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The Multifaceted Aspects of Ecosystem Integrity

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ABSTRACT

The need to reduce human impacts on ecosystems creates pressure for adequate response, but the rush to solutions fosters the oversimplification of such notions as sustainable development and ecosystem health. Hence, it favors the tendency to ignore the complexity of natural systems. In this paper, after a brief analysis of the use and abuse of the notion of ecosystem health, we address the problem of a sound definition of ecosystem integrity, critically review the different methodological and conceptual approaches to the management of natural resources, and sketch the practical implications stemming from their implementation. We show that there are merits and limitations in different definitions of ecosystem integrity, for each acknowledges different aspects of ecosystem structure and functioning and reflects the subjective perspectives of humans on the value, importance, and role of biological diversity. This evaluation is based on a brief sketch of the links among biodiversity, ecosystem functioning and resilience, and a description of the problems that arise in distinguishing between natural and anthropogenic disturbance. We also emphasize the difficulty of assessing the economic value of species and habitats and the need to use adaptive management policies to deal with uncertainty and ecosystem complexity. In conclusion, while acknowledging that environmental legislation requires objective statements on ecosystem status and trends, we stress that the notion of ecological integrity is so complex that its measure cannot be expressed through a single indicator, but rather requires a set of indicators at different spatial, temporal, and hierarchical levels of ecosystem organization. Ecosystem integrity is not an absolute, monolithic concept. The existence of different sets of values regarding biological diversity and environmental risks must be explicitly accounted for and incorporated in the decision process, rather than ignored or averaged out.

KEY WORDS: adaptive management; biodiversity; complexity and stability; conservation strategies; disturbance, anthropogenic; disturbance, natural; ecosystem integrity; ecosystem functioning; ecosystem structure; natural resource management; resilience; sustainable development.

INTRODUCTION

The simple and attractive notion of sustainable use holds great appeal for ecologists and economists alike (Levin 1996). A large literature has been developed around the notions of ecological economics (Daly 1990 Costanza 1991, Pearce and Warford 1993, Jansson et al. 1994) and ecological management (Gladwin 1992, Callenbach et al. 1993, Hawken 1993, Gladwin et al. 1995, Shrivastava 1995). Yet, the over-used notions of ecosystem health and sustainable development, and other ecological and economic concepts associated with them, remain vague and slippery, and have different meanings for different people (Gatto 1995). In the face of such ambiguity, decision makers require simple, user-friendly, cost-effective tools that permit the introduction of sustainability criteria into an economic framework and that promote ecologically sound business practices. The issue is not marginal; given the unprecedented rate of species extinction and habitat degradation due to pollution and overexploitation, we cannot wait long before taking actions against the impoverishment and disruption of life on our planet (Dobson 1996). The compelling need for analyses of the environmental effects of human activities creates pressure for answers. The rush to solutions fosters oversimplification of such notions as ecosystem integrity, and the tendency to suppress the complexity of natural systems in favor of simplistic and naive approaches to studying the ecological implications of social and economic development.

The physician's task is to evaluate and maintain healthy functioning of an individual; the environmental manager's, to evaluate and maintain healthy functioning of an ecosystem. The analogy is seductive, and has led to the development of the concept of ecosystem health (e.g., Costanza et al. 1992), which presupposes defining a normative state of natural systems and identifying limits of human intervention. Obviously, this notion is appealing. A healthy body is physically vigorous and free from disease. Similarly, a healthy ecosystem or community might be indicated by ranges of values considered to be normal, and by attributes that are regarded as stable and sustainable, whereas pathological conditions are indicated by the opposite (Schaeffer et al. 1988, Ryder 1990, Costanza et al. 1992, Rapport 1992, Freedman 1995). To large extent, however, this concept is rooted in the organismic theory of ecology promoted by Frederick Clements at the beginning of this century, and is based on the idea that biological communities are structurally and functionally like organisms. In the Clementsian view, communities are recognized as having their own identities that may change in time but eventually reach a fixed, normative balance state at the end of the successional process. This view of ecosystems thus directs attention to development of equilibrium theories that ignore dynamic features. Moreover, the "superorganism" paradigm ignores the degree to which ecological communities are open, loosely defined assemblages with only weak evolutionary relationship to one another (Levin 1992). This definition is highly dependent on the scale of description, and, GAIA notwithstanding, the ecological community is not an integral evolutionary unit in the sense that an individual is. Here the metaphor fails.

Furthermore, the emphasis put on stability, unique equilibria, and normative states has historically promoted a view of a "benign Nature" able to cope with any sort of anthropogenic interference and manipulation, because trials (and errors) of any kind can be made with the assurance that recovery is always possible once the source of disturbance is removed (Holling 1987). In reality, all natural ecological systems change over time, and it is extremely difficult to determine a normal state for communities whose measurable properties are often in flux, either because of natural disturbance or because of internal ecological mechanisms (Ehrenfeld 1993). Ecosystems are seldom close to equilibrium, a fact not recognized adequately in many environmental assessments (Reice 1994). Some communities may be consistently affected by high levels of localized disturbance that allow for the coexistence of species competing for the same limited resource (e.g., intertidal communities), whereas others may experience periodic catastrophic episodes, such as floods, forest fires, or pest outbreaks, that reset the timing of successional cycles. Furthermore, disturbance may occur on a wide range of temporal and spatial scales (Levin 1995). Therefore, in defining ecosystem health, it may be difficult to separate the effects of human and natural disturbance. To confuse matters more, the components of an ecosystem may be mutually connected in a variety of ways and, thus, may exhibit an ensemble of different functions. Hence, any attempt to evaluate ecosystem health will depend upon which functions and which components of the ecosystem we are considering.

