

CELL BIOLOGY. For the article “Mitochondrial potassium channel Kv1.3 mediates Bax-induced apoptosis in lymphocytes,” by Ildikó Szabó, Jürgen Bock, Heike Grassmé, Matthias Sodemann, Barbara Wilker, Florian Lang, Mario Zoratti, and Erich Gulbins, which appeared in issue 39, September 30, 2008, of *Proc Natl Acad Sci USA* (105:14861–14866; first published September 25, 2008; 10.1073/pnas.0804236105), the authors note that due to a printer’s error, the e-mail address for corresponding author Erich Gulbins appeared incorrectly. The correct address is erich.gulbins@uni-duisburg-essen.de. The online version has been corrected. In addition, in the Abstract, line 2, “Here, we show that mouse and human cells that are genetically deficient in either Kv1.3 or transfected with siRNA” should instead read: “Here, we show that mouse and human cells either genetically deficient in Kv1.3 or transfected with siRNA.” Also on page 14861, right column, third full paragraph, line 4, “Fig. 1C” should appear as “Fig. S1C.” On page 14863, right column, last line, “However, we expected this behavior” should instead read: “However, we expected the same behavior.” On page 14865, left column, in line 6, “Fig. 3D” should appear as “Fig. S8 A and B.” On the same page, left column, 8 lines from the bottom, “Fig. 5C” should appear as “Fig. 4C.” Finally, on page 14866, in the list of references, the reference number 6 appears twice, and the first instance should instead be numbered 5. The corrected references appear below.

5. Ardehali H, O'Rourke B (2005) Mitochondrial K(ATP) channels in cell survival and death. *J Mol Cell Cardiol* 39:7–16.
6. Dimmer KS, et al. (2008) LETM1, deleted in Wolf–Hirschhorn syndrome is required for normal mitochondrial morphology and cellular viability. *Hum Mol Gen* 17:201–217.

www.pnas.org/cgi/doi/10.1073/pnas.0809894105

PERSPECTIVE. For the article “Ecosystem Services Special Feature: An ecosystem services framework to support both practical conservation and economic development,” by Heather Tallis, Peter Kareiva, Michelle Marvier, and Amy Chang, which appeared in issue 28, July 15, 2008, of *Proc Natl Acad Sci USA* (105:9457–9464; first published July 9, 2008; 10.1073/pnas.0705797105), the authors note that on page 9459, right column, line 7, “1999” should have appeared as “1998.”

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An ecosystem services framework to support both practical conservation and economic development

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The core idea of the Millennium Ecosystem Assessment is that the human condition is tightly linked to environmental condition. This assertion suggests that conservation and development projects should be able to achieve both ecological and social progress without detracting from their primary objectives. Whereas “win-win” projects that achieve both conservation and economic gains are a commendable goal, they are not easy to attain. An analysis of World Bank projects with objectives of alleviating poverty and protecting biodiversity revealed that only 16% made major progress on both objectives. Here, we provide a framework for anticipating win-win, lose-lose, and win-lose outcomes as a result of how people manage their ecosystem services. This framework emerges from detailed explorations of several case studies in which biodiversity conservation and economic development coincide and cases in which there is joint failure. We emphasize that scientific advances around ecosystem service production functions, tradeoffs among multiple ecosystem services, and the design of appropriate monitoring programs are necessary for the implementation of conservation and development projects that will successfully advance both environmental and social goals. The potentially bright future of jointly advancing ecosystem services, conservation, and human well-being will be jeopardized unless a global monitoring effort is launched that uses the many ongoing projects as a grand experiment.

poverty alleviation | pro-poor conservation | sustainable management

Poverty and environmental problems are both children of the same mother, and that mother is ignorance.

Ali Hassan Mwinyi,
Tanzanian President in 1998

The Millennium Ecosystem Assessment (MA) contains a compelling argument that human well-being depends on the services provided by nature, and that these services have recently become so imperiled that we can expect negative feedbacks to people (1). In some ways there is nothing new in this message: people depend on nature, and people too often damage nature, thereby endangering their own health and well-being. The novel contribution of the MA is its championing of a new scientific focus, a focus on understanding how nature produces a wide array of ecosystem services, quantifying the rate and value of the delivery of these services, and modeling the connections between ecosystem services, human welfare, and economic systems (2).

Although the MA was a bold contribution that exposed huge gaps in the science of ecosystem services, the reality is that both the conservation and economic development communities have embraced ecosystem services for at least a decade, without explicitly labeling them as such. This melding of conservation and development comes from two distinct agendas: conservationists who seek to increase public support for biodiversity protection by integrating economic development, and develop-

ment agencies that seek to also provide for the stewardship of nature under the mantra of sustainable development.

