Colloquium

Human-modified ecosystems and future evolution

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Our global impact is finally receiving the scientific attention it deserves. The outcome will largely determine the future course of evolution. Human-modified ecosystems are shaped by our activities and their side effects. They share a common set of traits including simplified food webs, landscape homogenization, and high nutrient and energy inputs. Ecosystem simplification is the ecological hallmark of humanity and the reason for our evolutionary success. However, the side effects of our profligacy and poor resource practices are now so pervasive as to threaten our future no less than that of biological diversity itself. This article looks at human impact on ecosystems and the consequences for evolution. It concludes that future evolution will be shaped by our awareness of the global threats, our willingness to take action, and our ability to do so. Our ability is presently hampered by several factors, including the poor state of ecosystem and planetary knowledge, ignorance of human impact, lack of guidelines for sustainability, and a paucity of good policies, practices, and incentives for adopting those guidelines in daily life. Conservation philosophy, science, and practice must be framed against the reality of human-dominated ecosystems, rather than the separation of humanity and nature underlying the modern conservation movement. The steps scientists can take to imbed science in conservation and conservation in the societal process affecting the future of ecosystems and human well-being are discussed.

The Globalization of Human Impact

> Ecologists traditionally have sought to study pristine ecosystems to try to get at the workings of nature without the confounding influences of human activity. But that approach is collapsing in the wake of scientist's realization that there are no places left on Earth that don't fall under humanity's shadow.
>
> Richard Gallagher and Betsy Carpenter (1)

These opening remarks to *Science* magazine's special issue on Human-Dominated Ecosystems are long overdue. George Marsh (2) wrote his classic book *Man and Nature; or Physical Geography as Modified by Human Action* in 1864, before Haeckel (3) coined the word ecology and three quarters of a century before Tansley (4) gave us the ecosystem concept.

Ecologists' preoccupation with the pristine reflects a long tradition in western culture and a philosophy of separating humanity and nature (5), not to mention the humanities and science (6). The separation spilled over into conservation with its emphasis on setting aside pristine fragments of nature. Consequently, ecologists' recognition of the inseparability of human and natural realms could not be timelier in helping to bridge historical schisms, fostering sustainable development (7), and giving ecologists a new tool for investigating ecosystem processes (8).

Drawing a sharp line between the human and natural realms serves no purpose when our imprint is as ancient as it is pervasive. In the last few hundred thousand years, hunting and fire have shaped animal and plant communities across Africa (9). By the late Pleistocene, our shadow fell over every major landmass except Antarctica (10). The New World and Australia lost over two-thirds of their megafauna (>44 kg in body weight) within the last 10 to 50 millennia, and oceanic islands 50 to 90% of their birds in the last 3,000 years, largely because of human colonization and overkill (11). By the 20th century 40 to 50% of the world's land surface had been visibly transformed for domestic production and settlement (12). As we enter the 21st century, the earth's atmosphere, waters, and soils have been altered by human activity to the point of changing biogeochemical cycles and climate on a global scale (13).

What can we say about future evolution in a human-dominated world? We were invited to speculate freely. I suspect ecologists are uneasy about speculation because of their eschewal of human activity. I share the same uneasiness despite having studied humans as an integral part of African ecosystems for over three decades (14). But my uneasiness stems from a different concern—how little the fossil record can tell us about the future evolution because the future depends so much on human behavior. If we can't predict next year's economy, what can we say about evolution a thousand years from now, let alone millions?

Despite predictions of a mass extinction (15), the outcome is not inevitable. Human-induced extinctions are qualitatively different from previous mass extinctions (16). The threat is intrinsic, arising from a single species rather than an asteroid, volcanic activity, or other extrinsic agents. And, even though we can assume that human activity will affect future evolution by default or design, there is a world of difference between the two. Predictions based on past trends paint a bleak picture for our own species, let alone biodiversity. Yet even modest changes in fertility over the coming decades could see population growth level off (17). Ironically, scientists can change the course of evolution by persuading society to disprove their dire predictions! If my two cents worth helps, then I'm prepared to speculate in the interests of self-negation.

In reviewing human-dominated ecosystems I look at a number of interrelated topics. Each is vast and the subject of many reviews. These include ecosystem consequences of human impact (18–20), the consequences for humanity itself (7, 21), science applied to conservation (22), and science and conservation in society (23). My interest is not so much in the details as it is in showing the links and feedbacks among science, conservation, and society needed to avoid a dull homogenous planet fine for weeds and pathogens but not for the diversity of life or humankind.

