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Conservation of Biodiversity in a World of Use

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Abstract: *Biodiversity conservation has become the stated objective of national governments, state agencies, local communities, and scientific organizations. Yet despite this attention the term biodiversity remains poorly defined. One of the unfortunate consequences of this lack of definition is a proliferation of claims that biodiversity can be both used and conserved. This claim is difficult to assess without a more precise way of defining biodiversity. We offer a heuristic framework for measuring the consequences of human use for biodiversity. Our definition of biodiversity includes three components: genetic, population/species, and community/ecosystem. Each component has its own three attributes: composition, structure, and function. Using this definition, we assessed the effects of different types of human use on the different components and attributes of biodiversity. We show that (1) different degrees of human use or alteration result in differential conservation of biodiversity components; (2) some components and attributes of biodiversity are more sensitive to human use than others; and (3) only extremely limited use or virtually no alteration will protect all components.*

Conservación de la Biodiversidad en un Mundo de Uso

Resumen: *La conservación de la biodiversidad se ha convertido en un objetivo fijo reconocido por los gobiernos nacionales, agencias estatales, comunidades locales y organizaciones científicas. Sin embargo, a pesar de la atención brindada al término biodiversidad, este aún carece de una buena definición. Como resultado, se ha reclamado en muchas ocasiones que la biodiversidad puede ser utilizada y conservada. Es imposible evaluar esta afirmación sin contar con una forma precisa para definir la biodiversidad. En este artículo ofrecemos un enfoque heurístico para medir las consecuencias del uso humano sobre la biodiversidad. Comenzamos con una definición de la biodiversidad que incluye tres componentes: genético, poblaciones/especies y comunidad/ecosistema. Cada uno de los componentes cuenta con tres atributos: composición, estructura y función. Utilizando esta definición evaluamos los costos de diferentes tipos de usos humanos en los distintos componentes y atributos de la biodiversidad y demostramos que: (1) diferentes niveles de uso humano o alteración resultan en la conservación diferencial de los componentes de la biodiversidad; (2) algunos componentes y atributos de la biodiversidad son más sensibles que otros al uso humano; y (3) solamente el uso estrictamente limitado o virtualmente la ausencia total de actividades de alteración protegerá a todos los componentes.*

Introduction

Over the last decade the conservation of biodiversity has become an objective of international conventions, national governments, state agencies, nongovernmental or-

ganizations, local communities, school clubs, and individuals. Billions of dollars have been spent in the name of biodiversity, and over 150 national governments have signed a treaty committing themselves to biodiversity conservation (United Nations Environment Programme 1992). As biodiversity has become a common objective, the term itself has assumed an ever broader range of meanings (Takacs 1996; Sanderson & Redford 1997). As a result, the word has been pulled from its roots in the

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biological sciences and has become a political term with as many meanings as it has advocates (Redford & Sanderson 1992). Although this ambiguity may be convenient when it comes to signing treaties, a confusion of meanings can frustrate efforts to mobilize meaningful conservation efforts. Successful on-the-ground conservation relies on clear goals articulated with specific and commonly understood definitions and assumptions (Haila & Kouki 1994; DeLong 1996; Redford 1996).

Of the many confusing concepts in biodiversity conservation, few demand greater definition and scrutiny than "conservation through use," also commonly termed "compatible" or "sustainable" use. These terms are often used to imply that certain types or levels of human use incur little or no loss of biodiversity, that these uses are ecologically benign. Advocates of compatible use have suggested that substituting a compatible use for an incompatible one, or helping to perpetuate an existing use deemed as compatible, is in fact an attractive strategy for conserving biodiversity. Yet it remains difficult to know how to assess such suggestions, or how, in general, to measure compatibility or sustainability in biodiversity terms (Peters 1996).

We maintain that compatibility between human use and biodiversity conservation cannot be measured and should not be stated in binary terms as a "yes" or "no" condition. In reality, different kinds and intensities of human use will affect various aspects or components of biodiversity to differing degrees. Further, individual or societal decisions about the degree of biodiversity impact that is deemed "compatible" are value dependent and should be recognized as such.

We offer a framework both for assessing the biodiversity consequences of human use and for setting biodiversity goals based on those assessments. We use site-specific examples drawn from the conservation work of The Nature Conservancy, a large U.S.-based, non governmental organization, to illustrate how this framework could be applied to setting biodiversity goals at specific conservation sites.