Because different communities may exhibit completely different spatial and temporal patterns of species abundance and of functional activity (Levin 1995), the attempt to redefine the notion of health for any particular

system can weaken any larger, unifying idea of health. Most importantly, the organismic theory of ecology, on which the notion of ecosystem health is grounded, fails to recognize that ecosystems are not uniquely identified entities, nor are they defined by sharp boundaries (Karr 1994). Instead, they are loosely defined assemblages that exhibit characteristic patterns on a range of scales of time, space, and organization complexity. A more promising approach to ecosystem management is to recognize that various genetic, competitive, and behavioral processes (rather than states) are responsible for maintaining the key features of observed ecosystems, and that the dynamics of these processes vary with the scale of description. Holling (1992) proposes a dynamic view of ecosystem cycling through a spiraling developmental path, characterized by different phases. Here, the emphasis is on variability, spatial heterogeneity, and nonlinear causation.

Problems aside, it is essential that we develop measures of ecosystem functioning, for which we prefer the word "integrity." The notion of integrity must accept the dynamic view incorporating processes. It must recognize a human perspective, the ability of an ecosystem to continue to provide the services that humans expect. For managed ecosystems, the ability to supply products such as food or timber may provide the integration; for natural systems, other valuations will enter. It is important to recognize that these are imposed measures, conditional on a definition of "use" for a system. In this way, the notion of integrity differs fundamentally from a unique definition of "health" as an evolved aspect. It is a tool for management.

Ecosystem integrity is so complex an issue that a single indicator or operational definition is insufficient to grasp its multifaceted aspects. The aim of this paper is to review carefully the concept of ecosystem health and integrity; to identify links among biodiversity, ecosystem functioning, and resilience; and to stress and distinguish the effects of natural and anthropogenic disturbance. Throughout, we direct attention not only to theoretical aspects, but also to links between ecosystem theory and management, and to practical implications based on different notions of ecosystem integrity.

ECOSYSTEM INTEGRITY: theoretical aspects and practical implications

Although ecosystems do not represent evolutionary units, their importance for management is evident, conditioned by the manager's operational definitions. Holling's (1992) viewpoint that ecosystems periodically cycle through different successional states is a paradigm of broad, if not universal, applicability. It has been effective in promoting a new approach to the science of natural resource management that explicitly recognizes the existence of multiple modes of functioning and the potential for unexpected changes in system behavior. Accordingly, two main variants of ecosystem policies have been derived from this approach.

1) In resource-based systems, such as forests, fisheries, and croplands, decision makers are inclined to devote considerable effort to keeping the system within desirable stability domains that guarantee optimal exploitation rates. They attempt to prevent any shift toward a new mode of functioning, by reducing environmental stochasticity that could push the system away from its optimal state and cause undesirable economic or ecological effects. This imposed resiliency reduces the sensitivity of the system to exogenous factors that might adversely affect the exploited population(s), but at the cost of sacrificing information about the dynamic properties of ecosystems in changing environments.

2) Conversely, it is the dynamic processes themselves that guarantee the functioning of an ecosystem, and any successful effort to constrain natural variability will eventually lead to self-simplification and fragility. Therefore, it is neither desirable nor reasonable to eliminate the natural successional cycle of a natural system. Keeping one population at a constant level may lead to changes in other related species, so that features of the biophysical environment that usually have been perceived as constant begin to change and to produce a system that is structurally different from the original one. The resilience of the system to change is embedded in its heterogeneity and dynamic properties, and especially in these hidden variables.

Although they recognize the complex, dynamic nature of ecosystems, resource managers, therefore, often aim to achieve constancy through externally imposed regulations, attempting to reduce the probability of events that are perceived as ecologically or economically undesirable, such as floods, pest outbreaks, and fire (see [Appendix 1](#)). Unfortunately, policies to eradicate these natural nuisances have frequently led to dramatic impacts on communities. Numerous illuminating examples are described in Holling (1987), with reference to other managed systems, such as the salmon fisheries in North America; the conversion of the semiarid savanna ecosystem to productive cattle grazing lands in Africa, the United States, India, and Australia; and the malaria eradication programs in developing countries. All these examples share the common feature that a blind attempt to control some "undesired" ecological or economical effect has been successful only over a short span of time. However, the price paid to achieve this short-term objective has been a qualitative change in the behavior of the system; the alteration of natural, long-term cycles has led to a loss of resiliency and has produced system crises much larger than those occurring in unmanaged ecosystems.

Pickett and White (1985) state, "An essential paradox of wilderness conservation is that we seek to preserve what must change." On the other end, if ecosystems experience fluctuations and changes generated by internal ecological mechanisms, this does not mean that any change should be accepted. In contrast, Botkin (1990) states, "we must focus our attention on the rates at which changes occur, understanding that certain changes are natural, desirable, and acceptable, while others are not."

