Sustainability and Biodiversity

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Glossary

Biodiversity The variability among living organisms from all sources, including diversity within species, between species, and of ecosystems.
Ecosystem services Ecosystem functions involving exchanges of nutrients, energy, waste, and materials through the interactions of organisms and the physical environment that contribute to human well-being.
Human well-being Meeting of physical, psychological, and spiritual needs through material security, health, social relations, personal security, freedom, and other factors.
Inclusive wealth The summed total of capital assets or human and Earth system properties that can be used to provide the flow of goods and services that contribute to well-being.
Intergenerational equity Equality and fairness in well-being of people in future different generations relative to current generations.
Natural capital The capacity of the natural world to provide services that contribute to human well-being. These may include providing services including food and fiber production; regulating services, such as water flow and quality, or temperature regulation of the atmosphere; cultural services, such as recreation or meeting spiritual needs; and provision services such as soil formation and nutrient cycling.
Poverty A multidimensional concept that describes the inability to meet human needs; it includes economic, human, political, socio-cultural, and protective aspects of human capabilities, including income, livelihoods, health, education, empowerment, rights, status, dignity, and vulnerability.
Shadow prices The added value (or inclusive economic value) of an additional unit of a capital asset, such as widgets, regulation of the Earth's climate system, or human knowledge.
Social equity The fair, just, and equitable distribution of the stocks or flows of capital assets that contribute to human well-being.
Sustainable development The process of meeting human needs of the present without compromising the ability of future generations to meet their own needs.

Introduction: Biodiversity and Sustainability

Biological systems exhibit extraordinary diversity, whether considering the genetic variation within species, the differences among the more than 8 million recognized species found on the Earth, or the range of environments inhabited and shaped by those organisms. Over the past two centuries, the expansion of human populations, resource demands, and influence on the Earth's landscapes is the driving force behind a dramatic, planet-wide reduction in biodiversity at all of these levels (genes, species, and ecosystems). Estimates of species extinction over that time period range from 100 to 1000 times background levels (Millennium Ecosystem Assessment, 2005), a magnitude of biodiversity loss that has been matched only five times in Earth's history, and the first mass extinction known to be caused by a living species. That this catastrophic loss of diversity is linked with a dramatic increase in both the human population and its overall well-being raises fundamental questions for efforts to provide for human needs and preserve the planet's biodiversity, including whether the human population and its well-being can be maintained in the face of declining biodiversity.

The idea of sustainability – that the fruits of nature, if harvested at moderate rates, may be reaped indefinitely – is ancient wisdom. However, translating that verity into workable policies is difficult and elusive. As economies and human population (Figure 1(a)) have grown rapidly during the past 200 years, exploitation of ecosystems for human gain has usually ignored sustainability and often depleted biodiversity. This may change in the next several decades as land transformation and human appropriation of ecosystem services surge toward natural limits and the growth rate of the human population declines toward zero. Still, more than 950 million people face hunger during at least a part of each year (14% of world population) emphasizing the tension between priorities for human welfare versus those for the conservation of species and ecosystems.

Should attempts to improve the material conditions of human life be constrained by attempts to ensure the long-term survival of habitats and species? The connection between sustainability and biodiversity is neither conceptually clear nor practically straightforward, but it is of fundamental significance. Whether slowing the loss of biodiversity is necessary or sufficient for the transition to a sustainable society depends not only on the material relationships between diversity and the provision of ecosystems services to human society, but also on the philosophical basis for the value of biodiversity. The three central rationales that have motivated biodiversity