During our decades of applied conservation experience, we have repeatedly encountered a significant need for the sort of comprehensive assessment framework we advance here. We suggest that the consequences for biodiversity of human activities, particularly those heralded as ecologically compatible, need to be examined more rigorously. Our framework is designed to aid such evaluations, and we demonstrate its intended use. Our evaluations of a variety of human resource uses are based primarily on a review and synthesis of available literature; we filled literature gaps with our professional judgment. Unfortunately, the literature does not support full confidence in every individual evaluation embedded in our applications of the framework. We anticipate that other users will lament similar gaps in scientific understanding of human effects on the ecosystems

they study. We maintain, however, that these knowledge gaps should not discourage rigorous evaluation of human effects; the conservation biology community knows enough to say significant things about the impacts of human use. In cases where data are not available, evaluations necessitating professional judgment can be reframed as testable hypotheses begging attention from conservation biologists.

Definitions

To more accurately assess the impact of human use on the conservation of biodiversity, we must first start with clear definitions of the terms *conservation* and *biodiversity*.

The word *conservation* has a long and complicated history as applied to human use of the natural world (Hunter 1996). Conservation has been variously combined or juxtaposed with the term *preservation*, producing a terminological muddle (Robinson 1993; Norton 1994). We use a widely adopted definition of conservation from the "Global Biodiversity Strategy" (World Resources Institute, World Conservation Union, United Nations Environmental Programme [WRI, IUCN, UNEP] 1992): "the management of human use of the biosphere so that it may yield the greatest sustainable benefit to current generations while maintaining its potential to meet the needs and aspirations of future generations: thus conservation is positive, embracing preservation, maintenance, sustainable utilization, restoration, and enhancement of the natural environment." Ignoring some of the internal dissonance in this definition, we use conservation to mean "consumptive and nonconsumptive use without complete destruction/conversion" and distinguish it from preservation, by which we mean non-use.

Biodiversity refers to the natural variety and variability among living organisms, the ecological complexes in which they naturally occur, and the ways in which they interact with each other and with the physical environment. This definition and the elucidation below is based upon Office of Technology Assessment (1987), Noss (1990), Noss and Cooperrider (1994), Holling et al. (1995), Gaston (1996), and Sanderson and Redford (1997). Climate, geology, and physiography all exert considerable influence on broad spatial patterns of biotic variety; local ecosystems and their biological components are further modified by environmental variation (e.g., local climatic and stream-flow fluctuations) and interactions among native biota. This natural variety and variability is distinguished from biotic patterns or conditions formed under the influence of human-mediated species introductions and substantially human-altered environmental processes and selection regimes (Noss & Cooperrider 1994; Bailey 1996).

Biological diversity can be measured in terms of different components—genetic, population/species, and com-

munity/ecosystem—each of which has compositional, structural, and functional attributes. *Composition* refers to the identity and variety of elements in each of the biodiversity components. *Structure* refers to the physical organization or pattern of the elements. *Function* refers to ecological and evolutionary processes acting among the elements. We have modified the matrix presented in Noss (1990) and present some of the different measurable attributes of compositional, structural, and functional diversity for the three components of biodiversity (Table 1). We have concentrated on those measures that would be most useful in determining the potential effects of human use on biodiversity.

Diversity of the genetic component refers to the variability within a species, as measured by the variation in genes within a particular species, subspecies, or population. Composition of this component might be measured through allelic diversity, structure through heterozygosity, and function through gene flow.

Diversity of the population/species component refers to the variety of living species and their component populations at the local, regional, or global scale. Composition of this component might be measured through species abundance, structure through population age structure, and function through demographic processes such as survivorship.

Diversity of the community/ecosystem component refers to a group of diverse organisms, guilds, and patch

types occurring in the same environment or area and strongly interacting through trophic and spatial biotic and abiotic relationships. Composition of this component might be measured through the relative abundance of species and guilds within a community, structure through spatial geometry and arrangement of patch types, and function through disturbance regimes (e.g., fire and flood) and flows of water, nutrients, chemicals, and organic matter.