Toward a paradigm for ecosystem integrity

According to Webster's dictionary, "integrity" is "the state of being unimpaired, sound," "the quality or condition of being whole or complete." Therefore, a system subject to external disturbance will retain its integrity if it preserves all its components as well as the functional relationships among the components. Similarly, ecosystems are organized structurally into populations, species, and communities of organisms that interact with each other and with abiotic features of the environment, and functionally into production and consumption components that process energy and materials (Limburg et al. 1986). Measurable definitions of integrity include those of Cairns (1977): "the maintenance of the community structure and function characteristic of a particular locale or deemed satisfactory to society," and of Karr and Dudley (1981): "the capability of supporting and maintaining a balanced, integrated, adaptive, community of organisms having species composition, diversity, and functional organization comparable to that of natural habitats of the region." Integrity is a definition that reflects the capability of the system to support services of value to humans; even Karr and Dudley's definition reflects a human perspective.

The concept of ecosystem integrity is not free from criticisms (Anderson 1991, Rolston 1994). However, rather than engaging in endless debates over which is the best and most comprehensive definition of integrity, we agree with Noss (1995a) that it is much more useful to characterize in detail the functional and structural aspects of ecosystems to provide a conceptual framework for assessing the impact of human activity on biological systems and to identify practical consequences stemming from this framework.

Reductionism vs. holism

The inherent dualism of the structural and functional organization of ecosystems is not just a matter of philosophical debate, but has important practical implications concerning two different approaches to the study of earth's biota:

- 1) A reductionist approach emphasizes the structural aspects of natural systems and focuses on individual species and population dynamics of species within isolated ecosystems (Soulé 1986);
- 2) A holistic approach focuses on macro-level functional aspects (in particular, energy flows, nutrient

recycling, and productivity), to some extent neglecting historical and evolutionary factors and ignoring most of the details observed at smaller scales of functional organization and of the spatial and temporal distribution of organisms.

Of course, the structural and functional perspectives on biological systems are not mutually exclusive. They simply reflect broad streams in which many branches of ecological theories have flourished. In our context, they are useful in outlining two rather different approaches to the compelling issue of preserving ecosystem integrity (King 1993). In the extreme, in fact, they lead to very different definitions of integrity:

1) Strict attention to the structural aspects of ecosystems, as represented primarily in species composition, leads to a definition in which the loss of even one species or the damage of a link between some components implies a loss of integrity, because the ecosystem is no longer "complete" or "whole."

2) On the contrary, from the perspective of functional integrity, redundancies within functional groups make the biological composition less relevant.

There is merit in either definition of integrity, or in their combination; the relevance of either depends on the perspective of the investigator and on the way ecosystem services, resource species, aesthetic values, and other aspects are balanced (Levin 1997). Furthermore, structure and function are linked. Many macroscopic properties (primary productivity, in particular) are very resilient to changes in system structure, at least on short time scales. Even when subject to high levels of disturbance (and, thereby, to substantial changes in their structure), a system may be able to preserve its macro-level functions, such as primary productivity, and some macro-level indicators may not show any appreciable change.

An often-cited case is that of the American chestnut (*Castaneadentata*). This canopy species, once fairly dominant in the deciduous forest of eastern North America, has been wiped out by the introduced blight fungus *Endothia parasitica*. The population has been replaced by other shade-tolerant species (Hepting 1971, Spurr and Barnes 1980), without substantial changes in the primary productivity of the forest. Estuarine communities provide an example of biological systems subject to a high level of disturbance, such as hurricanes and floods, and characterized by a high variability in community composition over time. Yet some macro-level functions are amazingly resilient to alteration in structure: productivity rapidly recovers after major catastrophic events that completely reset the biological clock of the community (Costanza et al. 1993).

According to a strict interpretation of the functional approach to ecosystem integrity (King 1993), a change in ecosystem structure that does not appreciably change the qualitative and quantitative functional aspects should be interpreted, at most, as a minor loss of integrity. What is missed in this view, however, is that loss of diversity within functional groups may weaken the ability of the system to adapt to catastrophic changes on longer time scales.

Neither pure structuralism nor pure functionalism is completely appropriate; both contain validity, but within some boundaries. Putting equal emphasis on every piece of biodiversity is ecologically unsound and tactically unachievable (Walker 1992). On the other hand, the assessment of ecosystem integrity based only on a few macro-level indicators, such as primary productivity or other measures of energy and matter flows, may obscure other ecosystem properties that ultimately determine the resilience and stability of the ecosystem to several sources of disturbance. Indeed, the two extremes simply represent boundary points in a multidimensional continuum, in which a variety of measures of differing levels of detail may be applied.

In the following sections, we will briefly sketch some of the most widespread theories about the importance of species diversity and the relationship between biodiversity and ecosystem properties.

WHY PRESERVE BIODIVERSITY? Linking Biodiversity to Ecosystem Functions

The measurement of biological diversity is complicated by the fact that its valuation is a multidimensional concept (see [Appendix 2](#)). Aesthetic and intrinsic values are well understood in concept, albeit difficult to quantify and put into operation. Aesthetic values, in particular, can be of critical importance, because they resonate with the interests of environmental groups and organizations, the media, and a large part of the population. The direct valuation of resource species in fisheries, forests, and agricultural lands is the most apparent, even given the uncertainty about the value of undiscovered natural products of potential benefit for human health. Yet, the relationships among biodiversity, ecosystem function, disturbance, and resilience may be the most important and least understood (Tilman et al. 1996, Daily 1997). We thus turn our attention to this aspect.