Characteristics of Human-Dominated Ecosystems

Human impact on ecosystems can be looked at in several ways. Marsh (2), Tolba *et al.* (19), Heyward (19), and Vitousek *et al.* (12), for example, look at the outcome of using such measures as changes in habitat, species composition, physical characteristic, and biogeochemical cycles. Diamond (24) looks at the cause—the Evil Quartet of overkill, habitat destruction and

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Table 1. Some characteristics of intentionally modified ecosystems

High natural resource extraction
Short food chains
Food web simplification
Habitat homogeneity
Landscape homogeneity
Heavy use of herbicides, pesticides, and insecticides
Large importation of nonsolar energy
Large importation of nutrient supplements
Convergent soil characteristics
Modified hydrological cycles
Reduced biotic and physical disturbance regimes
Global mobility of people, goods, and services

fragmentation, impact of introduced species, and chains of extinction. Clarke and Munn (21) use systems models to explore human impact on ecosystems and its ramifications (19).

Although each approach has merit, none deals with motive. Did we create anthropogenic environments intentionally or not? Do they fulfill human goals? Ecologists are quick to judge the result without looking at cause, implying that we destroy nature without thought to the outcome. But, is our behavior really that aberrant? Would other species behave differently in the same situation?

I raise these questions because ignoring cause blinds us to the reasons for ecosystem modification. It also runs counter to the evolutionary perspective biologists apply to other species. What are the life-history and evolutionary strategies of *Homo sapiens*? How successful is that strategy in survival and reproductive terms? What are the costs? For consistency, we should look at human behavior as we do other species. After all, many, perhaps most, species modify their environment. Examples range from the crown-of-thorns starfish (25) to elephants (26). Problems of species overabundance, population crash, and ecological change are widely documented (27).

With these questions in mind, I have categorized human impact as either intended or unintended, fully recognizing the murky dividing line. My reason is 2-fold. First, the most universal and ancient features of "humanscapes" (28) arise from a conscious strategy to improve food supplies, provisions, safety, and comfort—or perhaps to create landscapes we prefer, given our savanna ancestry (29). The domestication of species, the creation of open fields, the raising of crops, and the building of shelters and settlements are the most obvious of intentional human activities, each practiced for millennia. Table 1 lists some ecosystem traits arising from deliberate human alteration of ecosystems. All of these characteristics are deliberate strategies to boost production and reproduction. As an evolutionary strategy, our success at commandeering resources and transforming the landscape to meet our needs has been phenomenal. Our numbers have grown from fewer than 4 million 10,000 years ago (30) to 6 billion today. Survival rates have risen, lifespan increased, and other indices of welfare improved in the evolutionary blink of an eye (18, 19).

But what of the negative consequences? Table 2 lists a few of the side effects. It can be argued that ecological side effects are not unique either, but stem from density-dependent effects widely reported in other species (27). The distinction between humans and other species thus lies not in our evolutionary strategy *per se*, but in the side effects or our global dominance. What then can be said about the consequences for ecosystems, evolution, and humans themselves?

Ecosystem Consequences

The more obvious consequences of human activity, such as the loss of species diversity and wild habitat, accelerated erosion, and sedimentation, have been extensively quantified (19, 20) and need no further elaboration. Harder to gauge are the consequences of human impact on such ecosystem properties as energy pathways, nutrient cycles, productivity, albedo, and, ultimately, the large-scale processes governing climate, hydrology, and biogeochemial cycles (31). The uncertainties over how human impact will affect large-scale ecosystem properties in turn clouds the evolutionary predictions we can make based on such species characteristics as ecological niche, demography, and adaptability.

Table 2. Some ecosystem side effects of human activity

Habitat and species loss (including conservation areas)
Truncated ecological gradients
Reduced ecotones
Low alpha diversity
Loss of soil fauna
Simplified predator–prey, herbivore–carnivore, and host–parasite networks
Low internal regulation of ecosystems due to loss of keystone agents
Side effects of fertilizers, pesticides, insecticides, and herbicides
Invasive nonindigenous species, especially weeds and pests
Proliferation of resistant strains of organism
New and virile infectious diseases
Genetic loss of wild and domestic species
Overharvesting of renewable natural resources
High soil surface exposure and elevated albedo
Accelerated erosion
Nutrient leaching and eutrophication
Pollution from domestic and commercial wastes
Ecological impact of toxins and carcinogenic emissions
Atmospheric and water pollution
Global changes in lithosphere, hydrosphere, atmosphere, and climate

An assessment of the ecosystem consequences is complicated by the question of the best measure. Should we use structural characteristics such as overall diversity, species composition, size-frequency, food web complexity, or trophic structure? Are ecological processes, whether resistance, resilience, perturbation, or some other measure more appropriate? Or should we use ecological functions such as overall productivity, water and nutrient cycles, and reflectance?