The Costs of Use

Human activities are highly variable in their influence on the components and attributes of biodiversity. Any human activity that results in substantial resource extraction or modification will always entail significant, often unknown, and almost always unappreciated consequences for one or more biodiversity components, primarily by redirecting matter and energy flows. This cumulative redirection is enormous at the planetary scale (Vitousek et al. 1997), as the following three examples illustrate: (1) Vitousek et al. (1986) calculated that 40% of the Earth's terrestrial primary productivity was being appropriated by humans; (2) Roberts (1997) estimates that 25–35% of the primary productivity of continental shelf marine ecosystems is consumed by humans; and (3) Postel et al. (1996) report that humans now appropriate 26% of total evapo-

Table 1. Attributes of each biodiversity component emphasizing those measures useful in determining potential effects of human use.*

<i>Biodiversity components</i>	<i>Attributes</i>		
	<i>Composition</i>	<i>Structure</i>	<i>Function</i>
Community/ecosystem	presence, richness, frequency, and relative abundance of patch types, guilds, and species; proportions of endemic, exotic, threatened, and endangered species; proportions of generalists and specialists; life form proportions (e.g., C4:C3 plants)	patch size-frequency distributions; patch spatial configuration and connectivity; trophic structure; vegetation physiognomy; seral stage diversity and areal extent; stream channel form; abundance and distribution of structural elements (e.g., pool-riffle-run ratios, abundance of large woody debris and snags)	extent/spread, frequency/return interval, predictability, timing, intensity, and duration of disturbance processes; patch turnover rates, energy flow rates and patterns; nutrient delivery and cycling rates; biomass productivity; herbivory; parasitism and predation rates; pollination success; geomorphic process rates; flux rates in water budget components; water chemistry and temperature variation
Population/species	abundance, biomass, or density; frequency, importance, or cover value	dispersion (i.e., microdistribution); range (i.e., macrodistribution); metapopulation spatial configuration; population structure	demographic processes (e.g., fertility, recruitment rate, survivorship, dispersal, mortality); metapopulation exchange rates; individual growth rates
Genetic	allelic diversity; presence of particular rare alleles, deleterious recessives, or karyotypic variants	effective population size; heterozygosity; chromosomal or phenotypic polymorphism; generation overlap; heritability	inbreeding depression; outbreeding rate; rate of genetic drift; gene flow, mutation rate; selection intensity

*Modified from Noss 1990.

transpiration and use 54% of all runoff in rivers, lakes, and other accessible sources of water. As W.E. Rees has said "in effect, thermodynamic law dictates that all material economic 'production' is really consumption, and in this simple reality lies the root of our environmental crisis."

Yet despite these statistics, many who study and practice conservation and sustainable development still maintain that it is possible to both use and preserve biodiversity (e.g., Huston 1993) with no costs to either side. This claim is made despite a record of human overexploitation of resources that began in prehistory (Goudie 1990) and is manifested most recently in the negative effects of tropical logging (Frumhoff 1995; Bawa & Seidler 1998) and marine fisheries exploitation (Dayton et al. 1995; Botsford et al. 1997; Pauley et al. 1998). This ahistorical and wishful thinking is extremely dangerous because it allows its adherents to believe that there exist easy, cost-free solutions to exploitation of the planet.

We developed a framework for evaluating the effects of human uses based upon the various components and attributes of biodiversity as described (Table 2). Along the vertical axis of our framework we array the three components of biodiversity: community/ecosystem, population/species, and genetic. For each component we list the associated attributes of function, structure, and composition, arranged in this sequence because it is suggested that human use will affect them in this order (Holling et al 1995; Folke et al. 1996). The horizontal axis arrays a continuum of degree of human alteration. In the example of Table 2, we applied the framework to both

riverine systems and forested terrestrial systems. To the far left are the most heavily altered ecosystems (dam-altered flow regime and channelized for riverine; converted-to-pasture for forested, to the far right those least altered (free-flowing, natural channel for riverine; large and natural for forested). We have scored each of the cells using the following categories: "completely conserved" when the parameter value is expected usually to stay within its range of natural variation for most of the genetic, species, or ecosystem components involved; "partially conserved" when the parameter value is frequently outside its natural range of variability for many genes, species, or ecosystems; and "not conserved" when the parameter value almost always falls outside the natural range of variation for most genes, species, or ecosystems.

This scoring process is strongly subjective; we have based it on our reading of the literature and our experience. We fully recognize that particular cases might have different patterns of scoring and emphasize that our purpose is to illustrate a useful analytical process rather than to obtain perfectly accurate scoring. We also emphasize that this framework serves to suggest many hypotheses that would be important research topics for conservation biologists from a number of different disciplines.

The body of the matrix (Table 2) illustrates the components of biodiversity that are completely conserved, partially conserved, or not conserved under different degrees of human alteration or use. Under this scheme, those systems in which human effects are most pronounced are those that do not conserve genetic, population/species, or community/ecosystem components. Only those systems that are altered either little or not at all can fully conserve genetic, population/species, and community/ecosystem components and attributes.