Keystone species and functional groups

To determine the ecological importance of biodiversity, we must focus attention on aspects of biodiversity that control resilience, i.e., the ability of the ecosystem to maintain its characteristic patterns and rates of process in response to the variability inherent in its climate regimes (Walker 1992). In some cases, attention may be directed to individual keystone species (Paine 1966) or groups of species whose removal may engender dramatic changes in the structure and functioning of its biological community. For example, in some regions, anadromous fishes in fresh water appear to be keystone food resources for vertebrate predators and scavengers, forming an ecologically significant link between aquatic and terrestrial ecosystems (Willson and Halupka 1995).

In most cases, it is indeed groups of species, rather than individual species, that assume importance, forming "keystone groups" or "functional groups," a generalization of the notion of keystone species. Functional groups (guilds) are collection of species that perform the same functions and that, to some extent, may be substitutable and viewed as a unit (Schulze 1982, Solbrig 1994). For example, removal of a numerically dominant species may result in its replacement by functionally similar competitors that had been suppressed, leaving untouched macro-level indicators of ecosystem functioning (like productivity, or the amount of matter processed). Yet, loss of species within a guild may reduce the long-term resilience properties of the system, and may lead to noticeable change in short-term system dynamics (Levin 1997).

The role of ecological redundancy

The functional redundancy of species within a guild should not be interpreted as a justification for their elimination. On the contrary, redundancy plays a fundamental role in maintaining an ecosystem's ability to respond to changes and disturbance and provides a hedge against stresses and catastrophes (Levin 1995, 1997). The best evidence to date that species-rich ecosystems are more stable than species-poor ecosystems is perhaps offered by Tilman and Downing (1994). In an elegant, long-term study of native and successional grassland in Minnesota, they have shown that species-rich grasslands were more resistant to drought than were species-poor ones, and that the loss of additional species has a progressively greater impact on the resilience of the community. Similar results have been obtained by Dodd et al. (1994) in the plant communities of the Park Grass Experiments.

Communities viewed in terms of functional groupings, in general, prove to be much more stable and predictable than when viewed in terms of species composition (Hay 1994); this is largely a property of averaging. For example, convergent biogeographical patterns in ecosystem organization have been clearly discerned when distinct species of subtidal algal communities in Maine, Washington State, and the Caribbean have been grouped

based on common morphological attributes (Steneck and Dethier 1994). In fact, changes in species populations within a functional group usually occur on a much faster time scale than dynamics among groups, allowing a hierarchical decomposition of the system dynamics (Simon and Ando 1961, Iwasa et al. 1987, 1989). Therefore, on the short time scale, a reduction of within-group heterogeneity is not likely to change ecosystem properties appreciably, and biotic detail is probably irrelevant. On the slightly longer scales, biotic diversity and consequent feedbacks may fundamentally alter the responses of systems to stress. Determining precisely what is "short" or "slightly longer" is, of course, very subjective. However, Bolker et al. (1995), modeling a forest in which shifts and feedbacks due to natural selection occur within and among functional groups, found that significant responses of the biota can be expected on time scales of 50–100 years, a relatively short time for forests and for the horizon of interest to humans.

Complexity and stability

It should be noted that simple generalizations about the relations between diversity or complexity and stability are elusive. Very complex ecosystems, such as tropical forests, may still lack resilience with respect to major anthropogenic perturbations. For example, pasture created from rain forest not only fails to return to rain forest, but often degrades into barren sites (Noss 1995a). Elegant mathematical analysis by May (1973) shows that increasing ecosystem complexity above a certain threshold simply increases the number of ways the system may be perturbed. Although the issue is still controversial (Hengeveld 1989), highly diverse ecosystems may be much less stable than predicted by the classical paradigm (Clements and Shelford 1939, Odum 1953). Controversy arises because of the many different meanings of complexity (in term of species richness, connectance, interaction strength, etc.) and stability (in term of resilience, persistence, resistance, variability, etc.) and the different levels of functional organization (individual species abundance, species composition, trophic level abundance, etc.) at which the notion of complexity and stability can be tested. The diversity of interpretations and issues maintains confusion (Pimm 1984).

A central question

In light of these findings, and given the accelerating rate of biodiversity loss due to human activity, the question we need to answer is how much, or rather how little, redundancy we can afford to lose without pushing the system to the edge of some irreversible and catastrophic change. The problem is once more tied up with the relationship between the structure and the function of ecosystems, and is complicated by the fact that there is no simple way to characterize the structural and functional properties of ecosystems. Different properties emerge at different spatial and temporal scales of observation, as well as at different levels of biological organization. This is a question for which no simple answer exists, but its resolution must underlie any management efforts.

Disturbance and temporal scale of investigation

A further problem of profound importance is that of sorting out endogenous and exogenous determinants of patterns in space and time (Levin 1992, Durrett and Levin 1994a, b, 1996). Many, if not most, natural systems are characterized by environmental variability whose effects on communities and ecosystems are expressed in different ways at different levels of biological organization and at different spatial and temporal scales of observation (Levin 1995). When choosing biological indicators, it should be borne in mind that the temporal scale of population change increases with body size, since this has very important implications for ecological investigations (Peters 1983). Some species may appear to be more stable only because they are physiologically incapable of great changes over a short time frame, whereas large fluctuations in abundance take place on longer

time frames. On the other hand, if small species are a matter of concern, a suitably short sampling interval should be used to monitor changes in population abundance. The choice of a suitable time scale for evaluating the effects of a proposed action is of paramount importance.