Here, rather than using a single measure, I stress ecological linkages. I do so because our historical local sphere of awareness still blinds us to the global ripples we cause today. Awareness lags far behind impact. Ecology cannot yet tell us the full consequences of our activity, deliberate or otherwise, but it can at least map its dimensions and alert us to plausible threats. I also stress biotic rather than abiotic processes, given the heavy emphasis on pollution, biogeochemical cycles, and climate change in environmental studies to date (13, 19). Following the ripples calls for new theories and tools and methods for detecting and predicting the outcome for ecosystems, planetary process, our own future, and ultimately the evolution of life on earth. Meanwhile, we must make informed guesses. I select a few of the larger stones we have cast into the ecosystem pond and, using evidence and theory, follow the ripples through a causal chain from impact on community structure to ecosystem process and function. I then follow one or two of the persistent ripples from ecosystem to biosphere to show how the backwash can affect species and communities locally.

I start with the most central issue in conservation biology today and the hallmark of human impact from genetic to landscape levels: the loss of biological diversity.

Diversity. What are the ecological consequences of reduced diversity? The evidence is inconclusive but tilts toward some predictable changes. So, for example, recent multisite studies across Europe show that productivity rises with species diversity (28, 29). The higher yields may arise from species complementary in resource use and perhaps positive species interactions (32). Whatever the cause, recent work points to the reverse phenomenon, a reduction in diversity leading to a loss of productivity (33). Diversity may also dampen variation in primary productivity during extreme stress such as droughts.

A great deal more experimental work is needed to clarify the relationships among diversity, food web structure and ecosystem properties (34, 35). Theoretical and experimental studies point to greater resistance to invasive species and pathogens as diversity increases (31, 36). Stability measured by return time (34) and compositional stability is not positively linked and may in fact be negative on theoretical grounds (37). Recent studies (38) show that external landscape factors and site history, rather than internal linkages, account for high stability in species-poor communities.

The difficulty of linking diversity and ecosystem properties probably tells us more about the inappropriateness of diversity as a generic measure than it does about human impact—or perhaps about the difficulty of drawing ecological generalities from the limited data so far available. Just as early debates over the link between diversity and stability floundered on the multitude of properties such as resilience, resistance, persistence, and variability (35), it is likely that we ask too much of diversity and miss the functional links between species composition and ecological process. The life history characteristics and the relative abundance of species is likely to tell us more about ecosystem change than species richness *per se* (39).

Functional Roles. Paine's (40) pioneering work on the role of the predatory starfish *Pilaster* in regulating species diversity in littoral communities was the first of many to highlight the role of keystone species in community structure and dynamics (41, 42). Recent work has broadened keystone species to functional groups. Functionally equivalent species contribute to keystone processes such as primary production by algal mats on coral reefs; here, individual species abundance may fluctuate, but the overall photosynthetic production remains relatively constant (43). It is quite possible that the maintenance of such functional groups is far more critical to the maintenance of ecosystem structure and properties than how many species are present, regardless of their role. Clarifying functional roles will help ecologists determine the ecological bottom line—those irreplaceable elements of ecosystems we cannot afford to lose.

The evidence already underscores the need to consider functional roles in tracing the ripple effect of human activity on ecosystem properties and points to a novel experimental tool for ecologists (44).

Structural Asymmetry. An obvious starting point is our differential impact on large species. The overharvesting of big species is our most ancient and persistent signature. Great Lakes fishery and New Brunswick forestry practices, for example, select large species because of their high price per unit mass. Overharvested species of trees and fish are further stressed by pesticides, acid rain, chemicals, and introduced species, causing a "general stress syndrome" (45). The outcome can be gauged from both theory and field studies. Size-scaling theory predicts such life history characters as growth rate, reproductive rate, intrinsic rate of natural increase, generation time, and turnover rate (39, 46). These life-history traits, derived from physiological scaling laws common to all plants and animals (47, 48), govern the demographic and population patterns for single species as well as their population cycle times and home ranges (39, 49). If community structure is the aggregation of species abundance, then ecosystem dynamics is the interactions of their relative abundance and life history traits—mediated by extrinsic environmental factors. So, for example, the size-frequency distribution of a species in an assemblage can be used to predict energy and nutrient turnover rates (39, 50). Scaling laws also explain packing rules that theoretically and empirically predict the relationship between diversity and productivity, and between species diversity and area (51).