These projects have variously been categorized as integrated conservation–development projects, community-based natural resource management, and, more recently, pro-poor conservation (3). Although these projects generally lack a formal foundation of ecosystem service science, they all are motivated by the general hypothesis that nature provides humans with benefits. In fact, an analysis of the vision and mission statements of major environmental organizations, including the major conservation nongovernmental organizations (NGOs), found that nature is typically portrayed as resources necessary for human well-being and sustainable development (4). Increasingly, the language used by conservation NGOs to discuss the value of nature is becoming more explicit in its reference to ecosystem services. Examining the web domains of four major conservation NGOs (Conservation International: <http://conservation.org>; The Nature Conservancy: www.nature.org; Wildlife Conservation Society: <http://wcs.org>; and World Wildlife Fund: www.worldwildlife.org), we found that, on average (± 1 SE), 7.8 \pm 1.3% of the pages that mention biodiversity also specifically mentioned one or more of the following terms: human welfare, ecosystem service(s), human well-being, drinking water (Google search engine; August 23, 2007). Thus, the conservation community assumes a connection between nature and human

well-being and increasingly designs projects in terms of the provision of ecosystem services.

An Unclear Record for Projects that Seek Both Conservation and Poverty Alleviation

There is no question that ecosystem services are now a focus for both scientists and conservationists, but interest and widely held beliefs do not necessarily mean that data and results support the feasibility of helping both people and biodiversity by maintaining ecosystem services. What lessons have been learned from the many projects already conducted by conservation NGOs in which efforts have been made to both improve human well-being and protect biodiversity? Answers are not as forthcoming as one would hope. For example, in the most thorough systematic review we know of regarding conservation projects, researchers were stymied by the lack of metrics of success for either conservation or poverty alleviation (5). Indeed, the major conclusion of this review was that projects tended to rely on overly simplistic definitions of both biodiversity and poverty, and few

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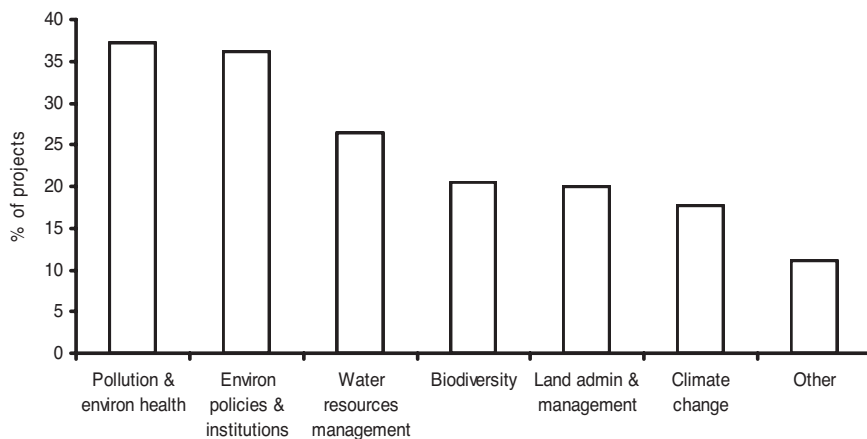


Fig. 1. Shown are the percentage of projects listing each environmental subtheme for the 1,961 World Bank projects with a major theme of environment and natural resources management (ENRM) and an approval date. The percentages sum to >100 , because nearly half of the ENRM projects listed more than one environmental subtheme. A maximum of five major themes or subthemes can be listed for each project.

projects directly examined the causal relationships responsible for the outcomes observed.

Arguably, the most consistently collected data regarding projects that seek improvements in human well-being and the environment (or biodiversity) are found in the records of the World Bank. Of the 11,155 economic development projects carried out by the World Bank since 1947 (www.worldbank.org; accessed December 17, 2007; limited to closed and active projects with an approval date listed), 17.6% have had “environment and natural resources management” as a major theme. From a conservation perspective, it is noteworthy that 20% of the World Bank’s environmentally oriented projects have specifically included biodiversity protection as a theme (Fig. 1). Moreover, the attention to biodiversity has been growing over the last 20 years, nearly quadrupling in frequency (Fig. 2). Thus, the World Bank has two decades of experience supporting projects with the dual goal of economic development and biodiversity protection (6). In addition, the World Bank uses a categorical scoring system by which it judges the degree to which each completed project achieved its stated goals. One can imagine three general categories of outcome for projects with both biodiversity goals and economic development or poverty alleviation goals: win–win (both goals are met), lose–lose (neither goal is met), and win–lose (only one of the goals is met). We searched the World Bank database for projects that (i) were approved between 1993 and 2007, (ii) listed biodiversity as a theme, (iii) had available an Implementation Completion Report

written between July 1998 and August 2006 (when the format was consistent), and (iv) stated environmental and poverty alleviation goals and outcomes. We found that relatively few, only five of 32 projects (16%), had substantial gains in terms of their stated environmental and poverty alleviation outcomes (Fig. 3). Thus, it is not impossible to make gains on both biodiversity and poverty fronts, but it is not easy. It is noteworthy that nearly half of the World Bank projects with biodiversity protection as a major goal had no objectives for poverty alleviation, which precluded them from being in our examination of win–win frequency.