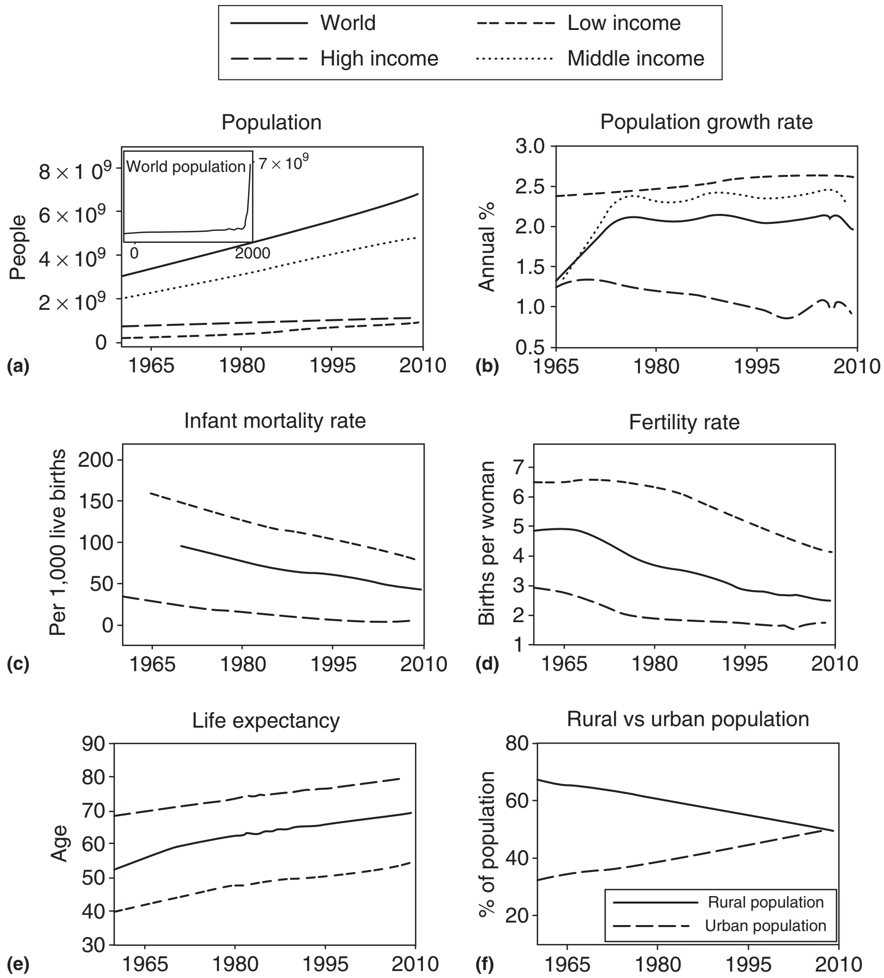

Figure 1 Human demography trends. In recent decades, world population has increased exponentially reaching 7 billion (a) although annual population growth has slowed (b) as human fertility rates have declined (d). Infant mortality rates have declined (c) whereas life expectancy has increased (e) providing an indication of increases in human well-being. Meanwhile, most humans now live in urban environments because the fraction of the population in rural regions has consistently declined whereas that in urban populations has consistently increased over the last half century (f). Data from the World Bank (www.worldbank.org) and the Population Reference Bureau (www.prb.org).

conservation can be summarized as: (1) the ethical perspective that other organisms that evolved over millennia have a right to exist and a claim to planetary resources irrespective of human needs, (2) spiritual and cultural practices that value the existence of other organisms, and (3) empirical linkages between biodiversity and the provision of ecosystem services. Although these rationales are philosophically compatible and even overlapping, they have divergent implications for the prioritization of biodiversity conservation and the meeting of human needs. The ethical perspective (1) suggests that preservation of biodiversity should be considered a priority equal to human well-being. The spiritual/cultural perspective (2) takes as given that human well-being is dependent on the preservation of other species. In either case, a trajectory of development that erodes biodiversity is, by definition, unsustainable. Although both views motivate biodiversity conservation, they do not consider the contributions of biodiversity to the material well-being of society. As such they are likely to fall short in conflicts over land-use that highlight immediate trade-offs between biodiversity conservation and production of goods and services for human consumption.

The ecosystem services justification is fundamentally anthropocentric, in that it makes the value of biodiversity contingent on its relationship to human well-being. Despite the weak philosophical protection it affords to biodiversity conservation, the potential for the ecosystem services perspective to align conservation and human development goals gives it the greatest prospects for widespread political adoption (MEA, 2005). In 1987, the World Commission on Environment and Development (WCED) chaired by Gro Harlem Brundtland declared: "Sustainable development is development that meets the needs of the present without compromising the ability of future generations to meet their own needs." Under this directive, the transition to sustainability will require that we understand the complex and reciprocal relationships between biodiversity and human well-being, both now and in the future.