Ecosystem Processes. By using life history theory, what can we infer about the ecological changes resulting from the extermination of large-bodied species? First, because large bodied species of predators and herbivores are keystone species, their extermination or reduction will further decrease species richness and habitat patchiness (26, 52). Second, the mean body size of species in a community will diminish. Third, population cycle times and overall community turnover rates will shorten. Fourth, nutrient flow rates will increase. Fifth, resilience will increase but resistance will decrease. Sixth, external agencies and stochastic events will increasingly govern community dynamics as the internal feedback linkages dominated by large animals weaken (53). Finally, the loss of important functional groups will also contribute to an overall loss in productivity.

The use of functional groups allows us test deductions about stability. We can deduce, for example, that resilience should decline with species succession—given the longer generation times of larger more competitive species—and, conversely, that resistance will decrease with species impoverishment because of a loss of niche specialization. We can also deduce that the loss of large mammals and their disturbance regimes will lead to further species loss and a weakening of internal stabilizing forces of herbivory, competition and predation.

Ecosystem Functions. I have used the example of asymmetrical impact of humans on species composition to trace the ripple effect of ecosystem structure and process. Whether such impacts show up in function is less clear (31). The causal linkage via size-structured communities suggests that nutrient cycles theoretically should be shortened and productivity lowered. Whether reflectance and water cycles are affected is also unclear. Large changes in biotic structure and process can occur without affecting ecosystem functions, and *vice versa*. So, for example, Schindler *et al.* (54) found in an experimental study of Canadian lakes that chemical perturbation causes large changes in species dominance, but that the functional properties of the ecosystem (productivity, water and nutrient cycles, reflectance) are unaffected. In contrast, sedentarization of livestock can change plant cover and reflectance through overgrazing in the absence of any increase in stocking levels. The mode of land use—the degree to which it mimics existing ecosystem properties—may, in other words, be more important than intensity.

I suspect that another problem clouding debate over the consequences of human impact biodiversity loss is the relatively small amounts of change ecologists study in natural systems. When it comes to the most extremely modified humanscapes—monocultures—the consequences of biodiversity loss are largely uncontested. Here, by almost any measure, ecosystem properties are profoundly simplified. Overall, diversity declines, the number of functional groups decreases, food chains are shortened and simplified, and resistance to invasive species and pathogens falls. Compositional stability alone may be higher, but only because of the ever-higher costs in terms of extrinsic energy and nutrients inputs.

So far I have focused on the direct impact of species removal on structure and internal ecosystem processes. The indirect and external effects are far greater for evolution. A few examples show the ripple effect of human impact in ecosystem, regional, and global processes.

Spatial Linkages. The unanticipated long-term consequences of fragmentation and loss of ecological linkages are only now becoming apparent. Dislocation of spatial links from ecosystem to continental level will see species extinctions progress up hierarchical scales starting locally in ecological time (decades to centuries) and extending into evolutionary time on a continental level (55). Fractal scales are important in resource partitioning and therefore in niche packing and diversity (51). Ecological gradients strongly partition niches and species in physical transition zones (56). Ecotones act as species refuges and speciation sites. Landscape fragmentation severs these spatial components vital to species diversity in space and time.

Spatial fragmentation also has a direct impact on individual species by snipping metapopulation connections, raising the risk of extinction through declines in species abundance, distribution, and interspecific interactions (57). The outcome is that smaller, less viable populations are vulnerable to stochastic processes such as disease, local environmental perturbations, genetic impoverishment, edge effects, and so on (58). Large species with low population densities and species with poor dispersal abilities across humanscapes are especially vulnerable to extinction.

Homogenization. Homogenization of ecosystems across the landscape reinforces the effects of fragmentation. The domestication of arable landscapes causes convergent ecosystem properties not only in species assemblage, but also in soil characteristics, nutrient and water cycles, and the dampening of stochastic events and perturbations. High nitrogen application on arable lands in moist climates and erosion-induced leaching in overgrazed arid lands are other example of large-scale homogenizing regimes. Based on Tilman's (59) resource ratio hypothesis, which predicts high species diversity at intermediate nitrogen levels, we might expect that species richness will diminish in both arable and arid lands.