We examined the effects of human use or alteration on biodiversity by determining how different types of resource use affect both the components of biodiversity and their attributes (Table 3). We drew upon illustrative examples from the literature (cited in Table 3) and recognize that effects will vary with intensity of use, biophysical setting, and history. Because the cited case studies did not directly evaluate all attributes and components of biodiversity use, we extrapolated from the information provided using our framework and our experience. We based our scoring on an assumption that the exploited system was unaffected by humans before the resource use began.

All consumptive use affects biodiversity in some attribute and component, commonly affecting not only the target resource but other components as well (Table 3). The genetic component has been shown to be affected by harvesting, be it fishing, logging, or trophy hunting (Ryman et al. 1981; Laikre & Ryman 1996; Buchert et al. 1997; Freese 1998). The population/species component is most

Table 2. Effects of human alteration (from heavily altered "built" to unaltered "natural"; Hunter 1996) of riverine^a and forested^b systems on the components and attributes of biodiversity.

Biodiversity component & attribute	Human alteration ^c			
	Built	Cultivated	Managed	Natural
Community/ecosystem				
function	0	X	XX	XX
structure	0	X	XX	XX
composition	0	0	X	XX
Population/species				
function	0	0	X	XX
structure	0	0	X	XX
composition	0	0	X	XX
Genetic				
function	0	0	X	XX
structure	0	0	X	XX
composition	0	0	X	XX

^aFor riverine systems, built means heavy dam alteration and channelization; cultivated means heavy dam alteration and flood disturbance but with original channel; managed means water diversion and natural channel; and natural means a free-flowing and natural channel.

^bFor forested systems, built means converted to pasture; cultivated means fire suppression and heavy management of natural forest; managed means selective logging and hunting; natural means large and natural forest.

^cXX, completely conserved; X, partially conserved; 0, not conserved.

Table 3. Effects of resource-use systems on the components and attributes of biodiversity.

Biodiversity component & attribute	Types of use ^a						
	Irrigation supply reservoirs ^b	Hydropower dams ^c	Intensive fishing on coral reefs ^d	Grazing in historically ungrazed forests ^e	Water diversion ^f	Harvesting nontimber forest products ^g	Wilderness river-running ^h
Community/ecosystem							
function	0	X	X	X	XX	XX	XX
structure	0	X	X	X	XX	XX	XX
composition	0	X	X	X	X	XX	XX
Population/species							
function	0	0	0	X	X	X	XX
structure	0	0	0	X	X	X	XX
composition	0	0	0	X	X	X	XX
Genetic							
function	0	0	0	X	X	X	XX
structure	0	0	0	X	X	X	XX
composition	0	0	0	X	X	X	XX

^aXX, completely conserved; X, partially conserved; 0, not conserved.

^bWestern North America: Rood & Maboney 1990; Poff et al. 1997.

^cGlobal: Cushman 1985; Moog 1993.

^dGlobal: Roberts 1995; Laikre & Ryman 1996.

^eWestern United States: Belsky & Blumenthal 1997.

^fSierra Nevada, California, U.S.A.: Harris et al. 1987; Stromberg & Patten 1992.

^gTropical forests: O'Brien & Kinnaird 1996; Peters 1996.

^hGlobal: Tejada-Flores 1978; B. D. Richter, personal observation.

commonly understood to be affected by use, as much work has demonstrated (Redford 1992; Noss & Cooperrider 1994; Witkowski et al. 1994; Peters 1996; Freese 1998; Pauley et al. 1998), although subtle effects are often missed (e.g., Garber & Burger 1995). Of increasing importance is an understanding of how the community/ecosystem component has been (Runnels 1995) and is being affected by human activities (Noss & Cooperrider 1994; Richter et al. 1997; Vitousek et al. 1997). The extent to which the different attributes are affected by use remains a little-understood and important topic for further work.

The primary points to gain from these analyses are that (1) different degrees of human use or alteration result in different negative effects on biodiversity components; (2) some components and attributes of biodiversity are more sensitive than others to human use or alteration; and (3) only extremely limited use or virtually no alteration will protect all components.

Much of what we have presented is based on the implicit assumption that nature is organized in a linear fashion. But increasingly, ecologists are appreciating the nonlinearity and complexity of nature. This makes it much more complicated to predict all the effects of human use or alteration. For instance, Johnson (1994) and Walker and Noy-Meir (1982) have documented cases where resource use has caused systems to flip into alternative stable states in which original patterns of biodiversity are altered irretrievably. Holling et al. (1995) conclude that management that applies fixed rules for achieving constant resource yields leads to systems that can break down in the face of disturbances that previ-

ously could be absorbed. It is also important to note that we treated each species as if it were equivalent to every other species and as if the impact of human use on the species would equally affect ecological systems. But as Walker (1992) and Power et al. (1996) have pointed out, some species play more important roles than others in structuring ecosystems, and their loss would have correspondingly greater effects.

