize important ecological relationships can result in counterproductive efforts. In the Mount St. Helens (Washington) blast area, for example, seeding slopes with grass and removing woody debris from streams actually hindered natural recovery processes (Franklin et al. 1988). On the other hand, many systems are remarkably responsive to appropriate restoration efforts. Years after a massive channelization project in the Kissimmee River in Florida, partial reestablishment of the flow regime quickly restored plant, invertebrate, fish, and bird assemblages (Toth 1993). As knowledge of ecological processes and the technology to mimic those processes advance, we expect ecological restoration to take its place as a successful discipline.

Policy implications

Despite spending hundreds of millions of dollars on endangered species, the United States continues to lose biodiversity. We ascribe much of this loss to ineffective policy that emphasizes piecemeal conservation of the elements of diversity rather than comprehensive protection of the integrity of systems supporting those elements. Two major shifts are needed to produce more effective resource policy. First, goals of biological conservation and restoration should focus on protecting integrity (Karr 1993), especially the organizational processes that generate and maintain all elements, rather than focusing on the presence or absence of particular elements. Such an approach is more likely to prevent endangerment of elements and should be more cost-effective than emergency efforts to pull them back from the brink of extinction after serious degradation. Emergency tactics may be necessary where a focus on integrity fails to protect an element, but they should not be the primary basis of conservation, as in current policy.

Adoption of policy goals to protect integrity would help avoid difficult resource allocation problems such as estimating specific flows needed to sustain populations of endangered fishes in the Colorado River or endangered birds in Platte River wetlands. In fisheries, managing for integrity would not allow the widespread practice of stocking nonnative fishes to be construed as enhancing biodiversity. In forestry, rather than using the range of stand ages in a forest or the range of tree ages in a stand (Lippke 1993) as measures of biodiversity, harvest schedules would mimic patterns of natural disturbance (Hunter 1990).

Appropriate roles of diversity in resource policy are in establishing conservation priorities, siting reserves, and indicating program success. However, policy makers must agree on which organizational levels and elements should be protected. Species and communities are commonly used to assess an area's conservation value, but genetic elements are rarely used. Gap analysis, for example, combines information on landscape-scale vegetation types with assumptions about the habitat associations of terrestrial vertebrates and butterflies to establish regional conservation priorities (Scott et al. 1993).

Policy effectiveness also could be improved by shifting focus from populations and species to landscapes. The organizational processes and ecological contexts that maintain populations typically operate at larger spatiotemporal scales than the populations themselves (Pickett et al. 1992). Because human impacts are applied at landscape scales, management prescriptions should be focused at the same scales. Landscape-scale approaches are especially important in managing aquatic systems, which can rarely rely on high-profile species (e.g., bald eagle or grizzly bear) to garner public support for protection.

Riparian zones and floodplains are critical landscape components linking aquatic and terrestrial systems; they regulate aquatic habitat formation, as well as entry of water, nutrients, and organic material into aquatic habitats (Gregory et al. 1991). Thus, management approaches focusing on strictly aquatic components (e.g., designation of a stream reach as wild and scenic or as critical habitat for an imperiled species) are unlikely to be effective over the long term. Application of integrity goals and landscape approaches are perhaps nowhere more important (or more politically challenging) than in estuaries or in anadromous fisheries, which depend on interactions among terrestrial, freshwater, marine, and even atmospheric systems.

Implementation of integrity goals is likely to challenge the leadership of government agencies. Protection of biological integrity could be enhanced by restructuring tax and subsidy programs to eliminate conservation disincentives for private landowners and to distribute conservation costs and benefits equitably (Carlton 1986). Traditional agricultural, fisheries, forestry, game management, and mining agencies must replace their narrow, commodity and harvest-oriented philosophies with innovative perspectives founded on a broader range of social concerns, longer time frames, and more interagency cooperation (Salwasser 1991). Critical steps toward managing for biological integrity include establishing scientifically defensible benchmarks and assessment criteria.