Disturbance Regimes. Loss of disturbance regimes is yet another route to ecosystem simplification. The dampening of disturbance regimes, including sedentarization, can cause habitat simplification (52). Spatial fragmentation, homogenization, and loss of disturbance regimes collectively create secondary cycles of simplification within ecosystems as species diversity falls and internally driven processes maintaining species diversity weaken. The outcome favors small, easily dispersed species able to invade human-dominated ecosystems with low species diversity and resistance—the tramp species, colonizers, nitrogen-tolerant species, pests, and pathogens.

By-Products. At the risk of simplifying the vast literature on the environmental impact of pollutants, sediment and nutrient load, heat production, and so on, I use a few examples simply to show the overt consequences for ecosystems, the growing ripples globally, and the repercussions on communities and evolution.

The impact of pumping exogenous nutrients and energy into ecosystems and disposal of by-products of human activity are well established for nitrogen. Eutrophication of lakes and the oceans is showing up in algal blooms, loss of species, and lowered immune resistance (60). Fossil fuels emit sulfurous and nitrogenous compounds distributed by air currents and redeposited as acid rain, causing lake and forest impoverishment in industrialized countries (19). Fossil fuels also emit greenhouse gases that have raised atmospheric CO_2 levels, causing global warming, and are likely to alter climate on a time scale that matches the most violent shifts recorded in the last ten million years or more (13). Ecosystems everywhere could be affected by changes in temperature and rainfall in a matter of decades. Both the rapidity of climate change and the barriers to species dispersal (many of them anthropogenic) will challenge species adaptations and block migration, with grave implications for species extinction (61).

Table 3. Some ecological consequences of human activity on ecosystem processes

Ecosystem structure
Loss of biodiversity
Structural asymmetry and downsizing of communities
Loss of keystone species and functional groups
Ecosystem processes
Low internal regulation
High nutrient turnover
High resilience
Low resistance
Low variability
Low adaptability
Ecosystem functions
High porosity of nutrients and sediments
Loss of productivity
Loss of reflectance
Global processes
Modified biogeochemical cycles
Atmospheric change
Accelerated climatic change

The consensus on exogenous human impact is that every major planetary process, whether in biosphere, lithosphere, hydrosphere, or atmosphere, is already altered or dominated by our activity (12). Table 3 summarizes the main consequences of human activity on ecosystem properties.

The Evolutionary Implications

Human domestication of ecosystems greatly reduces species diversity. Of equal or greater importance, asymmetrical selective pressure on large species downsizes communities. Relatively small changes in keystone species and functional groups will have greater repercussions on ecosystem process than diversity as a whole. Downsized communities accelerate population, energy, and nutrient turnover rates, increase resilience, decrease resistance, and reduce overall productivity.

The dominant species—domesticated animals and plants—are heavily selected for specific traits and have reduced genetic heterogeneity and adaptability. Maintaining these traits and enhancing production in adverse environments and in the face of mounting disease and pathogen attacks will require ever-increasing energy inputs and environmental modification.

The expansion and intensification of domesticated landscapes will shrink habitats of nondomestic species, reduce population sizes, and fragment their range by imposing physical or biological barriers to dispersal. The resulting population declines and barriers select against poor dispersers, including big species. Small, easily dispersed species able to tap into the production cycle of domesticated landscapes and heavily harvested natural resources are selectively favored. These are typically r-selected weedy species and pathogenic and competitive microorganisms.

The selective pressures exerted by indirect human impact reinforce species extinctions and create deeper asymmetries and gaps in downsized communities. Three agencies of human activity reinforce these selective pressures:

(*i*) The secondary influence of fragmentation and homogenization of the landscape by reinforcing large-scale barriers at a regional and continental level. These large-scale barriers reduce periodic dispersal (due say to climate change) from continents to ecosystems and communities and vice versa, weakening the hierarchical links that maintain species richness (55).

(*ii*) The loss of disturbance regimes, either generated internally by keystone and functional species, or by external perturbations such as stochastic hydrological events.

(*iii*) The impact of human by-products such as heat, particulate matter, chemicals, and nutrients.

These three forces, among others, further amplify extinctions and asymmetries in community structure and favor small, high-dispersion species able to invade human-dominated ecosystems. The outcome will also accelerate speciation in small species able to survive fragmentary habitats in high enough densities to form viable founder populations and perhaps, ultimately, secondary specialization (62).

Finally, human activity will dominate biogeochemical cycles and affect major planetary processes such as climate through the greater porosity of energy flow and nutrients cycles across ecosystem boundaries and increased reflectance. One example is the impact of nitrogen overload on oceans through eutrophication and phytoplankton blooms (60) and their diminished resistance to invasive species (36).