Box 1 Sustainability and the theory of inclusive wealth

In theory, inclusive wealth considers all the contributions to human well-being from all planetary resources. These "capital assets" support, provision, and regulate goods and services now and in the future. The well-being or utility of individuals (U_i), who exist within a social state, x, where the social state characterizes everything that might influence well-being. Social well-being at time t $V(x(t))$ is an aggregate function of the well-being of individuals in society

$$V(x(t)) = V(U_1(x(t)) \;\; U_2(x(t)) \; \ldots \; U_n(x(t))$$

Social well-being from time t forward is measured by

$$V(t) = V(x(t)) + V(x(t+1))/(1+\delta) + \cdots$$

where δ is the discount rate by which future values are discounted when compared to present values. The discount rate is an area of much controversy. Perhaps the well-being of future generations should not be discounted at all, or perhaps discounting is reasonable. Leaving aside the controversy, sustainability is said to be achieved when the flow of well-being is nondeclining, $\mathrm{d}V/\mathrm{d}t \geq 0$. Since well-being is subjective and not directly observable sustainability cannot be measured in this way. However, we can attempt to measure assets and their values. The theory becomes more tangible if we consider human well-being in terms of all of the capital assets or system properties, $K(t)$, that can be used to provide the flow of goods and services that contribute to well-being

$$V(t) = V(K(t), M)$$

where $K(t) = (K_1(t), K_2(t), \ldots, K_H(t))$ and M is the evolving political economy or the resource allocation mechanism that involves institutions. Capital assets that contribute to well-being come in many forms, including manufactured capital, natural capital, human capital, social capital, and knowledge capital. Taking the derivative of $V(K(t), M)$ with respect to time generates the following expression:

$$\frac{\mathrm{d}V(K(t), M)}{\mathrm{d}t} = \sum_{h=1}^{n} \frac{\partial V(K(t), M)}{\partial K_h} \;\; \frac{\mathrm{d}K_h(t)}{\mathrm{d}t}$$

The added value of an additional unit of capital asset h is its 'shadow price' P_h and can be defined as

$$P_h(K(t), M) = \frac{\partial V(K(t), M)}{\partial K_h(t)}$$

Inclusive savings or investment in capital asset h is

$$I_h(t) = \frac{\mathrm{d}K_h(t)}{\mathrm{d}t}$$

Inclusive wealth, which is the value of all capital assets, is

$$W(t) = \sum_{h=1}^{H} P_h(K(t), M) K_h(t)$$

and the change in the value of inclusive wealth through time is given by

$$\frac{\mathrm{d}W(t)}{\mathrm{d}t} = \sum_{h=1}^{n} p_h(K(t), M) \frac{K_h(t)}{\mathrm{d}t} = \sum_{h=1}^{n} p_h(K(t), M) I_h$$

Nondeclining social well-being through time is equivalent to nondeclining inclusive wealth, so that we can summarize sustainability from the perspective of the theory of inclusive wealth as being a trajectory through time where the total value of all capital assets that contribute to human well-being is nondeclining:

$$\frac{\mathrm{d}V(K(t), M)}{\mathrm{d}t} = \frac{\mathrm{d}W(t)}{\mathrm{d}t} = \sum_{h=1}^{H} P_h(K(t), M) I_h(t) \geq 0$$

A major challenge for the integration of biodiversity conservation and providing for human well-being through the framework of sustainability is the appropriate valuation of biodiversity. This challenge begins with determining the relationships between biodiversity and ecosystem function, and between ecosystem functions and their value of in terms of well-being, relationships which are incompletely understood. But it also extends to and ultimately resides in questions of scale and equity, both within and among generations. That is, measures necessary to meet human needs locally may compromise biodiversity globally and vice versa, and measures necessary to meet human needs or maintain biodiversity today may compromise one or both of these aims in the future. How can we determine the course that provides greater benefit to human welfare now or for humans in generations to come? A framework that considers inclusive wealth (**Box 1**), or the contributions of all natural and human-derived systems to human well-being, may help guide this search.

At the heart of potential tradeoffs between biodiversity conservation and human well-being are decisions about alternative land-uses, which must balance conservation against uses that contribute immediately and directly to human welfare, such as agricultural production (Foley *et al.*, 2011). These are entangled with issues of equity by the fact that the world's biodiversity hotspots tend to be found in countries with the highest human population density and the lowest per capita income (**Figure 2**). These same countries, mostly in the tropics, have seen much of their best agricultural land committed to the production of sugar, tea, coffee, chocolate, and other luxury goods for temperate-zone markets for centuries, and increasingly to meet rising global demand for soya and palm oil in biodiversity hotspots such as Indonesia and Amazonia. Ultimately, the possible paths toward sustainability are constrained by the realities of the history and geography of human society and Earth's biodiversity.