Unfortunately, this simple tally of World Bank scores cannot reveal what strategies or factors tend to lead to failure. Failures could be caused by poor project design or intrinsic tradeoffs between ecosystem services. For example, development of more productive agriculture, which is often a route by which rural poverty is alleviated (7), may inexorably harm biodiversity. Alternatively, failures may be driven by external problems such as civil conflict or weak governance that were not anticipated in project design and have nothing to do with ecosystem services. Understanding the factors that determine the outcome of projects with dual biodiversity and economic development goals is crucial. One path to understanding these outcomes is to develop a framework for assessing the connections between ecosystem services and economic development on a project-by-project basis and suggest indicators and metrics that could increase the likelihood of win–win outcomes.

A Framework for Analyzing Ecosystem Service Projects Aimed at Human Well-Being and Biodiversity Protection

A number of authors have recently argued that there are strong links between ecosystem services and sustainable development, particularly development efforts that aim to reduce rural poverty (8–10). We see two distinct routes by which the science of ecosystem services can contribute to both nature conservation and sustainable development. First, a thorough accounting of ecosystem services and a better understanding of how and at what rates ecosystems produce these services can be used to motivate payment for nature conservation. At least part of the generated funds can be used to compensate people who suffer lost economic opportunities to protect these services. For example, if rural poor are asked to take actions that reduce farm productivity to protect and regulate water supply, those farmers could be compensated for the reduced productivity they experience. When the benefits of natural ecosystems are explicitly quantified, those benefits are more valued both by the people who directly interact with the ecosystems and the governmental and other agencies that would have to pay for substitute sources of these services if these ecosystems should become impaired. Appreciating the value of ecosystem services can motivate increased conservation investment to prevent having to pay for substitutes later. This approach could be characterized as a “government investment” approach because the payments will generally come from beneficiaries outside of the local area, and a governmental or other agency is typically responsible for collecting and redistributing the funds.

Second, a focus on the conservation of ecosystem services could improve the success of projects that attempt to both conserve nature and improve the welfare of the rural poor by fostering markets for the goods and services that local people produce or extract from ecosystems. These projects could be characterized as more “community-based” because the goal is to foster the more organic, or grassroots, development of cottage industries, such as ecotourism, or the production of bushmeat or nontimber forest products, that are enhanced by better protection of local ecosystems.

Using this framework, we discuss the factors that may have contributed to failure or success for several projects (Table 1). The scale of our analysis is local or project level. Often the hyperbole of “pro-poor conservation” might

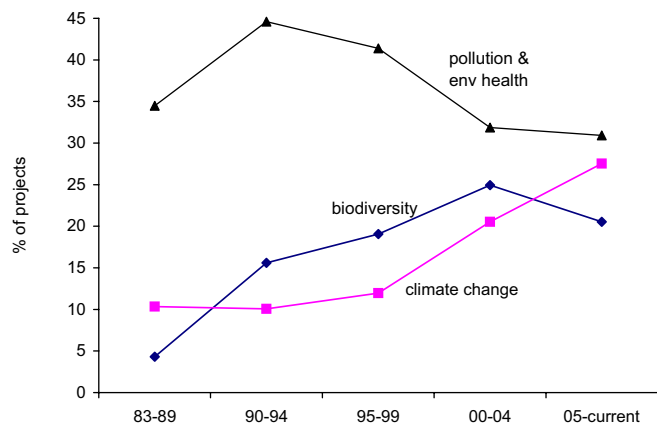


Fig. 2. For the 1,961 World Bank projects with the ENRM major theme, the percentage of projects with a pollution and environmental health theme has remained flat or declined, whereas the percentage of projects with subthemes of biodiversity and/or climate change has increased. The numbers of projects with the ENRM theme are: 1983–1989, 116; 1990–1994, 417; 1995–1999, 493; 2000–2004, 521; and 2005–present, 414.

be mistaken for a claim that conservation is a global strategy for poverty alleviation. It is not (11). The plight of urban poor and many of the world's poor has little to do with the production functions of ecosystem services. But for rural poor, at the local level, the status of ecosystem services can make a big difference in their daily lives.

Government Investments in Ecosystem Services

When there is clear information that ecosystem services of obvious value (like clean water or flood control) are imperiled, governments often invest in their protection. The money for these investments may come from charging beneficiaries for the use of ecosystem services, such as clean water, and then using the payments either to improve enforcement of protected areas or to compensate those whose livelihoods are diminished by the conservation efforts (12). These arrangements typically involve payments from beneficiaries outside of the immediate area. Here, we highlight two projects that demonstrate how ecosystem services can be used to motivate payment for nature conservation.

The Quito Water Fund. Quito, the capital city of Ecuador, houses 1.8 million people in a region of extremely high biological diversity and endemism. In the most strained regions around Quito, 63% of water needs are not met, and in 1999, most of the city's 14 monitored watersheds flowed with undrinkable water. The Condor Biosphere Reserve, situated upstream of Quito, has the potential to alleviate social struggles around water resources and environmental struggles around biodiversity loss. However, enforcement of park restrictions was weak,

and unsustainable land use practices surround the reserve, leading to continuing declines in biodiversity and water quality.