Managing for the Full Spectrum of Biodiversity

A Portfolio or Network of Conservation Sites

Our analyses (Tables 2 & 3) suggest that preservation of all components of biodiversity can be attained only in areas largely free of human alteration. In many parts of the world such places are rare, however, with little native landscape remaining, genetic information having been lost, species extirpated, communities rearranged, and ecosystem processes substantially altered. As a result, many areas affected by human alteration also must play a role in efforts to conserve the components and attributes of biodiversity.

But how, given both the many areas affected by humans and the limited nature of conservation resources, can the conservation practitioner know what places are likely to make the largest possible contribution to biodiversity conservation and hold the greatest promise for long-term ecological sustainability? Obviously, sites that retain much of their native biodiversity at all levels of bi-

ological organization should be highly valued in any ecoregional or national conservation strategy. Consideration of the three biodiversity components and of the ways in which various types and degrees of human use or alteration can degrade or may already have degraded biodiversity at different levels can help in selecting those places at which conservation resources should be directed.

Managing a Site for Biodiversity

Once a site is targeted for conservation activity, it should be managed to retain and regain as much of its native biodiversity components and attributes as is feasible. The Nature Conservancy (TNC) has developed a site conservation planning framework (Poiani et al. 1997) designed to guide conservation practitioners through a process of explicitly defining conservation targets (e.g., species and community types), articulating ecological goals for these targets (e.g., to maintain minimum population or relative abundance levels), assessing threats to the targets related to existing and potential human uses of lands and waters, and designing conservation strategies for ameliorating those threats.

Although TNC's conservation efforts focus on species and natural communities as conservation targets, these site conservation plans explicitly consider the ecosystem processes and conditions necessary to sustain the targets (TNC 1996). Thus, by conserving species and communities in their ecosystem context, many of the ecosystem and genetic components within a conservation site also will be conserved. In addition, TNC has recognized the need to conserve each species and community type in a variety of ecoregional settings for the purpose of "maintaining the genetic and ecological variation necessary for long-term survival" of conservation targets (TNC 1996, 1997). Arguably, adequate conservation of sites selected to include genetic and ecological variation of targeted species and communities will lead to conservation of all three of the components of biodiversity we have characterized.

Ecologists are becoming increasingly aware of the extent to which alterations of ecosystem processes and patterns may influence the genetic variability or genetic structure of species (e.g., Weiner 1994). In practice, it is difficult to discern the degree to which ecosystem patterns and processes can be altered without affecting the genetic variation of targeted species. This argues for adequate protection of the whole system of which a species' population is a part. The compatibility of various human activities within a conservation site should be evaluated with the rigor suggested by our analytical framework, which explicitly considers all components and attributes of biodiversity.

Site conservation goals should be founded on a realistic yet ambitious assessment of the maximum contribution a site can make to biodiversity conservation. For example, a site may retain its full complement of native

species even though certain environmental processes have been irretrievably altered, so all genotypes may not be conserved. Conservation goals should address the prevention of further loss of certain biodiversity components associated with increased levels and types of human use. And conservation goals should reflect a strong commitment to regain as much native biodiversity as is possible at the site. A framework, such as that in Table 2, should prove useful in assessing a particular site's current biodiversity condition and future potential.

Site-Based Biodiversity Conservation

The utility of our framework can be best illustrated with some real-world examples in which TNC has been involved: the lower Roanoke River in North Carolina, U.S.A., and the middle Pantanal in Brazil (Tables 4 & 5).

THE ROANOKE RIVER

The Nature Conservancy selected a site along the lower Roanoke River in North Carolina as a place to conserve numerous species and community types in one of the "highest-quality, most extensive floodplain forest ecosystems remaining on the Atlantic Coastal Plain" (TNC 1991). Major threats to this site and its associated biodiversity include (1) substantial alteration of the natural hydrologic regime associated with upstream dams (Richter et al. 1997); (2) water diversion to growing cities on the Atlantic Coast; (3) degraded water quality associated with pulp mills, municipal discharges, agriculture, and reservoir operations; (4) forest fragmentation associated with timber harvest and agricultural clearing activities; and (5) commercial and recreational hunting and fishing.