Although these steps are potentially contentious, current uses of integrity goals indicate that success is attainable. Management programs for Kissimmee River, Ohio surface waters, and Canadian national parks are grounded in the goal of protecting or restoring biological integrity. The current shift in management of US national forests and parks should also involve a goal based on integrity. Emphasis on a method of management (i.e., ecosystem management) without a well-defined goal could be counterproductive.

Reserves alone are unlikely to sustain all biodiversity or even all species. Partnerships between government agencies and the public are essential to maintaining integrity and diversity across landscapes that include public and private lands. Noss and Harris (1986) proposed a promising conceptual approach in which interconnected networks of protected and multiple-use landscape components are managed to provide economic benefits yet protect ecological processes. Conservation biologists are exploring applications of this approach to regional landscapes such as the Pacific Northwest and Southern Appalachia (Mann and Plummer 1993). Similar management schemes could be effective in protecting the integrity of many ecosystems and landscapes, but where such preventive approaches fail, agencies should establish safety-net measures analogous to the Endangered Species Act to prevent important or unique ecosystems and landscapes from being destroyed.

Societal choices

The causes of environmental degradation and loss of biodiversity are rooted in society's values and the ethical foundation from which values are pursued (Orr 1992). Solutions are likely to emerge only from a deep-seated will, not from better technology. Adopting biological integrity as a primary management goal provides a workable framework for sustainable resource use, but fostering integrity requires societal commitment well beyond government regulations and piecemeal protection. Such a commitment includes self-imposed limits on human population size and resource consumption, rethinking prevailing views of land stewardship and energy use, and viewing biological conservation as essential rather than as a luxury or nuisance.

Shifting our everyday thinking in this direction forces us to face the hard choices for which political rhetoric so often calls. Those choices are not likely to favor biological diversity unless people recognize the inherent value of unique biological elements and processes at all organizational levels. Conservation biologists should play a major role in articulating the value of biota, demonstrating links between biological integrity and economic stability, and dispelling the myth that technology can replace biodiversity or essential life-support services.

The decision to conserve or exhaust biotic resources is before us. It can be informed by science and influenced by government policy, but conservation primarily depends on a societal will grounded in recognition of its obligation to the future.

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References cited

Allan, J. D., and A. S. Flecker. 1993. Biodiversity conservation in running waters. *BioScience* 43: 32–43.

Allen, T. F. H., and T. W. Hoekstra. 1992. *Toward a Unified Ecology*. Columbia University Press, New York.

Angermeier, P. L. 1994. Does biodiversity include artificial diversity? *Conserv. Biol.* 8: 600–602.

Bormann, F. H. 1985. Air pollution and forests: an ecosystem perspective. *BioScience* 35: 434–441.

Carlton, R. L. 1986. Property rights and incentives in the preservation of species. Pages 255–267 in B. G. Norton, ed. *The Preservation of Species*. Princeton University Press, Princeton, NJ.

Deegan, L. A., J. T. Finn, S. G. Ayvazian, and C. Ryder. 1993. Feasibility and application of the index of biotic integrity in Massachusetts estuaries (EBI). Final Project Report, Ecosystem Center, Marine Biological Laboratory, Woods Hole, MA.

Ehrlich, P. R., and H. A. Mooney. 1983. Extinction, substitution, and ecosystem services. *BioScience* 33: 248–254.

Ehrlich, P.R., and E. O. Wilson. 1991. Biodiversity studies: science and policy. *Science* 253: 758–762.

Eisner, T. 1992. The hidden value of species diversity. *BioScience* 42: 578.

Environmental Protection Agency (EPA). 1990. Biological criteria: national program guidance for surface waters. EPA-440/-90-004. EPA, Office of Water, Washington, DC.

______. 1991a. Biological criteria: state development and implementation efforts. EPA-440/5-91-003. EPA, Office of Water, Washington, DC.