In 2000, The Nature Conservancy in collaboration with the U.S. Agency for International Development worked to establish a water fund that directs money from water users to improve protection of the Condor Biosphere Reserve (12). In 2004, the fund was worth \$2.1 million, paid into by the Quito Municipal Water and Sewage Agency, the Quito Electricity Company, and the Andina Beer Company (12). In this case, the government and its municipal utilities chose to redirect current fees and taxes rather than raise the price of water.

The project reports successes on both social and ecological fronts. The nearly \$5 million raised for conservation action have been used to plant 3.5 million trees, hire nine new park guards that provide new jobs and increase enforcement, build local capacity for monitoring and conflict resolution, fund hydrologic modeling and monitoring, and provide environmental education to children (12). Financial support for conservation came not from individuals concerned about biodiversity or some particularly charismatic species on the verge of extinction. Rather the support came from an appreciation of the role healthy forests play in supplying and regulating the availability of clean water. A key to the success of this project may have been a long record of flow and sedimentation monitoring data collected by hydropower operations, which provided a clear signal of a degrading ecosystem service before any catastrophic event.

Payment for Ecosystem Services in China.

The government of China has implemented several payment for ecosystem service programs. One of the better known is the Sloping Land Conversion Program. This program was motivated by large floods on the Yangtze River in 1999 that many presume were worsened by sedimentation that has reduced the flood mitigation potential of dams on this river. The State Forestry Administration linked sedimentation to erosion from intensively farmed sloping lands in the upper reaches of the watershed.

The Sloping Land Conversion Program, also known as the Grain to Green Program, pays farmers in cash or grain to abandon farming and restore forests on steep slopes along key rivers (refs. 13 and 14 and www.forest-trends.org/documents/publications/ChinaPES%20from%20Caro.pdf). The State Forestry Administration runs this program and projects that 14.6 million hectares in 24 provinces will be improved through this program by 2010 (13). The upper watershed regions targeted by this program are often home to some of the most socially marginalized minority groups in the country, coincidentally allowing social, economic, and ecological benefits to flow from this program.

To date, payments for ecosystem services in this and other programs have come primarily from China's central government. In 2004, 92% of the accumulated value of the Sloping Lands Program (\$7.6 billion) was provided by the national government. It is expected that the high costs of the program will soon spur the development of privately funded payment schemes (14). As with the Quito Water Fund, this program was not motivated by biodiversity, but rather by interests in ecosystem services such as flood mitigation. If China had not suffered severe floods in 1999 it is unlikely that the Sloping Lands Program would have been launched; there first needed to be strong evidence of a connection between land use and degraded ecosystem services.

Aligning Conservation of Ecosystem Services with Local Economic Activity

Many early projects that integrated conservation and development used ecotourism, which offers market-based income and a natural alliance between conservation of an ecosystem service and economic development. Participants in these programs typically receive funds directly from corporations or others in the private sector, rather than from governments or nongovernment organizations. Here, we briefly outline two

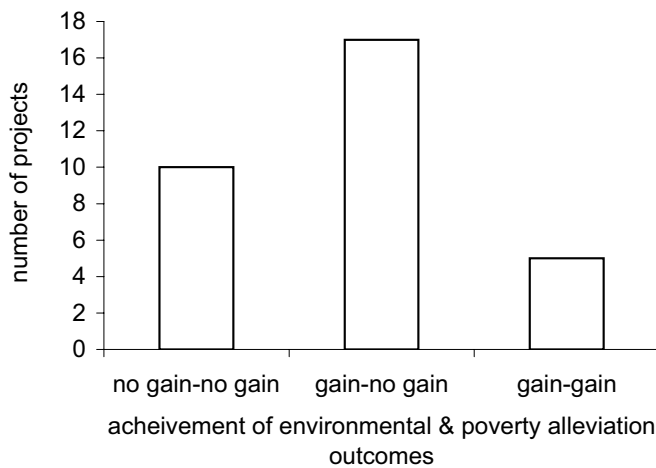


Fig. 3. The World Bank database was searched for projects that (i) were approved between 1993 and 2007, (ii) listed biodiversity as a theme, (iii) had available an Implementation Completion Report written between July 1998 and August 2006 (when the format was consistent), and (iv) stated environmental and poverty alleviation goals and outcomes. A total of 32 projects were found. Projects rated as having high or substantial achievement of environmental and/or poverty alleviation outcomes are considered to have made a gain, whereas those rated as having modest or negligible achievement are considered to have made no gain.

programs that have successfully taken this approach.