These current human uses of the Roanoke ecosystem, and data available for certain species and physical conditions over time, lead us to hypothesize that community- and ecosystem-level composition, structure, and function have been altered to some degree, populations substantially changed, and genotypes likely compromised by current human uses of ecosystem processes and products. Key ecosystem functions have been altered, such as the delivery of nutrient-enriched sediments to high terraces; hydroperiod (flood inundation) regimes; and the reworking of the floodplain that destroys and regenerates secondary channels, oxbow lakes, and natural levees. These perturbed ecosystem processes will likely lead to increasing alterations at the population/species and genetic levels as the ecosystem proceeds through a process of relaxation and biosimplification over time. Table 4 portrays our current understanding of the "current condition" of this site, depicting those biodiversity components and attributes that are being conserved to varying degrees under current conditions.

As with the majority of ecosystems currently or historically exploited for human uses, we can only speculate

Table 4. Current and potential resource uses of the Roanoke River, North Carolina, U.S.A., and their effects on the components and attributes of biodiversity.^a

<i>Biodiversity component & attribute</i>	<i>Management options, Roanoke River^b</i>					
	<i>Channelize</i>	<i>Increase water diversion, flood control, and forest clearing</i>	<i>Current conditions</i>	<i>Restore flood regime</i>	<i>Restore hydro regime and water quality, change game management</i>	<i>Remove dams</i>
Community/ecosystem						
function	0	X	X	XX	XX	XX
structure	0	X	X	XX	XX	XX
composition	0	X	X	XX	XX	XX
Population/species						
function	0	0	0	X	XX	XX
structure	0	0	0	X	XX	XX
composition	0	0	0	X	XX	XX
Genetic						
function	0	0	0	0	X	XX
structure	0	0	0	0	X	XX
composition	0	0	0	0	X	XX
Option space	feasible	feasible	feasible	feasible	feasible	not feasible

^aArrayed across the top are types of current and potential resource uses, from most intense at the left to least intense at the right. At the bottom is our perception of which of the options are politically feasible. See Table 1 for types of variables used in determining rating.
^bXX, completely conserved; X, partially conserved; 0, not conserved.

about the full magnitude and nature of human-induced changes to the biodiversity components and attributes along the Roanoke. Little historical data exist to quantitatively document changes that have transpired over time. Linking those data and trends to specific human uses or human-induced changes to ecosystem processes such as flood regimes is extremely difficult. We briefly explain our ratings for the Roanoke River in Table 4 by referencing existing documentation and by offering extrapolations that extend beyond that documentation.

Because daily streamflows have been measured on the Roanoke River since 1913, we were able to quantify ecologically relevant changes in flow characteristics such as flood disturbances and low flows since dams were constructed in the 1950s (Richter et al. 1997). Researchers at the University of North Carolina then used satellite imagery, obtained at various flooding levels, and correlated mapped areas of inundation with the respective flow levels to produce quantitative estimates of hydroperiod (floodplain inundation) changes associated with the

Table 5. Current and potential resource uses of the Pantanal, Brazil, and their effects on the components and attributes of biodiversity.^a

<i>Biodiversity component & attribute</i>	<i>Management options, Pantanal^b</i>				
	<i>Channelize (Hidrovia)</i>	<i>Massive landscape conversion (e.g., agriculture)</i>	<i>Increase fishing and hunting pressure</i>	<i>Current conditions (ecotourism and commercial fishing)</i>	<i>Eliminate commercial fishing</i>
Community/ecosystem					
function	0	X	XX	XX	XX
structure	0	X	XX	XX	XX
composition	0	X	XX	XX	XX
Population/species					
function	0	0	X	XX	XX
structure	0	0	X	X	XX
composition	0	0	X	X	XX
Genetic					
function	0	0	X	X	XX
structure	0	0	X	X	XX
composition	0	0	X	X	XX
Option space	feasible	feasible	feasible	feasible	feasible

^aArrayed across the top are types of current and potential resource uses, from most intense at the left to least intense at the right. At the bottom is our perception of which of the options are politically feasible. See Table 1 for types of variables used in determining rating.
^bXX, completely conserved, X, partially conserved; 0, not conserved.

measured changes in streamflow regimes (Townsend & Walsh 1997). These hydroperiod changes were subsequently linked to vegetation data that suggest changes in seedling survival within certain floodplain forest communities and reduction or elimination in coverage of vegetation types that require periodic inundation (Rice & Peet 1997; S. Pearsall, personal communication).