______. 1991b. Biological criteria: research and regulation. EPA-440/5-91-005. EPA, Office of Water, Washington, DC.

Franklin, J. F., P. M. Frenzen, and F. J. Swanson. 1988. Re-creation of ecosystems at Mount St. Helens: contrasts in artificial and natural approaches. Pages 1–37 in J. Cairns Jr., ed. *Rehabilitating Damaged Ecosystems*. Vol. II. CRC Press, Boca Raton, FL.

Frey, D. 1975. Biological integrity of water: an historical perspective. Pages 127–139 in R. K. Ballentine and L. J. Guarraia, eds. *The Integrity of Water*. EPA, Washington, DC.

Gore, J. A., ed. 1985. *The Restoration of Rivers and Streams*. Butterworth, Boston, MA.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *BioScience* 41: 540–551.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: a brief history and conceptual domain. *Biol. J. Linn. Soc.* 42: 3–16.

Hoover, S. R., and A. J. Parker. 1991. Spatial components of biotic diversity in landscapes of Georgia, USA. *Landscape Ecol.* 5: 125–136.

Howarth, R. W. 1991. Comparative responses of aquatic ecosystems to toxic chemical stress. Pages 169–195 in J. Cole, G. Lovett, and S. Findlay, eds. *Comparative Analyses of Ecosystems*. Springer-Verlag, New York.

Hunter, M. L. Jr. 1990. *Wildlife, Forests, and Forestry*. Prentice-Hall, Englewood Cliffs, NJ.

Karr, J. R. 1991. Biological integrity: a long neglected aspect of water resource management. *Ecological Applications* 1: 66–84.

______. 1993. Protecting ecological integrity: an urgent societal goal. *Yale Journal International Law* 18: 297–306.

______. 1994. Landscapes and management for ecological integrity. Pages 229–251 in K. C. Kim and R. D. Weaver, eds. *Biodiversity and Landscapes*. Cambridge University Press, New York.

Karr, J. R., and D. R. Dudley. 1981. Ecological perspective on water quality goals. *Environ. Manage.* 5: 55–68.

Karr, J. R., K. D. Fausch, P. L. Angermeier, P. R. Yant, and I. J. Schlosser. 1986. Assessing biological integrity in running waters: a method and its rationale. Special Publication 5. Illinois Natural History Survey, Champaign, IL.

King, A. W. 1993. Considerations of scale and hierarchy. Pages 19–45 in S. Woodley, J. Kay, and G. Francis, eds. *Ecological Integrity and the Management of Ecosystems*. St. Lucie Press, Delray Beach, FL.

Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pages 87–123 in M. E. Soule, ed. *Viable Populations for Conservation*. Cambridge University Press, New York.

Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967.

Lippke, B. 1993. Focus on preserving old growth is counterproductive to achieving biodiversity. *Northwest Environ. J.* 9: 10–15.

Livingston, R. J. 1991. Historical relationships between research and resource management in the Apalachicola River estuary. *Ecological Applications* 1: 361–382.

Lubchenco, J., et al. 1991. The sustainable biosphere initiative: an ecological research agenda. *Ecology* 72: 371–412.

Mann, C. C., and M. L. Plummer. 1993. The high cost of biodiversity. *Science* 260: 1868–1871.

Mares, M. A. 1992. Neotropical mammals and the myth of Amazonian biodiversity. *Science* 255: 976–979.

Master, L. 1990. The imperiled status of North American aquatic animals. *Biodiversity Network News* 3(3): 1–2, 7–8.

Milton, S. J., W. R. J. Dean, M. A. duPlessis, and W. R. Siegfried. 1994. A conceptual model of arid rangeland degradation: the escalating cost of declining productivity. *BioScience* 44: 70–76.

Myers, N. 1979. *The Sinking Ark*. Pergamon Press, New York.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries (Bethesda)* 16(2): 4–21.

Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conserv. Biol.* 4: 355–364.