The Il'Ngwesi Ecologde. In Kenya, the Maasai culture and highly diverse biological communities have been under threat from the same forces: cattle rustling and poaching, alongside pressure from the government to subdivide and develop land (15). Subdivision would have led to the end of pastoral life for the Maasai and fragmentation of some of the largest remaining tracts of wildlife habitat in Kenya. In 1995, 8,000 members of a Maasai community at Il'Ngwesi agreed to establish an ecolodge and promote tourism (15). As a result, security in the region has increased, income from the ecolodge is funding the local school, poaching has been halted, 13 of the region's 19 large mammals (including the endangered Grevys zebra) have returned to the area, and some wildlife populations have increased by as much as 500% (15). Obviously all ecotourism projects do not turn out so well, with failures commonly occurring because of either poor business planning or poor ecological management. Nonetheless, ecotourism is well established as a joint development and conservation strategy, and the world's two largest conservation NGOs (World Wildlife Fund and The Nature Conservancy) have developed special planning processes to help their field staffs promote ecotourism (16, 17).

Namibia's Conservancy Program. In many cases, ecotourism markets are not easily accessible because of regulatory struc-

tures or entry costs. Some integrated conservation and development projects have found success in reducing these barriers by granting local control of the management of biological resources to communities or individuals. In Namibia, a global biodiversity hotspot (the Cape Floristic region) overlaps with high hunting and poaching pressure, high poverty, and socially marginalized populations of indigenous people. Game populations have declined, large-scale animal migrations have ceased, and black rhino populations have plummeted (18). As part of the institutional change associated with Namibia's independence, the Nature Conservation Act was passed in 1996. The World Wildlife Fund became involved in supporting communities who wanted to enter into a "conservancy program" established by the act.

Enrollment in the program gives communities rights, for the first time, to hunt game and revenues from game products and tourism (18). The act has fundamentally changed the landscape in Namibia. More than 60 communities now participate, supporting 31 conservancies that cover some 70,000 km², or 17% of Namibia's land area (18). In this case, new revenue streams were created by opening access to existing international markets.

Again, this project has been a success on both social and ecological fronts. Many of the conservancies are on lands that now act as corridors between protected areas (18). Wildlife populations have increased dramatically on conservancy lands. Namibia now houses the world's largest free-roaming black rhino

population and game species such as elephants, zebra, oryx, and springbok have increased 600% in some places (18). For the first time in 30 years, seasonal migrations have resumed between Botswana and Namibia. The program was a major development success, with local incomes increased by a total of \$2.5 million in 2004 and Namibia's net national income up by \$9.6 million (18). Overall, 3,250 part-time and 547 full-time jobs were created, and the fact that the majority of these jobs were obtained by women meant that gender equity was substantially improved (18).

Projects that Failed to Advance Conservation and Development

The case studies described above indicate that both conservation and enhancement of human well-being can be accomplished as part of one project. It is important, however, to ask about failures. Failures are quite common. In a random sample of 194 Implementation Completion Reports for World Bank projects, 16% were judged to be unsatisfactory or highly unsatisfactory overall performance. Political or economic factors outside the control of the project frequently contribute to their failure (Table 1). It would be extremely foolish to neglect the influence of external forces and global markets and corruption and governance on the ability of ecosystem service projects to enhance human well-being. Here, we describe two examples of projects that have failed on both environmental and poverty alleviation fronts.

West African Wildlife Project. Like Namibia's Conservancy Program described above, the West Africa Pilot Community-based Natural Resources and Wildlife Management Project sought "a common solution to both development and conservation concerns by involving local communities in the sustainable, profitable exploitation of wild resources and assisting them to manage their wild land areas for their own economic benefit and for the benefit of biodiversity." This, however, is an example of an effort that failed to achieve both its biodiversity and development goals (19). Supported by the World Bank and initiated in 1995, the project faced many difficulties including an initially very low level of training among villagers, a deeply rooted mistrust of central government within local governing bodies, and the resumption in 2004 of civil conflict in one of the participating nations, Cote D'Ivoire.

The project's antipoaching program failed because of the lack of a legal basis for villagers to apprehend poachers;

Table 1. Examples of projects that have used ecosystem services to advance both conservation and development or poverty alleviation

Project	Conservation	Development/poverty alleviation
Successes		
Quito's Water Fund	3.5 million trees planted Nine park guards added Hydrology monitoring program started	Alternative income, nine new jobs Education Clean water Conflict resolution training Technical capacity building
China's Sloping Lands Program	14.6 million hectares reforested (2010)	Alternative income Targeted ethnic minority groups Flood control
Kenya's Il'Ngwesi Ecodge	Increasing wildlife populations Poaching controlled	Alternative income Way of life Education (school funded) Security (poaching controlled)
Namibia's Conservancy Program	Increasing wildlife populations Overgrazing controlled Landscape connectivity improved	Property rights Income Cultural equality Gender equality Way of life
South Africa's Cape Peninsula Biodiversity Project	Invasive plant eradication Antelope species reintroduction Increasing raptor populations Establishment of protected area	Improved infrastructure Income
Failures		
West African Wildlife Project	Poaching Livestock encroachment No monitoring	Insufficient legal power Insufficient communication infrastructure Civil unrest Insufficient capacity Governmental distrust
India's Shrimp Aquaculture Development Program	Habitat destruction Overharvest	Unsustainable jobs Unstable market
Azov-Black Sea Corridor Program	Unenforced protected areas Unsustainable agriculture Habitat destruction	Insufficient legal power Uninformed agricultural practices Dysfunctional environmental institutions
Kerinci Seblat Conservation and Development Project	Poaching and wildlife decline Agriculture encroachment Logging threat Habitat destruction and fragmentation	Insecure land tenure Insufficient infrastructure Unsustainable agriculture and nontimber forest products harvest Weak and uncoordinated governance

insufficient investment in high-quality weapons, which put village teams at a major disadvantage in conflicts with poachers; and insufficient investment in a communications infrastructure, which caused slow response times. Moreover, weak and incomplete implementation of ecological and sociological monitoring made it impossible to assess what was working or not working. In the end, there was no compelling evidence that the wildlife or the local villages had benefited from the project, and there was anecdotal evidence that poaching and livestock encroachment had resumed in wildlife zones.