The complexities of relationships among biodiversity and human well-being present fundamental challenges to defining the objectives of a sustainable future; thus a transition toward sustainability must be a search rather than a march. Regardless of the specific path, a transition toward sustainability – in which biodiversity and the ecosystem services they provide are sustained and human needs met now and in the future – will require significant social, political, and technological changes during the next few generations. The good news is that this is a time period in which human population is expected to level off within the century due to declining fertility rates (**Figure 1(d)**); hence, it is possible to think of a sustainability transition on the timescale of the demographic transition drawing to a close during the twenty-first century. At the same time, even present levels of human population and consumption have proven devastating to the planet's biota. Understanding how past and future biodiversity loss influence the ecosystem and environmental services that contribute to human welfare is critical to the search for a sustainable future. Awareness of long-term trends and transitions, together with indicators to inform our searches, are important contributions that science can provide in addition to developing means for

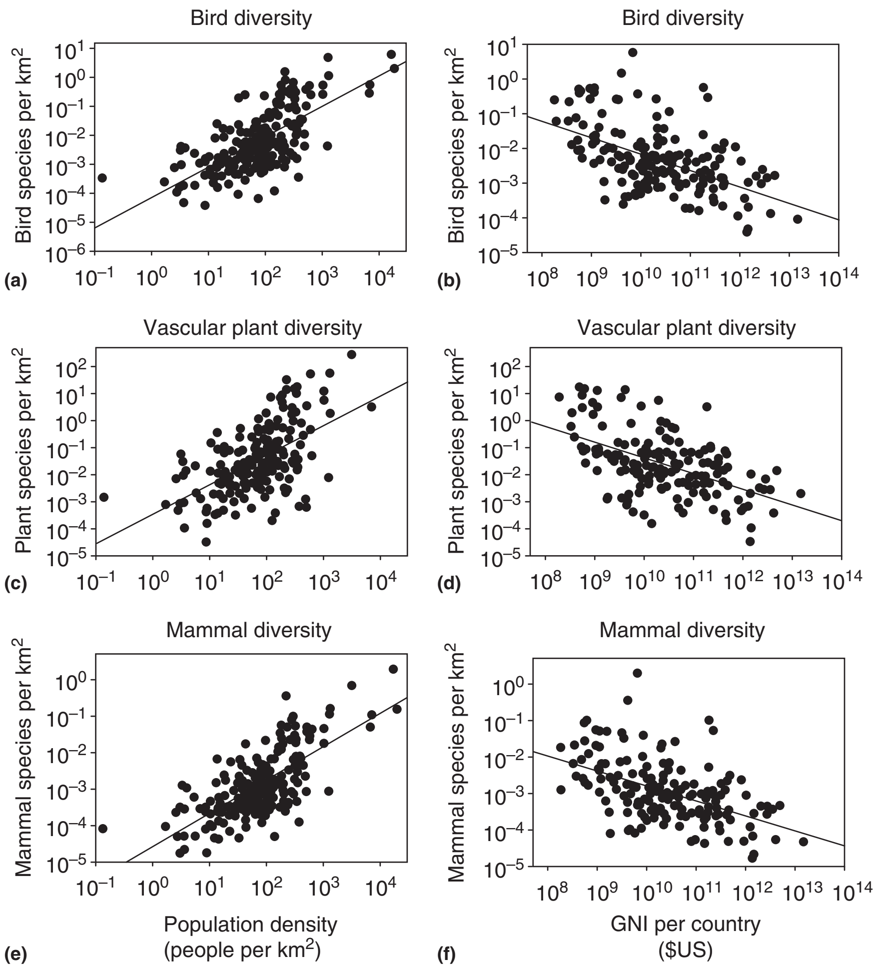

Figure 2 Bird diversity (a, b), vascular plant diversity (c, d), and mammal diversity (e, f) by country in relation to population density (people per km^2) and Gross National Income (GNI; $US), respectively. GNI is the value of all products and services generated within a country in one year (GDP) plus the income lost to or gained from other countries through debt and interest payments. The relationships show that species diversity, one measure of biodiversity, is highest in countries where population density is highest and income is lowest, posing challenges for biodiversity conservation. In a–f, each point represents a single country. Lines are least squares regressions fitted to the data. Species per km^2 are calculated from the number of species per country divided by the total area of the country. Data on bird, mammal and plant diversity are from the World Resources Institution (earthtrends.wri.org); population density and GNI data are from the World Bank.

reconnecting human prosperity to the diverse and essential riches of the natural world.