These changes lead us to postulate that under current conditions community/ecosystem function, structure, and composition are only partially conserved (Table 4). Each of these attributes at the community/ecosystem level, however, could be largely restored by reinstating larger floods and associated hydroperiods, as depicted in Table 4. We do not believe that current levels of other threats, such as water pollution, timber harvest, and fishing, substantially influence attributes of the community/ecosystem component or limit the potential restoration of these attributes to "completely conserved" under the "Restore Flood Regime" column of Table 4. We recognize that some species and ecosystem functions would remain impaired after flood regimes are restored, but we expect that most attributes of the community/ecosystem component would usually stay within their ranges of natural variation (completely conserved). Similarly, modest increases in other threats would not cause our ratings in the "increased water diversion, flood control, and forest clearing" column of Table 4 to change to "not conserved," but additional effects associated with channelization certainly would.

We are not so optimistic about current effects at the population/species level (Table 4). Species-specific research has included analysis of changes in the population structure and reproductive success of striped bass using the Roanoke River. This research has documented substantial reductions in recruitment of young bass associated with changes in springtime flows (Zincon & Rulifson 1991). In addition, qualitative observations of macroinvertebrates inhabiting the Roanoke's stream edge suggest that these fauna have been heavily affected by flow alterations (S. Pearsall, personal communication). These species observations, the vegetation changes described previously, and our familiarity with flow alteration research conducted on other rivers lead us to believe that functional, structural, and compositional attributes of the Roanoke's populations and species distributions almost always fall outside their natural range of variability for most species (not conserved).

Restoring the Roanoke's flood regime would benefit many aquatic and floodplain species. Nevertheless, it would not lead to complete conservation at the population/species level (Table 4) because of continuing problems with water quality, heavy recreational and commercial fishing, and other aspects of flow alteration such as rapid water-level fluctuations associated with hydropower dam operations. Attributes at the population/species level would remain frequently outside their natural range of variability for many species (partially conserved).

The impacts described for the Roanoke's species undoubtedly are having even more pronounced effects on genetic attributes. Flow regimes present strong selective forces in aquatic ecosystems (Poff et al. 1997). Alteration of these forces on the Roanoke River is likely translating into genetic changes due to their strong influence on reproductive success in vegetation, fishes, and many other floodplain and aquatic species. As described above, many of the attributes at the population/species level would be partially or substantially restored by restoring hydrologic regimes and water quality; we believe that genetic conditions would improve for many species as well. The presence of dams, however, will continue to limit many species' potential for genetic restoration because of the dams' influence on metapopulation dynamics within the Roanoke River basin. Thus, genetic attributes cannot be completely conserved until the dams are removed (Table 4).

The Nature Conservancy's conservation goals for the Roanoke site include the intent to "restore and maintain the relative abundance and variability of the full suite of viable community types, and allow no human-induced extirpation of native species" (TNC 1991). To attain these goals, substantial restoration of key ecosystem functions will be necessary. In particular, restoration actions would need to move the community/ecosystem ratings in Table 4 toward "completely conserved," requiring restoration of the flood regime. The Conservancy is presently advocating that natural flow restoration be pursued in the context of a multi-agency adaptive management program designed to test a number of hypotheses about the dependence of certain species and community types on specific aspects of natural flow regimes (Richter et al. 1997). By pursuing these restoration actions with scientific rigor and adequate monitoring, the degree to which flow alteration has compromised different attributes of the Roanoke's biodiversity components can become better understood from the responses of the system to restoration.

Table 4 portrays different management options and the different components of biodiversity conserved under those options. Restoration actions could move the Roanoke site's position on the matrix toward the right side, a highly desirable management outcome. Implementation of more radical management options will be constrained by perceptions about the political and economic feasibility of limiting or eliminating current human uses of the Roanoke. As discussed previously, full conservation of the genetic component on the Roanoke cannot be achieved with the dams in place; despite this, it is not realistic to remove the dams at this time. The range of management options available to biodiversity managers on the Roanoke might be called their "option space" (denoted in the bottom row in Table 4; option space does not include dam removal). Such option space reflects both the opportunity presented with adoption of ambitious yet realistic management goals and the biodiversity consequences of

increased human use (e.g., water diversion, forest clearing) of the Roanoke's resources.

THE PANTANAL

Our second example comes from the Pantanal region in southwestern Brazil. The centerpiece of the Pantanal region is an extensive, 140,000-km² wetland complex that includes seasonally inundated grasslands, gallery forests along river corridors, and perennial lakes. The wetland complex supports a spectacular diversity of wildlife, including the jaguar (*Panthera onca*), the giant otter (*Pteronura brasiliensis*), 260 species of fishes, 650 species of birds, and huge populations of caimans (*Caiman* sp.), capybaras (*Hydrochaeris hydrochaeris*), and innumerable other species.