Noss, R. F., and L. D. Harris. 1986. Nodes, networks, and MUM's: preserving diversity at all scales. *Environ. Manage.* 10: 299–309.

Odum, E. P. 1985. Trends expected in stressed ecosystems. *BioScience* 35: 419–422.

Office of Technology Assessment (OTA). 1987. *Technologies to Maintain Biological Diversity*. Congress of the United States, OTA-F-330, Washington, DC.

Ohio Environmental Protection Agency (Ohio EPA). 1988. Biological criteria for the protection of aquatic life. Ohio EPA, Division of Water Quality Monitoring and Assessment, Surface Water Section, Columbus, OH.

O'Neill, R. V., A. R. Johnson, and A. W. King. 1989. A hierarchial framework for the analysis of scale. *Landscape Ecol.* 3: 193–205.

Orr, D. W. 1992. *Ecological Literacy*. State University of New York Press, Albany, NY.

Osborne, L. L., P. B. Bayley, and L. W. Higler, eds. 1993. Lowland stream restoration: theory and practice. Special issue. *Freshwater Biol.* 29: 187–342.

Palmer, T. 1992. The case for human beings. *Atlantic Monthly* 269(1): 83–88.

Pickett, S. T. A., V. T. Parker, and P. L. Fiedler. 1992. The new paradigm in ecology: implications for conservation biology above the species level. Pages 65–88 in P. L. Fiedler and S. K. Jain, eds. *Conservation Biology*. Chapman & Hall, New York.

Ray, G. C., and J. F. Grassle. 1991. Marine biological diversity. *BioScience* 41: 453–457.

Redford, K. H., and S. E. Sanderson. 1992. The brief barren marriage of biodiversity and sustainability? *Bull. Ecol. Soc. Am.* 73: 36–39.

Regier, H. A. 1993. The notion of natural and cultural integrity. Pages 3–18 in S. Woodley, J. Kay, and G. Francis, eds. *Ecological Integrity and the Management of Ecosystems*. St. Lucie Press, Delray Beach, FL.

Reid, W. V., and K. R. Miller. 1989. *Keeping Options Alive*. World Resources Institute, Washington, DC.

Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241: 1460–1466.

Salwasser, H. 1991. In search of an ecosystem approach to endangered species conservation. Pages 247–265 in K. A. Kohm, ed. *Balancing on the Brink of Extinction*. Island Press, Washington, DC.

Schaeffer, D. J., E. E. Herricks, and H. W. Kerster. 1988. Ecosystem health: I. measuring ecosystem health. *Environ. Manage.* 12: 445–455.

Schindler, D. W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos* 57: 25–41.

Scott, J. M., et al. 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monograph No. 123. The Wildlife Society, Bethesda, MD.

Soule, M. E. 1985. What is conservation biology? *BioScience* 35: 727–734.

Taylor, J. N., W. R. Courtenay Jr., and J. A. McCann. 1984. Known impacts of exotic fishes in the continental United States. Pages 322–373 in W. R. Courtenay Jr. and J. R. Stauffer Jr., eds. *Distribution, Biology and Management of Exotic Fishes*. Johns Hopkins University Press, Baltimore, MD.

Toth, L. A. 1993. The ecological basis of the Kissimmee River restoration plan. *Fla. Sci.* 56(1): 25–51.

Vane-Wright, R. I., C. J. Humphries, and P. H. Williams. 1991. What to protect? Systematics and the agony of choice. *Biol. Conserv.* 55: 235–254.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57: 7–13.

Williams, J. E., and R. J. Neves. 1992. Introducing the elements of biological diversity in the aquatic environment. *Trans. N. Am. Wildl. Nat. Resour. Conf.* 57: 345–354.

Wilson, E. O. 1985. The biological diversity crisis. *BioScience* 35: 700–706.

Woodwell, G. M., ed. 1990. *The Earth in Transition*. Cambridge University Press, New York.