Sustainability, Sustainable Development, and Carrying Capacity

The definition of a sustainable material economy remains problematic: Which stocks must be preserved? Which flows must be conserved and at what levels? Is there a single numeraire that can indicate sustainability or its opposite? There are no definitive answers to these questions, but the definition of sustainable development put forward by the Brundtland Commission (meeting the needs of the present without compromising those of future generations) contains within it two key concepts: The concept of needs, in particular the essential needs of the world's poor with an emphasis on alleviating poverty; and the idea of limitations imposed by the state of technology and social organization on the environment's ability to meet present and future needs.

In a simple consumer–resource interaction, resource use, or consumption is sustainable when the rate of extraction is equal to or less than the rate at which the resource can replenish itself. In such systems, for a given extraction rate and replenishment rate, there exists a finite limit (or carrying capacity) of the size of the consumer population, which can be sustained. When consumers exceed the carrying capacity, this can result in a self-limiting feedback, because with a decline of the resource base, the consumers' abundance also declines. In this light, ecosystems are essentially suites of resources that support both human and other organisms. And as such, they also have a finite limit (or carrying capacity) to support other populations. However, for humans, self-limiting feedbacks rarely manifest themselves as they would in a simple consumer–resource relationship. People obtain highly diverse and complex portfolios of resources and services from ecosystems, which allows numerous forms of buffering from self-limitation. Some resources can substitute for others in maintaining livelihoods. Thus, with some notable exceptions, the birth and death rates of human populations are rarely in lockstep dependence with a single ecosystem service. Also, our consumer–resource interactions are frequently spatially buffered. Humans live and work in virtually all parts of the planet, exchanging goods in a global economy. Richer societies have often transferred the burdens of their unsustainable practices onto poorer ones by harnessing goods and services produced in poor regions, and avoiding some of the costs of those goods in the form of environmental degradation. Humans have also developed technological innovations that buffer us from the harsh consequences of exceeding carrying capacities by enhancing the rate of resource replenishment, as is the case with fertilizer use on crops. And there is of course temporal buffering, wherein the consequences of unsustainable resource use do occur but are unobserved because the feedbacks take decades to play out.

For nearly all human populations, trends during the past several decades in indicators of well-being, such as declining infant mortality rates (**Figure 1(c)**) and increasing life expectancy (**Figure 1(e)**, income and education, indicate that human welfare is increasing. However, given the many ways by which we buffer and escape direct suffering even when we exceed carrying capacities for ecosystem services, this outcome may not be entirely surprising. Buffering mechanisms, changes in social organizations, technological advances, and the values we place on different indicators of well-being can all obfuscate the finite nature of resource availability. However they do not change the fact that resources are still ultimately finite. They also do little or nothing to direct attention to the ways that overutilization of one resource can impact the availability of other resources and services. The destruction of biodiversity may be deemed a negligible cost to increasing ecosystem services like food production, but when we reduce a resource's abundance, we reduce the carrying capacity for other organisms that rely on the resource. This can lead to cascading losses of biodiversity, which comes full circle to limit resources on which humans depend. This cycle can be seen in the collapse of fisheries, the loss of species in logged tropical forests, and loss of agricultural soil productivity – all cases where exploitation of one resource has led to unexpected losses of other resources and services.

As human numbers and consumption of natural resources increased over the last century, so did concern that the impact of our species on the natural world would have irreversible, ultimately self-destructive effects. Using the idea of carrying capacity as a framework, ecologists have estimated that humans now appropriate slightly less than half the net primary production on land and approximately the same fraction of fresh water (Vitousek *et al.*, 1986). Such estimates indicate that further economic growth or improvements in human well-being – even if they occur – may not continue to increase the size of the material economy on which life depends. Indeed, it seems likely that achieving sustainable economies will require decreasing the burdens of wasted energy, discarded materials, and pollution that are now imposed on the environment. Technology plays a strategic role in this aspiration.