Shrimp Aquaculture in Former Mangrove Forests. The clearing of coastal mangrove forests for shrimp aquaculture in coastal regions of Asia provides another

example of a lose–lose situation in which neither people nor nature benefited from a well intentioned project. The original idea of a project subsidizing shrimp aquaculture in Andhra Pradesh, India was to create economic opportunity for local communities through shrimp farming, which can be enormously profitable. Unfortunately, the clearing of mangroves for shrimp farms can have negative impacts on the environment and the industry itself.

In many parts of the world, including Andhra Pradesh, shrimp aquaculture is done with the shrimp species *Penaeus monodon* (20). Because it is difficult to bring this species to reproductive maturity in captivity, hatcheries rely on wild broodstock to maintain production (20). The wild shrimp populations, in turn, rely on mangrove habitats. Thus, the

ecology of the farmed species sets up a conflict between shrimp pond development, which is largely done by clearing mangroves, and shrimp production, which requires mangrove habitat for the provision of wild broodstock.

Overdevelopment of the shrimp industry in the Andhra Pradesh region has poised both economic and ecological systems on the brink of collapse. The area's 61 hatcheries are suffering from a widely fluctuating market with alternating low demand and limited supplies of broodstock (20). In fact, broodstock are at times so rare in this region that the price for a single reproductive female shrimp can be as high as \$2,000 (20). A careful assessment of the ecological and economic capacity of the system for shrimp production could have identified the optimal number of farms the region

could support at maximum capacity and low broodstock prices. Operating at this optimal level would have saved subsidy funds that were used to develop the farms, provided sustainable jobs for the region, and retained more of the natural mangrove habitat that is key to storm protection (21) and the provision of other ecosystem services. This project failed in large part because the myriad services provided by intact mangrove ecosystems, and the tradeoffs among these services, were not fully appreciated.

Scientific Understanding that Could Improve the Likelihood of Win-Win Outcomes

Projects that use ecosystem services to simultaneously advance conservation and human agendas could benefit from improved scientific understanding of four key overriding issues: sustainable use of ecosystem services, tradeoffs among different services, the spatial flows of services, and economic feedbacks in ecosystem service markets. Better quantification of ecosystem services will reduce the transactional costs of policies based on ecosystem services, will promote greater equity, and reduce the risk of unintended consequences or surprises. Better quantification of ecosystem services can also help to identify those situations where the economic benefits are sufficiently large to counterbalance money that can be made from illegal abuses of an ecosystem (such as poaching or illegal timber harvest).

Any time a human endeavor seeks to derive something of value from our natural world, there is the possibility that overuse or overexploitation could result in failure. One of the most basic principles of ecology is the notion of a maximum sustainable yield (MSY) derived from intermediate levels of use. If this level of use is exceeded, the ecosystem or natural resource is degraded and both nature and humans lose (22). One important lesson from the MSY concept is that levels of extraction that provide meaningful amounts of income may be feasible only under particular ecological conditions. Consider, for example, a project similar to the conservancy program in Namibia that aims to increase local income and wildlife populations by encouraging a relatively low level of legal trophy hunting of kudu (*Tragelaphus strepsiceros*), a large antelope. If the local kudu population has a low population growth rate, even a very low level of hunting (ecosystem service use) could lead to a decline in the population and a lose-lose outcome. Alternatively, the same project could provide a win-win situation if it were initiated in an area where the kudu population has a high