Natural and anthropogenic disturbance

There are substantial differences, shaped by the evolutionary histories of species, between natural and anthropogenic disturbance. In general, natural disturbance can randomly affect several species that share some functional or structural characteristic, and is generally of a scale that species have experienced over evolutionary time. Conversely, human activities, such as fires and logging, may have dramatic impact and wipe out individual species or even functional and structural categories of species (Baskin 1994). The scale is often too fast for evolutionary adjustment. Forestry is a well-known example; disturbances caused by timber extraction are qualitatively and quantitatively different from natural disturbances (Boot and Gullison 1995). Mortality rates of trees in forests with only natural disturbances are on the order of 1–2% per year (Swaine et al. 1987). Conversely, selective logging, a harvesting policy recently in vogue because it is supposed to promote sustainability, can kill up to 55% of the residual stems in a forest (Boot and Gullison 1995). Selective logging obviously affects the various species of a plant community unevenly. This is particularly true if density-dependent processes apply at the guild level, rather than at the single species, as pointed out by Boot and Gullison (1995). In this case, increased productivity due to the reduced density of the exploited species will spread over the entire guild. The tree species that is heavily harvested may experience virtually no benefit in terms of increased productivity, because of compensatory increase in other species. Selective mortality implies a substantial competitive disadvantage of the target species with respect to species not subject to exploitation; the target species will form a proportionately smaller part of the guild after harvest, and its subsequent regeneration will be reduced accordingly. Selective logging may also cause soil compaction, erosion, and changes in drainage, all of which will disrupt normal succession (Gullison and Hardner 1993). Pioneer species, which are of no commercial value, may be released as a consequence of high levels of disturbance caused by extraction. The lessons derived from forest management have general validity and can be applied to a variety of other communities, as suggested by Beddington (1986) for tropical fisheries.

Ecosystems affected by human activity usually exhibit reduced resistance to natural stresses, such as fires, droughts, pests, and diseases, in a positive feedback fashion. When a native grassland is converted to a monoculture of corn, for instance, the resulting system (which is highly simplified with respect to the original one) is inherently unstable and needs huge inputs of energy and material, such as fertilizers and pesticides, to remain in the desired condition (Noss 1995a). On the other hand, human disturbances that mimic or simulate natural disturbances are less likely to threaten ecological integrity than are disturbances radically different from the natural regime. Therefore, in managing ecosystems, the goal should not be to eliminate all forms of disturbance, but rather to maintain processes within limits or ranges of variation that may be considered natural, historic, or acceptable (Noss 1995a).

ASSIGNING ECONOMIC VALUE TO BIODIVERSITY

Biodiversity questions are complex, but effective legislation and ecosystem management require objective statements rather than subjective considerations about the potential future utility of particular species. It has been argued that it would be helpful to assign an economic value to species and habitats. This would allow ecological integrity to be incorporated in an economic framework, where a cost-benefit analysis could be applied to discriminate among alternative actions.

To conservation biologists, putting an economic value on biodiversity may seem both arrogant and useless. Aldo

Leopold (1953) wrote: "The last word in ignorance is the man who says of an animal or plant: What good is it? ... To keep every cog and wheel is the first precaution of intelligent tinkering." Placing an economic value on biodiversity prevents us from coping with the root causes of loss of diversity and from recognizing the value of the environment, other than as a commodity to be exploited (Meyer and Helfman 1993); it forces us to accept the old economic paradigm that assumes a perfect substitution between the natural capital and market capital, and it reinforces the technological premise that makes the biological impoverishment of the planet inevitable (Ehrenfeld 1988). Given the present interest rate on money, there is no hope that traditional economic approaches will preserve natural systems. Clark (1973a) elegantly proved the fallacy of this approach, demonstrating that it could be economically preferable to kill every blue whale left in the ocean and to reinvest the profits in the stock market, rather than waiting for the species to recover to the point at which it could sustain an annual catch. An economist might argue that the problem, in this example, is an inadequate evaluation of the resource; if aesthetic values are important, simply put a price on them. In practice, however, this ignores the complexity of valuation, including the problem of who speaks for the less powerful or for future generations.

Leaving apart the fact that many, if not most, species do not seem to have any conventional value, even a hidden one (Ehrenfeld 1988), it should be borne in mind that the true economic value of any piece of biodiversity cannot be determined without considering the value of biodiversity in the aggregate. Classification of diversity by species is only one possibility, and other forms of diversity, should be taken into account during the evaluation process (see [Appendix 3](#)). The patchiness and diversity of ecosystems across the landscape (forest, wetland, grassland, estuarine, and marine ecosystems) play a crucial role in retaining soil and nutrient availability and purifying the air and the water.

In conclusion, assigning an economic value to species is extremely complicated, highly subjective, and very simplistic. It is difficult to attach levels of probability of potential benefits in the absence of appropriate information. The process of assigning values, especially ones that reflect potential future use, is extremely subjective and is inevitably affected by the present poor scientific knowledge of ecosystem structure and functioning. Instead of arrogating to themselves the valuation of species, scientists should limit their advice to science, informing the decision-making process, but leaving complex trade-offs to be resolved by the stakeholders. This is a highly controversial area, of course, and it is essential to find new mechanisms for inserting science into the decision-making process. Multisector partnerships involving science, industry, the public, and decision makers offer great hope for the future.