The Inclusive Wealth Framework for Sustainability

There are many perspectives from which to consider sustainability ranging from single indicators of human well-being that mimic Gross Domestic Product (GDP) to composite indicators to even more complex approaches. One type of approach, dubbed the 'dashboard' (Stiglitz *et al.*, 2009) involves gathering and analyzing a series of indicators that are relevant to evaluating environment, social, and economic progress simultaneously. At small spatial scales, particularly in agroecosystems found in many regions of Latin America, once such dashboard approach, the Framework for the Evaluation of Natural Resource Management Systems Incorporating Sustainability Indicators (MESMIS) has demonstrated promise (Speelman *et al.*, 2007). MESMIS considers indicators to evaluate system sustainability in the environmental, economic, and social arenas and provides criteria for sustainable management systems that emphasize (1) productivity, (2) stability, resilience and reliability, (3) adaptability, (4) equity, and (5) self-reliance. The effort has provided critical guidance in decision-making at the community level over the past decade. At larger spatial and sociopolitical scales, such as at national or global levels, the inclusive wealth economic framework (Arrow *et al.*, 2004; Dasgupta, 2008), provides a theoretical framework for developing composite indicators and charting a path for sustainability (**Box 1**). The inclusive wealth framework follows an economic approach that defines sustainability as nondeclining human well-being over time. In doing so, it takes a strictly human-focused perspective thereby ignoring the value of planetary resources for other species unless they benefit humans. However, it does allow for valuing of biodiversity to humans spiritually, materially, and for their importance in providing ecosystem services. Acknowledging this tension, the inclusive wealth framework offers guidance for human decision-making for achieving sustainability considering resource use, ecosystem services, and human well-being.

Human well-being is difficult to define, given its subjective nature. It is a function of material security, health, social relations, personal security, freedom, and other factors. Essential to human well-being is that physical, psychological, and spiritual needs which are met. In keeping with the United Nations World Commission on Environment and Development (WCED) (1987) definition of sustainable development, a sustainable development path is one in which human well-being is nondeclining. A sustainable economy, therefore, is one which follows a development trajectory in which intergenerational well-being is nondeclining.

Inclusive wealth includes the contributions to wealth from all capital assets and the value of these assets is determined by their contribution to the current and future production or provision of goods and services (**Box 1**). In other words, sustainability is achieved if the change in the total value of all capital assets that contribute to human well-being and investment in those assets is nondeclining.

Theoretically, it is possible to calculate changes in well-being through time by tracking the change in inclusive wealth, which is a function of both the shadow prices of capital assets and investment or depreciation in the capital assets that contribute to well being (**Box 1**). The theory provides an elegant means to focus attention on what needs to be measured to evaluate sustainability. Actually measuring inclusive wealth, however, presents an extreme challenge given that it requires quantifying shadow prices, a process fraught with difficulties and unknowns. Evaluating shadow prices for natural resources, for example, requires evaluating losses in terms of all present and future well-being that would result reductions in these resources. This necessitates understanding exactly how assets contribute to provision of goods and services and how goods and services contribute to human well-being; achieving such estimates for spiritual, aesthetic, or nontangible goods may be particularly problematic. Provisioning of environmental services depends also on systems dynamics and how evolving conditions will impact the stocks and flows of capital assets. In particular, the risks associated with catastrophic changes (i.e., tipping points) are difficult to assess and therefore to manage appropriately. Present formulations of inclusive wealth do not generally include how capital and services are distributed within or among economies. Although equity considerations can be incorporated into this framework, the real challenge is achieving societal agreement on how this is best done. Despite the many challenges, which highlight the nature of the search rather than a march toward sustainability, the inclusive wealth framework provides one approach to considering sustainability that incorporates the stocks and flows through time of the major forms of capital assets that contribute to human well-being.

Table 1 Examples of ecosystem services

Supporting	*Regulating*
Nutrient cycling	Global Climate regulation
Soil formation	Flood regulation
Primary production	Disease regulation
Oxygen production	Water purification
Pollination	Shade/temperature regulation
Provisioning	*Cultural*
Food	Aesthetic
Freshwater	Spiritual
Wood and Fiber	Educational
Fuel	Recreational
Pharmaceuticals	Identity