There will, of course, be more that is unknown than known. By far the greatest uncertainty lies in predicting the scale and tempo of human land use changes. If these are slow, spatially homogenous, and persistent, species loss will be high. If the changes are local and transient, species may be able to disperse temporally and avoid mass extinction. The rate and scale of change in the mosaic of human land uses will have huge and as yet unpredictable consequences for evolution.

The Human Consequences

Assessing the implications for our own future is no simpler than it is for ecosystems. The future can be gauged from several points of view—from human carrying capacity, capacity for a given standard of living, or for the diversity of future options, for example (15). Should our horizon be measured in ecological or evolutionary time—in decades and centuries, or in millennia and millions of years? Cohen (17) has elegantly exposed the simplicity of Malthusian thinking in making projections over decades let alone centuries, given the sensitivity of the outcome to small changes in initial assumptions and the complex interactions involved in modeling human developmental scenarios.

One could well argue that our very success evolutionarily is proof of our ability to modify ecosystems to our advantage—and that we can take care of the environment in due course, when we can afford it. This is where the distinction between intentional modifications and side effects (Tables 1 and 2) becomes important. Kusnet's U-curve of wealth and environment, postulating that environmental clean-up follows wealth creation, has been development dogma for decades. There is now sufficient evidence to show that the Kusnet curve doesn't apply to fisheries and forestry in the developed world, let alone the poorer nations (63).

The challenge for ecology and environmental studies is to gauge the outcome of human action on ecosystem processes and on our own future. If there is no link between biodiversity and human well-being, then the future may be bleak for diversity but not necessarily for humanity. If that is the case, the fate of diversity will depend on human compassion, esthetics, and emotions rather than on human welfare.

Linking Ecological Impact and Human Welfare. Is there any link between biodiversity and human welfare? At best the connection is weak. Have we evidence to convince rural farmers that intensified monoculture is less productive and sustainable than biodiversity extraction? This is a dubious assertion, given the low limits on extractivism relative to intensive farming (64). Our intentional modification of food webs and landscapes is hard to fault based on evolutionary success to date. These modifications take on a different complexion, however, when the growing problems of overconsumption, ecological side effects, and rising costs are considered.

The cost of overconsumption can be measured in falling yields and rising costs. Nearly half of the world's marine fish populations are fully exploited and another 22% are overexploited (65). The real costs of food, resource, energy, and materials production are heavily disguised by massive subsidies, amounting to 1.5 trillion dollars globally each year (66). Stripped of subsidies, the costs of agriculture in the United Kingdom and perhaps many other developed countries already exceed the benefits (67). The mounting costs have been discounted in conventional gross domestic product measures, leading to calls for full-cost disclosure in valuing natural capital and ecological services (68). Removing these perverse subsidies would in itself improve economies and environment alike (66).

National governments share the academic's view of overconsumption to the point where environmental sustainability and security have risen to rise to top of the post-Cold War agenda. The Biodiversity Convention and a plethora of national biodiversity strategies testify to the consensus on the environmental threats of overconsumption and the need for sustainable practices (69).

We are on firmer ground yet when it comes to the side effects of our evolutionary strategies. A decline in environmental quality (measured by ecosystem process and function and build-up of deleterious waste products) does have a direct bearing on human health and well-being, as a few examples illustrate.

The rising health cost is the gravest concern because it does directly threaten our very survival, production, and reproduction—in short, our evolutionary success. Concerns over ozone thinning and increased UV levels, toxic pollutants, endocrine mimicking substances, immune suppression (70), and the spread of resistant and exotic infectious diseases including HIV, Ebola, and Marburg's virus are some examples (71).

Less important, but climbing the list of human concerns, is the quality of life. Urban living, the welter of human activity, and global travel will push the world tourism trade past the 4 trillion dollar mark in 2000. By 2020, some 20% of the global population is expected to take international trips (72). As awareness of environmental deterioration widens and appreciation of open space and more natural landscapes builds, the demand for quality of life will intensify. Environmental connections are being made where they matter most, in people's minds (14).

The Inadequate Response. The environmental connection could be construed as a turning point for conservation. It could further be argued that conservation is in place and showing success through protected area expansion, global agreements on greenhouse gases and ozone thinning, and perhaps even the plethora of national biodiversity strategies. Added to that is the good news of a worldwide demographic and economic transition and the improvement in numerous environmental indicators since the 1970s (19).