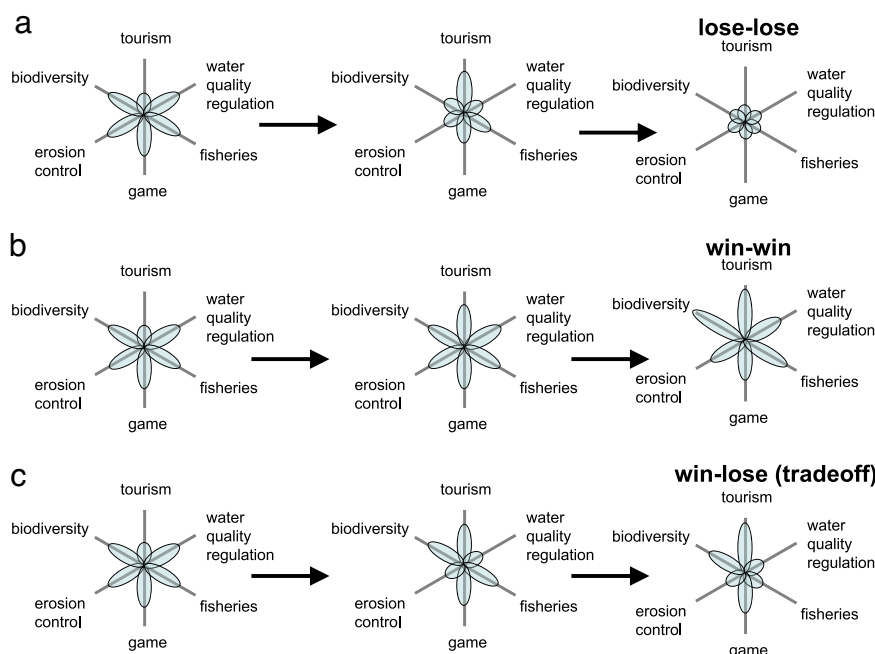


Fig. 4. “Tradeoff flowers” depicting alternative scenarios for ecotourism projects aimed at biodiversity protection and economic growth. (a) Unrestrained ecotourism can lead to infrastructure and human traffic that degrades many ecosystem services, and ecotourism itself collapses. (b) Ecotourism develops with good management of biodiversity and ecosystem services, so that income flows from tourism, biodiversity is enhanced, and ecosystem services are not lost. (c) Ecotourism develops and biodiversity is protected in nature reserves, but the increase in roads and hotels undermines water quality and fisheries, causing tradeoffs among ecosystem services and development. Which outcome is realized is largely a matter of a good management plans and making sure the intensity of human use is not too high.

growth rate. Because the success of a project depends to a large extent on the starting conditions and use levels, any given strategy will not be equally effective in all places. Further, it is relatively trivial to show that extreme impacts arise from extreme actions, but we lack the ecological production functions that quantify the impacts of more incremental changes. For example, it is well understood that total deforestation yields erosion, impaired water quality, and diminished flood control, but we do not have the ability to predict how the provision of these same services would be affected by 10% versus 20% deforestation (23). Given the extensive literature describing dramatic changes in ecosystem function in response to such things as complete deforestation or extreme runoff of fertilizers into waterways, we should be able to design projects that avoid such severe consequences. What is not well understood is how one might pinpoint the extent to which a resource can be exploited without pushing an ecosystem over its tipping point.

Most real-world conservation, development, and ecosystem service projects have paid attention to only a select few services that represent a narrow slice of the full spectrum provided by nature. Other services also deserve the atten-

tion of both conservation and development agencies. For instance, habitat loss and landscape change are documented to have played a major role in the increased prevalence of vector-borne diseases such as Lyme disease (24), West Nile virus, Chagas disease, and tick borne encephalitis. Although claims are commonly made about human health benefits from well managed natural systems (25), no conservation projects have yet taken advantage of our growing understanding of the link between landscape change and human diseases or health. Also largely absent from on-the-ground ecosystem service projects are any of the supporting services such as soil formation, nutrient cycling, and pollination. We must simultaneously consider multiple ecosystem services and multiple production functions, not just to obtain a more complete understanding of the benefits and losses, but because any one ecosystem service might be related, either positively or negatively, to other services (26, 27). For example, developing ecotourism can bring income to local communities and this added revenue could foster improved community stewardship of the natural features that attract ecotourists (e.g., biodiversity for wildlife viewing or sports fisheries), providing a win-win

Table 2. The relationship between nature and human well-being from the websites of major conservation NGOs

NGO	Relationship between nature and human well-being
Conservation International	"The rural poor within hotspots depend on the products of healthy ecosystems, harvesting wild plants for food, fuel, clothing, medicine and shelter. These services also help maintain energy and infrastructure activities that underpin economic development. For example, coral reefs, wetlands and mangroves can buffer beaches and prevent storm surges and coastal flooding. The value of these ecological services is tremendous and we are only beginning to measure their significance." (http://web.conservation.org/xp/CIWEB/strategies/humanwelfare)
The Nature Conservancy	"Nature has tremendous assets that are key to human-well being and that have concrete economic value...it's becoming increasingly clear that the goals of conservation and the goals of alleviating poverty and improving human health are deeply interwoven." (www.nature.org/tncscience/bigideas/people/art19846.html)
World Wildlife Fund	"The world's poorest people bear the brunt of forest loss, since forest resources sustain most of the 1.2 billion people in the world who live in extreme poverty. WWF is working locally, regionally and globally to address this threat and at multiple levels - with communities, governments and industry. In partnership we can ensure forests are protected for the people and species that depend on these habitats for their livelihoods." (www.worldwildlife.org/forests)

situation for nature and people (Fig. 4*b*). On the other hand, excessive development of infrastructure to support tourism, or excessive tourism activities such as hiking and fishing, can cause the decline of the very resources tourists seek to enjoy, resulting in a lose–lose situation (Fig. 4*a*). For instance, rapid development of trekking in Nepal has resulted in unsustainable overharvest of firewood for cooking, thereby damaging local ecosystems (28). Exactly how people manage ecosystems as they increase the intensity of use in any natural system can result in win–win, lose–lose, or tradeoff outcomes (Fig. 4*c*). Although scientists are now vigorously examining multiple ecosystem services, the practice of conservation is still almost entirely designed to focus on one service at a time. Interlocking production models of the full suite of ecosystem services are needed.