Source: Adapted from the Millennium Ecosystem Assessment: www.MAweb.org

Capital assets that contribute to human well-being go far beyond resources that are typically valued in monetary terms. All of the planetary and human-created resources that influence human welfare must be considered. These assets can be broken down into major categories, including (1) manufactured capital, which includes all the goods and services produced by humans, (2) human resources and capabilities, such as human health, human knowledge, and governmental, social, and cultural institutions, and (3) natural capital, which includes all the goods and services provisioned, regulated, and supported by Earth systems (e.g., the atmosphere and climate; terrestrial, freshwater, and oceanic ecosystems; and so forth) (**Table 1**). Natural capital assets, for example, include system properties such as soil, hydrology, vegetation, habitat, interactions between species and trophic levels, etc. that provide ecosystem/environmental services that contribute to human well-being. Such services include plant pollination, pest regulation, pollution reduction, renewable resource conservation, soil fertility, food and fiber production, freshwater, regulation of water flow and quality, flood regulation, nutrient regulation, carbon sequestration, disease regulation, recreation, aesthetics, pharmaceuticals, etc. Biodiversity is a critical component of natural capital assets from which these services flow (section Biodiversity as a Form of Natural Capital). Ecosystems and Earth systems, more generally, provide services in often complex and interacting ways that are often poorly understood and monitored. The maintenance of natural capital assets and their ability to provide services are influenced by human use and management. The governance, institutions, cultural values, social relations, incentives, regulations, markets, and so forth that drive how humans use and manage these assets are thus critical to the maintenance of and investment in natural capital.

Biodiversity as a Component of Natural Capital

Biodiversity represents a distinct component of natural capital and is often considered essential to sustainability. Species extinction is one of the only indications of irreversible environmental loss widely accepted by laypersons; what is its practical significance, both biologically and socially? Is human well-being dependent on the survival of biodiversity, and if so how?

First, it is worth remembering that whereas biodiversity is often used to refer to the richness of species in a given region, it is a much broader term that includes the sum total of the living resources on Earth. According to the 1993 Convention on Biodiversity, biodiversity is the variability among living organisms from all sources, including diversity within species, between species and of ecosystems. The variety of life this encompasses as well as the complex and dynamic relationships among components of biodiversity make it much more than simply the number of species per unit area.

Second, an increasing number of scientific studies demonstrate empirical linkages between biodiversity and ecosystem services that contribute to human well-being (see article from Quijas and Balvanera, *Links between biodiversity and ecosystem services*). Quantitative syntheses of the large amount of experimental studies that have manipulated species richness and measured multiple ecosystem functions have shown that higher biodiversity provisions more services such as increased stability in the face of perturbation, higher productivity and thus higher provision of food fodder or wood, and better regulation of erosion, pests, and pathogens.

Ehrlich and Ehrlich (1981) hypothesized that losses of biodiversity have consequences for ecosystem function much like losses of redundant rivets in airplane wings: Initial losses of species should be accompanied by minimal change in the functioning of ecosystems because some fraction of species are redundant in the processes they perform in nature. However, at some point, loss of species lead to rapid declines in ecological function, much like the loss of one too many rivets can lead to failure of an airplane wing. Of the hundreds of scientific studies that have examined the empirical links between biodiversity and ecosystem functions, such as nutrient cycling and productivity, the vast majority support the rivet-redundancy hypothesis for individual ecosystem functions (Cardinale *et al.*, 2011). In agricultural systems, for example, different crop varieties that can adapt to altered climates or are resistant to different diseases provide redundancy and reduce risks. In the face of climate change or invasive pathogens, if one crop variety fails, another may persist. If one pollinating insect species declines, a similar species may provide the same service. Meta-analyses that have examined multiple ecosystem services simultaneously (Hector and Bagchi, 2007; Isbell *et al.*, 2011) demonstrate, however, that many more species are required to provide multiple ecosystem services than a single service alone. Such multidimensional investigations demonstrate that although each ecosystem function or service may depend on only a fraction of the species in the ecosystem, the number of critical species continues to increase as more functions and services are considered. The end result is that that most species, including rare species, turn out to be critical to the integrity of ecosystems.

Despite the wealth of evidence linking biodiversity to human well-being in experimental and theoretical contexts, at landscape, regional, within country, and among countries spatial scales, biodiversity, and ecosystem services may be at conflict, given competing land-uses. Agriculture, for example, contributes to food provision at the cost of preserving habitat for other species. In contrast, a forest preserve allows for the maintenance of multiple species, which contributes to the maintenance of carbon stocks and the regulation of water-availability and related services, but does not allow for the extraction of timber or other products for human consumption.