On the downside, these improvements come at a time when ecologists and conservationists alike realize that we have underestimated the magnitude of our environmental impact and the mitigation needs. Existing measures are far too paltry to save biodiversity or reverse environmental degradation. The global network of protected areas is too small to avert a rash of extinctions. Overharvesting of forests, fisheries, and wildlife continues unabated. Poverty and resource depletion is growing worse over much of the world, sapping the will and means to implement conservation measures.

How can conservation take hold under these conditions to avoid ecological homogenization, simplification, and degradation? How can we break past behavior patterns and change the projected course of evolution?

Applying Science to Conservation

The consequences of human impact, although largely unknown, are already troubling enough. The unknowns, no less than the immense amount of information needed to mitigate anticipated trends, pose the biggest of all challenges for science. Ayensu *et al.* (73), among others, have recognized the information gap in setting up an International Ecosystem Assessment (IEA) to conduct regular audits of human impact. The IEA is a fast-track solution to forecasting trends and integrating biological, physical, and socioeconomic studies for decision-making.

The need for information is growing critical. And yet, as Holling (49) points out, more information in itself is not the solution. Ecosystem models with ever more detail do not necessarily improve predictability. Arcane theories that fail to connect with reality are worthless. The Ecological Society of America (74) recognized the environmental and intellectual challenge in 1991 when it laid out an ecological research agenda for its Sustainable Biosphere Initiative. A decade later, some real progress has been made, but the challenge is more formidable than ever.

How can scientists keep up with such information demands? Perhaps a better way to phrase the question is: Given the catch-up problem, how can scientists provide better tools for environmental decision-making? Several interlinked steps are needed; I touch on them briefly.

Macroecological Theories. Ecological theory is essential in providing a robust, yet relatively simple explanation of ecosystems and their response to human activity. Community assembly rules and the relationship between ecosystem structure and process and how they vary biogeographically are basic to explaining overall diversity and ecosystem properties. In recent years, promising progress has been made on macroecological approaches (75–77). These nascent theories underscore the importance of scale and process in maintaining species diversity and ecological processes—and the links to continental scales (49, 55, 78).

Such models can help address question such as: Are there critical levels of diversity for a given ecological process? How much redundancy is there in ecological systems? What species or functional groups are vital to ecosystem structure and process? Can we use surrogate species to restore ecosystem properties? What critical thresholds exist for ecosystem properties in terms of species, processes, and area?

Ecological Principles. The maintenance of diversity, process, and function in ecosystems will depend on the identification of these critical properties and thresholds (49). Identifying threshold levels of tolerance provides the guidelines (or principles) on which sustainable development and conservation must be founded (79). Ultimately, simple principles are the basis of international agreements, conservation and development strategies, and management plans for all natural resources and biodiversity.

These questions only scratch the surface by touching on immediate threats and ecological time. Conservation biology has made a singular contribution by adding an evolutionary perspective to conservation (80). By identifying the selective forces of human impact and their consequences, ecologist are in a position to state principles for minimizing the evolutionary consequences of our action. I consider development of principles of sustainability that avoid evolutionary sclerosis to be the biggest task for ecologists. Table 4 illustrates some examples based on maintaining the ecosystem processes threatened by human activity (Table 3).

Methods. *In situ* restoration and *ex situ* management and tools and methods for improving data collection, monitoring and analyzing results, assessing risk, and defining minimum critical ecosystem parameters are vital for applying such principles to management (81). In recent years, cheap, accessible, high-resolution imagery has made large-scale environmental monitoring a reality. Techniques such as Population Viability Analysis and rapid techniques for biodiversity assessment have helped bridge the gap between time-consuming surveys and arbitrary judgments. Environmental Impact Assessments (EIA) and environmental monitoring have become prerequisites of development around the world in a remarkably short period. Further improvements in EIAs will depend on better ecological tools, methods, and application criteria.

Table 4. Ecological principles for conserving ecosystem processes

Maintain or replicate
Species richness, structural symmetry, and keystone processes
Internal regulatory processes (e.g. predator–prey interactions)
External diversifying forces
Large habitat areas and spatial linkages between ecosystems
Ecological gradients and ecotones
Minimize
Erosion, nutrient leaching and pollution emissions
Landscape simplification
Landscape homogenization
Mimic
Natural process in production cycle

Criteria. Finally, there is a dearth of criteria for identifying, safeguarding, or restoring biodiversity and ecological processes and gauging when and how to apply ameliorative measures (81). Such criteria help build consensus and develop a biological basis for conserving and managing biodiversity.