MANAGING AND MISMANAGING ECOSYSTEMS

A large body of scientific literature is available on theoretical and applied aspects of renewable resource management and sustainable harvesting (e.g., Clark 1976, 1990), but political and sociological considerations generally override scientific recommendations (Ludwig et al 1993). Because unregulated open-access resources (fisheries, in particular) have proved economically and biologically inefficient (Gordon 1954), several methods have been proposed to shift over-exploited resources from unacceptable bioeconomic equilibria to more acceptable conditions. Normative methods have been implemented in the form of time, place, and catch restrictions, total and allocated quotas, harvesting tool restrictions, and license limitation. Another category of regulation instruments results from a different philosophy, namely financial disincentives such as subsidy cuts and taxes, or royalties on effort and harvested biomass (Anderson 1977, Berck, 1981, Clark 1985, De Leo et al. 1991.)

This subject has been so thoroughly studied, in theory and practice, that it is certainly one of the best understood areas of environmental science. Unfortunately, there are very few ecosystems in which sustained exploitation has proved to be successful (Clark, 1973b, Ludwig et al. 1993). All over the world, renewable resources have been systematically overexploited and diminished to local decimation or extinction. It has been argued that the causes of mismanagement are rooted in the inherent complexity of biological communities and in the high level of environmental stochasticity that confounds any effort toward an ecologically sound exploitation practice. On this

point, one of the most attractive notions is that of implementing adaptive methods of management (Holling 1978, Walters 1986) that focus on the links and the mutual interactions among biological factors, economic considerations, and natural variability. The use of modern decision theory (Berger 1985, Lindley 1985, Mangel 1985, Hilborn 1987) allows natural resource managers to include environmental uncertainty explicitly in the decision process, by continuously monitoring the managed system and recursively upgrading management protocols in response to observations. Yet, with some exceptions, adaptive management remains more a hope than a realization.

Resource management, even when included in an adaptive framework, traditionally has focused on relatively small scales of spatial and functional organization, ignoring the broader ecological and environmental context in which exploited resources are often, if not always, embedded. Second-order, indirect, and sometimes irreversible impacts have been systematically neglected in the effort to mitigate first-order direct impacts on target resources, and to increase production and possibly reduce fluctuations in the exploited biomass. Consequently, resource exploitation may be sustainable with respect to the commercial species, but may seriously threaten the viability of other components of the ecosystem. For instance, Mangel et al. (1993) reported that the current worldwide catch of penaeid shrimp might be sustainable, yet an estimated 89–90% of shrimp trawlers' catches are nontarget species. One of the nontarget species most affected by shrimp exploitation is Kemp's Ridley turtle (*Lepidochelys kempi*), which has experienced a 99% decline in population size in the last 50 years (Pritchard 1990); several other species are accidentally caught (Andrew and Pepperell 1992), although their decline is far less likely to be noticed.

Focusing strictly on target or endangered species is rarely the best strategy: the species-by-species approach may be inefficient for several reasons (Carroll et al. 1996). First, it may be difficult to advocate the importance or need for a particular piece of biodiversity, as long as the relative importance of specific species to the overall functioning of the ecosystem is not known. Second, conservation measures may be activated only when most of the damage has been done already, and the detrimental effect of human activity has finally been manifested. As Noss (1995b) pointed out, "many endangered-species conflicts that polarize society ... arguably could have been prevented if management agencies had taken steps to protect adequate amounts and distributions of habitat before populations declined to where listing was legally required." Species at the brink of extinction must be managed intensively, at great cost, and may require immediate and extreme changes in land use that may be strongly opposed by economic interest groups (Noss 1995b). Conversely, a community-level conservation strategy may protect up to 85–90% of species by conserving representative natural communities without a separate inventory of individual species (Noss 1987). Ecosystem-level planning, such as that by the Natural Community Conservation Planning Process of California, may be an efficient way to "avoid the eleventh-hour crises that force choices between losing species and shutting down regional economies" (Mantell 1992, after Noss et al. 1995).

CONCLUSION

We are facing unprecedented loss of biodiversity at all levels. To ignore the impact would be foolhardy, not only for humans, but also for the support of life itself. Loss of species and habitats and ecosystem degradation due to pollution and overexploitation occur on such rapid time scales that we need not wait long before realizing their impacts. We need measures and concepts to characterize the status and trends in ecosystems and to provide a standard for management. There is no relevant notion of ecosystem health, however, as there is for humans: a set of properties that have been selected through evolution because they maximize fitness. Ecosystems are loosely defined, dynamically changing associations of biotic and abiotic components. Measures of integrity must reflect the ability of ecosystems to maintain services of value to humans.