Protected conservation areas have been established near the confluence of the Cuiaba and Paraguay Rivers. Ecotourism is popular in the area, with little or no measurable consequences for the area's biodiversity associated with the use of watercraft. The primary current threat to biodiversity appears to be commercial fishing, although other areas of the Pantanal are under substantial threats from agriculture, urbanization, and ranching. Although such fishing has not yet resulted in the documented extirpation of any species, it may well be changing the population structure of commercially desirable species, changing biotic interactions among species, and thereby substantially altering the genetic component of the population/species (Table 5; Laikre & Ryman 1996). Eliminating commercial exploitation of the Pantanal's fishes likely would restore population/species-level structure and lead to substantial restoration of the genetic component as well (Table 5).

Current levels of human use in parts of the Pantanal therefore present an extraordinary and rare opportunity to completely conserve all three components of biodiversity across an immense landscape. This circumstance is highly vulnerable to changes in human use, however (Table 5; note the large range of available options). Fishing and hunting pressure could easily increase as local human populations grow, resulting in the extirpation of commercially desirable species. Some agribusiness proposals considered for the region could lead to massive conversion of the Pantanal landscape, with dire consequences for all components of biodiversity. Most serious at present, however, is a five-nation proposal to channelize the Paraguay River to facilitate increased barge transport of goods from the interior of the continent. This channelization proposal, known as the "Hidrovia" or waterway project, could lead to lowering of water levels throughout large areas of the Pantanal wetland and forever change ecosystem patterns and processes.

The depiction of management option spaces and the placement of each site's current condition in Tables 4 and 5 has proven to be a useful heuristic exercise. Most im-

portant, we are hopeful that the framework we present will prove useful for engaging our colleagues and resource managers in constructive discussions about compatible human uses at conservation sites.

Conclusion

We follow in a long history of those who advocate that all biological entities and their environments have intrinsic value independent of their usefulness to humans (Wilson 1992; Noss & Cooperrider 1994). This value applies not just to species, communities, or ecosystems, but to the complex and intertwined web of life that has come to be called biodiversity. In such a value system, the preservation of biodiversity for its own sake, in its entirety and in its component parts, is a legitimate objective in itself (Ehrenfeld 1981). As we have shown through our framework, biodiversity in its entirety can be conserved only in areas of limited human use. But the majority of both the terrestrial and aquatic world have been, and will continue to be, vital sources of resources for the human population. We live in a world of use.

It was the assurance that such human use would serve as the basis for conservation that brought so many different interest groups to agree on the importance of biodiversity conservation (Sanderson & Redford 1997). The value of biodiversity was largely to be determined by economic criteria, and maintenance of biodiversity and sustainable development not only could go together but were part of the same process (Robinson 1993).

In our daily work we confront the discordance between the view that humans can use biodiversity without causing any harm and our own experience, shared by many of our peers, that this is not possible. Belief in the existence of ways to use biodiversity without affecting it continue despite strong counsel from the conservation biology community: "Human intervention in an ecosystem for commercial purposes inevitably alters and generally simplifies, at some scale, ecosystem structure, composition and function" (Freese 1998).

We must move beyond the sterile argument of "use conserves" versus "use destroys" and into the complicated terrain between these two positions. The framework we are proposing is designed to do exactly this, enabling an approach to answering the question posed by Freese (1998): "... what criteria or measurements do conservationists use to understand the biodiversity tradeoffs that commodity uses of wild ecosystems may entail?" It is now possible to gain a good general understanding of the effects that specific human uses have, have had, and could have on biodiversity. We disagree with an eminent panel of scientists who concluded that "in many, if not most, cases it will not be possible to accurately predict the effects of various types and levels of resource use on the targeted resource or other ecosystem components" (Mangel et al. 1996).

The literature we sampled for this paper is part of an ever-growing body of evidence that pinpoints the effects of specific human uses on specific components of biodiversity. By incorporating this evidence into an analytical framework, conservation biologists can work to provide critical, a priori assessments of the biodiversity costs of resource use. Such an approach would also support working with resource harvesters to improve the effectiveness of their harvesting methods to ensure that those components and attributes that can be conserved under their use regimes are conserved.

It is time for conservation biologists to overcome their methodological differences and the limitations of their data and unite to provide answers and approaches to one of the major issues confronting humans and the other inhabitants of our world.

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