Until the last decade or so, ecological theory and conservation principles did no more than provide reactive short-term and small-scale solutions to ecological threats. Recent advances on both fronts offer better ways to determine sustainable harvests, set protected area priorities (82), and conserve entire ecological provinces through a minimum conservation area system nationally and regionally (83).

Applying Science and Conservation to Society

The Convention on Biological Diversity (CBD), adopted by over 120 nations, is the broadest conservation agreement ever reached. Its three goals—biodiversity, sustainable development, and equity—will guide global initiatives well into the 21st century. Achieving these goals will be difficult.

On the positive side, CBD shows high-level political commitment to the environment. Scientists have a central role to play in developing the ecological principles for CBD, national biodiversity strategies, EIAs, and sustainable development. On the negative side, the specialist nature of science and its aversion to the human-dominated landscapes distance it from society. Poor civic understanding of science echoes in conservation and the political arena. How can science-based conservation position itself to become a foundation for sustaining development and biodiversity in the 21st century? Ecologists have pointed out one flaw in our present strategies—inadequate concern with space and provision for the dynamical processes underlying biodiversity. Other challenges arise from changing society itself.

The Challenge of Change and Pluralism. The inherent weakness of conservation lies in big centralized government schemes (84) in the face of growing environmental threat and diminished treasury allocations. Governments simply cannot do everything everywhere by using the command-and-control method on which the modern movement was founded.

Societal change is also chipping away at the foundations of command-and-control conservation itself, particularly in the developing world. Here the spread of democracy in the post-Cold War era has raised awareness of rights and cultural identity. Pluralism in views and demands for equity in conservation benefits has intensified resistance to coercive conservation. The one-size-fits-all western conservation model is too doctrinaire today, ignoring cultural differences in philosophy, knowledge, society, and often what works already. Science is often seen as part of the top-down doctrine that disenfranchises local and rural communities, which bear the costs of conservation (85, 86).

These problems cut to the heart of CBD's goals of biodiversity, sustainable development, and equity. How can these goals be reconciled and implemented? How can they be achieved across human-dominated landscapes soon enough to maintain biodiversity and evolutionary adaptability? How can science-based conservation contribute more effectively to global and national development plans and local conservation efforts?

Balancing Local and Global Scales. The new conservation framework must address the hierarchical scales linking global and ecosystem processes by using mutually reinforcing top-down and bottom-up approaches (83). I touch briefly on both approaches to show the opportunity and need for science-based conservation.

Community-based conservation (CBC) has emerged over the last two decades in response to weakening governmental programs and new opportunities (85, 87). CBC is based on participation and emphasizes access rights, equity, and social responsibilities in conservation. It builds on local knowledge, skills, and institutions. Despite some success in watershed management, forestry, and wildlife conservation, CBC suffers from a lack of incentives, secular knowledge, self-organizing institutions, and local regulation.

In contrast, government efforts cover global conservation agreements, national policies, and strategic plans. These instruments set conservation principles, policies and strategies, legislation, incentives, and enforcement by using a variety of national institutions and public education. The transition from sectoral conservation (forestry, fisheries, wildlife, soil, water) to integrated landscape conservation and from centralization to devolved and interlinked efforts overseen by government will not be easy (84). Nongovernment agencies, universities, and the corporate world can help bridge top-down and bottom-up approaches, as shown in pluralism-by-the-rules negotiations on pollution abatement in the United States (88).

The role of science is central in developing the principles, criteria, methods, and overall accountability for sustainable development and biodiversity conservation linking top-down and bottom-up conservation approaches. However, creating spatially explicit linkages between institutions to match the scale of ecological and planetary processes calls for the best available information rather than exact science. How, then, can science be made applicable given the ignorance, uncertainty, urgency, lack of finance and human resources, social complexity, political realities, and cultural differences inherent to conservation?

Cultural perspective, local knowledge, and existing skills determine land use practice. Some practices are sustainable and compatible with conservation, others are not. The same can be said of ecological theories and conservation policies and practices.

Getting conservation going on a global and local scale in the face of these realities calls for rapid assessment techniques, setting up the basis for negotiation and partnerships, initiating a cycle of exchange, and procedures for reconciling science and local knowledge (83). We must make allowances for uncertainty and put in place adaptive management procedures to learn from successes and failures (89), whatever the source of knowledge or practice. How well we succeed will largely decide the outcome of future evolution.

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