Our knowledge of the factors maintaining ecosystem integrity is still incomplete, mainly because of the intrinsic complexity of natural systems. The task of preserving ecosystem integrity is challenging. Even when not influenced by human activities, ecosystems show a high degree of variability, at different temporal and spatial

scales, in diversity, structure, and functioning. Such variability reflects changes in the community and physical environment due to internal and external disturbance (Ravera 1991). This inherent variability often makes it extremely difficult to separate the relative effects of natural and anthropogenic perturbations. However, absence of (scientific) evidence should not be interpreted as evidence that environmental impacts are absent. Clear yes–no answers are rarely available and decisions must be made in the face of uncertainty. There are costs in assuming an effect of human activity on ecosystem integrity when there actually is none, but the consequence of assuming no effect when there really is one is often far greater. In a strictly statistical sense, the null hypothesis that human activity does not appreciably affect the integrity of ecosystems can rarely be rejected (Peterman 1990). Waiting for a scientific consensus may delay any decision about conserving the environment, with possibly irreversible consequences. This becomes crucially important if we accept that, in extent and intensity, human exploitation of natural resources seriously threatens the earth's natural capital; too much indulgence in risk–taking could be very dangerous (Woodwell 1989).

Pressure for adequate answers creates a need to devise conceptual tools, such as ecological integrity, to help scientists and resource managers grasp the complexity of biological systems (Bernstein and Goldfarb 1995). The concept of integrity is far from a panacea for any management problem. Its definition simply reflects the capability of ecosystems, however defined, to support services, including pure aesthetics, that humans value. Ecosystem integrity is not an absolute, monolithic concept, but a multidimensional, scale–dependent abstraction; there is no unequivocal way to apply it in decision making. Measures of integrity must recognize the importance of maintaining processes that support those critical services.

What are the practical implications of these discussions? How should a manager implement notions of ecosystem integrity? The first step is to recognize that this is not the domain of the manager or of the scientist alone. Integrity reflects the ability of ecosystems to sustain services to humans, and the identification of those services can best emerge from multisector partnerships, in which all stakeholders seek agreement on the uses to which an ecosystem will be put, recognizing the linkages with other ecosystems. From such agreement on uses can come the identification of a set of measures that represent the status and trends of those services. A basic research question then arises: how to characterize the relationship between structural features of ecosystems (such as biodiversity or trophic linkages) and measures of functioning? This is an inchoate and nascent area of investigation, but one that holds tremendous potential for advancing the science of management (Daily 1997, Levin 1997, Levin and Ehrlich 1997).

RESPONSES TO THIS ARTICLE

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APPENDIX 1

OVERRIDING THE COMPLEXITY OF NATURAL SYSTEMS: two examples of the revenge of nature

Control of forest fires

Forest fires are especially frequent in boreal forests and other seasonally dry ecosystems, such as prairies and savannas. In Canada, $\sim 3 \times 10^6$ ha of forest burns each year, mainly due to natural ignition by lightning (Wein and MacLean 1983, Honer and Bickerstaff 1985). Natural forests are characterized by a mosaic of patchy, uneven-age stands and high heterogeneity in species abundance and distribution (Shugart 1984). Consequently, not all patches are equally susceptible to fires. Fires are usually limited to restricted areas and confined to the ground or understory. They are relatively modest in intensity; the high frequency of fire episodes prevents accumulation of fuel and reduces the probability of major catastrophic events. Fire suppression policies have been implemented in an attempt to reduce the frequency of fires in several U.S. National Parks. Remarkable side effects have followed the reduction in fire frequency, such as major changes in habitat structure and species composition, abundance, and spatial distribution. Some cases have been extensively documented: early successional forests in Oregon formerly had ~ 74 trees/ha and an average ponderosa pine (*Pinus ponderosa*) diameter >43 cm; after several decades of successful fire suppression, tree density has experienced a 10-fold increase (Daniel 1990), whereas average tree diameter has dropped to ~ 25 cm. The consequences of such changes in forest structure may be dramatic, because very high tree density implies increased vulnerability to insect pests and diseases and decreased resistance to drought (Habeck 1990). Furthermore, the ensuing

accumulation of fuel in the forest greatly increases the system's susceptibility to catastrophic fire in drought years. Fire control in a mature forest eventually becomes too sensitive to monitoring errors: a small fire that is not localized and suppressed at once can rapidly spread over huge areas. Indeed, fires have occurred to an extent never before experienced: the well-publicized 1988 Yellowstone fires burned 570,000 ha, including ~50% of Yellowstone National Park.

The spruce budworm

This example relates to management of North American forest subject to periodic outbreaks of the spruce budworm (*Chorisonema fumiferana*). This important lepidopteran defoliator of conifers is responsible for tremendous damage to North American forests. Mature forest stands dominated by balsam fir (*Abies balsamea*) are believed to be particularly vulnerable to budworm outbreaks, but stands of white spruce (*Picea glauca*) and red spruce (*P. rubens*) may also suffer substantial damage. An outbreak may kill up to 75–90% of trees in a fir stand, whereas impacts on spruce are less catastrophic. Only small trees usually survive budworm infestation. When the epidemic episode dies out, young understory trees enter a series of successional stages, at the end of which a new mature community of fir and spruce is reestablished. This stand is again susceptible to a new outbreak that can eventually wipe out part of the forest and start a new trend of successional phases. The dynamic of the budworm–forest system thus can be viewed as a cyclic succession with long-term dynamic stability (Freedman 1995). Outbreaks of budworm have probably recurred on the landscape for thousands of years (Baskerville 1975, MacLean and Erdle 1984, Blais 1985, Freedman 1995). After the second World War, however, as a way to cope with this resource crisis, considerable effort was devoted to controlling budworm outbreaks by intensive spreading of insecticide. Initially, this policy led to higher biomass production by constraining the budworm population, limiting defoliation, and substantially reducing tree mortality. Eventually, it promoted an increasingly large biomass of susceptible tree species, mainly dominated by mature stands of balsam fir and white spruce. Since 1974, insecticide spraying has not been effective in controlling budworms; in subsequent years, an outbreak has covered an area of an extent and intensity never experienced before. On the basis of this experience, Clark et al. (1979) have devised an instructive lesson for ecologically sound policy design that enables resource managers to account explicitly for natural variability, spatial heterogeneity, and nonlinear causation due to the combination of the multiscale, dynamical mechanisms of the exploited ecosystem.