If policy and financial incentives for conservation of ecosystem services are to be successful and equitable, we will also need a solid scientific understanding of how services flow from one region to another, what human groups benefit from ecosystem services, and what groups or populations would need to be compensated for protecting those services. The science of ecology made huge advances when it began to consider dispersal and the importance of movement in governing the dynamics of ecological communities (29). However, the science of ecosystem services has not yet made this transformation, and as a result typically depicts ecosystem services as site-bound on static maps (ref. 30 and www.nj.gov/dep/dsr/naturalcap). Only when we have the scientific foundation to map the flows of ecosystem services, can we hope to meld conservation with delivering benefits to the poorest of the poor.

In addition to ecosystem services, there are economic feedbacks to consider. Market expansion can affect prices, and there are often feedbacks between economic development, social change, and environmental condition. We see the challenges of dealing with these complexities even in the examples we have outlined as successes. As supply in any product increases, prices are likely to fall. Because the goal of these projects is not to achieve an efficient market, but rather to encourage a livelihood that is good for nature and people, low prices may cause failure. For instance, low prices for hunting and tourism in Namibia may make these livelihoods insufficient for well-being, and landowners may turn back to domestic livestock rearing or other more destructive practices. The Namibian government may want to limit the number of communities that can participate in the program so that prices remain high and participants receive enough income to continue their investment in sound game management. This example points out the need to understand the focal market and the nature of demand for the product of interest.

We also need to understand how the growth of a market will affect the larger social system and vice versa. For instance, expanding tourism in attractive natural areas can stimulate immigration of people hoping to benefit from expanded economic opportunities. This can lead to a "tourism-income-population growth spiral," which obviously increases pressure on local resources and the environment (31) and can degrade the natural beauty that people initially traveled to view and enjoy. In Quito, the population continues to grow at 1.6% per year (35). When will the needs for residential development or demand on the water supply outstrip the capacity of

one watershed to provide clean water for the masses? What happens when that threshold is passed? Will construction of a water treatment plant remove the incentive for protection of the Condor Biosphere Reserve?

Finally, good governance, rule of law, and democracy may well be important for achieving joint success in conservation and economic development. Statistical analyses of economic growth in poor countries hint at a connection between democracy and governance and economic success (32). It would not be surprising to find a similar link to win–win ecosystem service projects. In Table 1, all of the win–win examples entail strong functioning governments, whereas poor governance is implicated in three of the four lose–lose failures. We hypothesize that a thorough study of many case studies would uphold this trend.

The Absence of Data Jeopardizes the Success of Future Projects

Increasingly, conservation organizations and development groups are in the business of providing hopeful visions of people and nature jointly benefiting from conservation efforts (ref. 4 and see Table 2). However, the enthusiasm for ecosystem services as a strategy for enhancing conservation support is far outpacing credible evidence of what is possible and how to best achieve the much desired win–win outcomes. Conservation that is justified on the basis of enhanced ecosystem services cannot afford to neglect rigorous evaluation of both ecology and social well-being. Indeed, there are enough projects in place around the world that if some simple metrics were collected on each, it would be possible to treat these efforts as a grand experiment. The natural science, social science, and practitioner communities jointly need to establish a stan-

standard set of measures and approaches for quantifying and monitoring ecosystem service levels and values. Minimally, projects should track what money funds the protection of ecosystem services and who provides it, who benefits from the ecosystem services, and whether the project results in an impact on the delivery of ecosystem services.

An added challenge with ecosystem service projects is that economic returns and signals respond relatively quickly to any action, whereas changes in ecosystem function may lag by decades. For example, the productivity gains in the Mississippi River valley that resulted

from heavy fertilizer application yielded immediate economic benefits. However, the dead zone in the Gulf of Mexico did not appear until 20 years after those initial gains in agricultural productivity. Different ecosystems services will respond on different temporal and spatial scales, and efforts to track interactions will have to anticipate these different scales.

Beyond the missed scientific opportunity, conservation groups are risking damaged reputations because they have largely failed to deliver data that provide evidence of a link between their actions and any improvement in the status of biodiversity or ecosystem services

(33, 34). This is a significant mistake, and a mistake that is even more grievous in the case of ecosystem service projects. Whereas biodiversity cannot complain if it is not well served by a conservation project, people supposedly benefiting from an ecosystem service effort will be quick to ask for evidence of their enhanced well-being. Much of the current enthusiasm for ecosystem service projects in the conservation world is an act of faith. At some point, however, that faith will need to be backed up by irrefutable data showing that these projects benefit both people and nature.

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