APPENDIX 2

FOUR CLASSIC CRITERIA FOR EVALUATING BIOLOGICAL DIVERSITY

Intrinsic value

In this view, all species have genuine intrinsic value, which is independent of any direct or indirect utility to human beings (Callicot 1986, Naess and Rothemberg 1989). All species have an equal right to exist and to be protected from human-induced extinction. In this view, it would be arrogant to attempt to judge the relative rights of species to exist. Of course, the species is an abstraction, a convenient classification device invented by humans. Thus, the intrinsic value approach must also look within and above the species level, creating in the extreme and impossible definition dilemma.

Aesthetic value

Species and habitats may be perceived as amenities, to be valued for their beauty and potential for recreation. We can experience joy when we see a tropical landscape or a seal pup, and similarly value Central Park, Yosemite Park or the California Condor as part of our heritage. This amenity argument is not free of limitation: it can be criticized for being rather vague, brazenly anthropocentric, and too inconsistent, since aesthetic appeal is a highly subjective category and can undergo remarkable changes over time, driven by contingent cultural and economic forces. Indeed, amenity is largely associated only with "charismatic megaverbrates," rather than fungi, nematodes, or soil microorganisms. The difficulty in determining aesthetic values is evident in debate over recreational development in potential wilderness areas; but the importance of the concept remains evident.

Direct value of natural resources for humans

So far, this has been basically the only way living resources have been valued on the marketplace: biomass is harvested and molded into a product that can be bought or sold, according to market laws and constraints. Resource-based systems (fisheries, forest, and agricultural lands) are basically valued according to this mechanism. In 1988, fisheries provided 100 x 10 kg of food worldwide (FAO 1988), and wild species contributed ~4.5% to the U.S. Gross Domestic Product (Prescott–Allen and Prescott–Allen 1986). The loss of such resources is the most evident and pressing aspect of biodiversity loss. From an investment perspective, biodiversity provides both realized and potential direct services. Many of today's pharmaceuticals have been discovered from the study of natural products. R.S. McCabel, President of the Herb Research Foundation, states that about one in 125 plants that are thoroughly studied yield a major new medicine (*personal communication* at the Biodiversity Conference, Washington, D.C., 3–4 April 1995). In contrast, only one in >10,000 chemicals synthesized in laboratories turns out to be a drug of potential benefit for humankind (Dobson 1995). Moreover, Miller and Tangle (1991) report that prescription drugs containing active ingredients from angiosperm plants contributed ~ \$14 billion per year to the U.S. economy and \$40 billion per year worldwide between 1965 and 1990. F. Grifo, of the American Museum of Natural History, has shown that 118 out of the top 150 prescription drugs in the United States are derived from natural products: 74% are based on plants, 18% on fungi, 5% on bacteria, and 3% on vertebrates (Rosenthal and Grifo 1996). Nine of the 10 top prescription drugs in the United States are based on natural plant products. The World Health Organization estimates that > 80% of the world's human population relies upon traditional plant medicine for primary health care.

Indirect value through maintenance of ecosystem services

Biodiversity keeps the planet habitable and its ecosystems functional. The diversity of species and their communities provides essential ecological services of many types (Freedman 1995), including nutrient cycling, biological productivity, trophic function, cleansing of water and air, control of erosion, provision of atmospheric oxygen and removal of carbon dioxide, control of the vast majority of agricultural pests and organisms that can cause disease, pollination of many crops, and "maintenance of nature's vast "genetic library," from which humanity has already drawn the very basis of civilization"(Ehrlich and Ehrlich 1991). Biodiversity is tightly intertwined with the ecosystem's ability to withstand stress and disturbance, such as drought, disease, and global warming.

APPENDIX 3

INDICATORS OF BIODIVERSITY AT DIFFERENT LEVELS OF SPATIAL AND HIERARCHICAL ORGANIZATION

The simplest indicator of biological diversity is the number of species in a community (richness); yet, this measurement of biodiversity is of limited utility and misses much that is relevant (Walker 1992, Levin 1997). Indices such as Simpson's, Shannon–Wiener's, and Margalef's (Pielou 1977) involve not only the number of species, but also their relative abundance, and provide information about the distribution of importance of the species in a community. The scale of investigation is also important: point, alpha, beta, and gamma diversities address the problem of measuring biological diversity at different spatial scales, namely from a few square meters to hundreds of square kilometers. Moreover, as Wilson (1992) pointed out, "although the species is generally considered to be the 'fundamental unit' for scientific analysis of biodiversity, it is important to recognize that biological diversity is about the variety of living organisms at all levels." For example, the genetic diversity within a population is an important indicator of the range of phenotypic responses to various environmental conditions. Functional diversity is based on functional classification rather than taxonomic classification; it is a measure of how organisms are distributed across functional groups. Finally, community diversity is computed by using the number, sizes, and spatial distribution of communities (sometimes referred to as patchiness).

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