It is possible to design landscape management schemes that allow for the simultaneous maintenance of biodiversity and agricultural areas (Porter-Bolland *et al.*, 2011). Diverse agroecosystems can be established within a matrix of conserved forest patches that allow for multiple species to find suitable habitat, while food is produced. Also, it is possible to design a network of sites for conservation that could maximize the conservation of biodiversity and that of ecosystem services. By identifying the key areas for conservation of biodiversity and those for the provision of ecosystem services, sites can be chosen to maximize both. Well-managed natural ecosystems that conserve biodiversity can provide income and jobs through trade, tourism, crafts, and sustainable food production. At the same time, productivity of existing agricultural systems in regions where they fall woefully short of possible production could prevent unnecessary expansion of land conversion to agriculture (Vandermeer and Perfecto, 2007; Foley *et al.*, 2011; Tilman *et al.*, 2011). Polasky and colleagues (2008) modeled an "efficiency frontier" of possible land-use scenarios in which biodiversity and economic output can both be increased far beyond current land management practices. Such options provide a path forward toward sustainability while recognizing that there are challenges, costs, and both winners and losers in the transition.

Biodiversity, Poverty, and Equity

Around the world, the Convention on Biological Diversity has unified nearly every country in a commitment to reduce the loss of biodiversity. Likewise, there is almost universal adoption of poverty reduction as a national goal, as evidenced by the widespread embracement of the Millennium Development Goals (Barrett *et al.*, 2011). These may seem on the surface to be independent endeavors, but they are important, complex interactions between the dynamics of poverty and biodiversity, occurring across spatial and temporal scales.

The well-known latitudinal gradient in biodiversity from the poles to the equator corresponds to a latitudinal gradient in poverty and human population, such that hotspots of biodiversity are found in some of the worlds' poorest and most densely populated nations (**Figure 2**). The interactions between biodiversity and poverty can lead to complex feedbacks that: synergistically benefit both biodiversity and poverty; create tradeoffs between aims to alleviate poverty or conserve biodiversity; or create detrimental feedbacks that eventually lead to worsening human and environmental conditions (Roe *et al.*, 2011). Therefore, the dual aims of biodiversity conservation and poverty reduction cannot be addressed independently of each other, nor can they be strictly pursued within nations without considering global dynamics. Instead, we must recognize and understand the relationships that exist between biodiversity and poverty, and evaluate them integratively at local, regional, and global scales. Social and economic equity arises as a cross-cutting issue, shaping the trajectories of human–environment interactions and thus affecting sustainability.

At global, continental, and many national levels, trends indicate increases in average standards of human well-being despite declines in biodiversity (MEA, 2005). This would suggest that biodiversity conservation is not relevant to, or not necessary for, human development. However, such aggregated scales blur the fact that national average indicators of well-being can increase whereas the economic welfare of the poorest is stagnant or decreasing. Furthermore, when we focus on regions with extreme poverty, these areas are frequently regions of the greatest rates of biodiversity loss. Numerous factors contribute to this troubling co-occurrence.

Such regions are most commonly located in the tropics and in developing countries, where people often engage in traditional subsistence or small-scale production systems. These segments of society tend to rely heavily on local biodiversity to meet an array of their livelihood needs – food, fiber, fuel, construction materials, medicine, pollination services, cultural services, etc. Also, these societies also tend to have high levels of multiple indicators of poverty, such as little wage employment or cash income, poor access to education, health, and social services, and political marginalization (**Figure 3**). This leads to a spatial correlation of biodiverse areas and poverty.

A major driver of biodiversity loss globally is demand and consumption of natural resources from urban areas and from the developed or rapidly developing world (DeFries *et al.*, 2010). Urban populations have continued to increase in all parts of the globe over the last century (**Figure 1(c)**) with increases in consumption that put pressure on agriculture and the natural resource bases at the expense of biodiversity. The loss of biodiversity in poor rural areas of developing countries occurs as local residents and governments are driven by such demands to exploit their natural capital to increase national economic growth. Natural resource extraction and land conversion – such as timber extraction, mineral extraction, expansion of agriculture or aquaculture, and urban growth – are often undertaken in environmentally irresponsible ways, due to some combination of weak governance, perverse incentives, and economic desperation. Whether out of economic necessity,

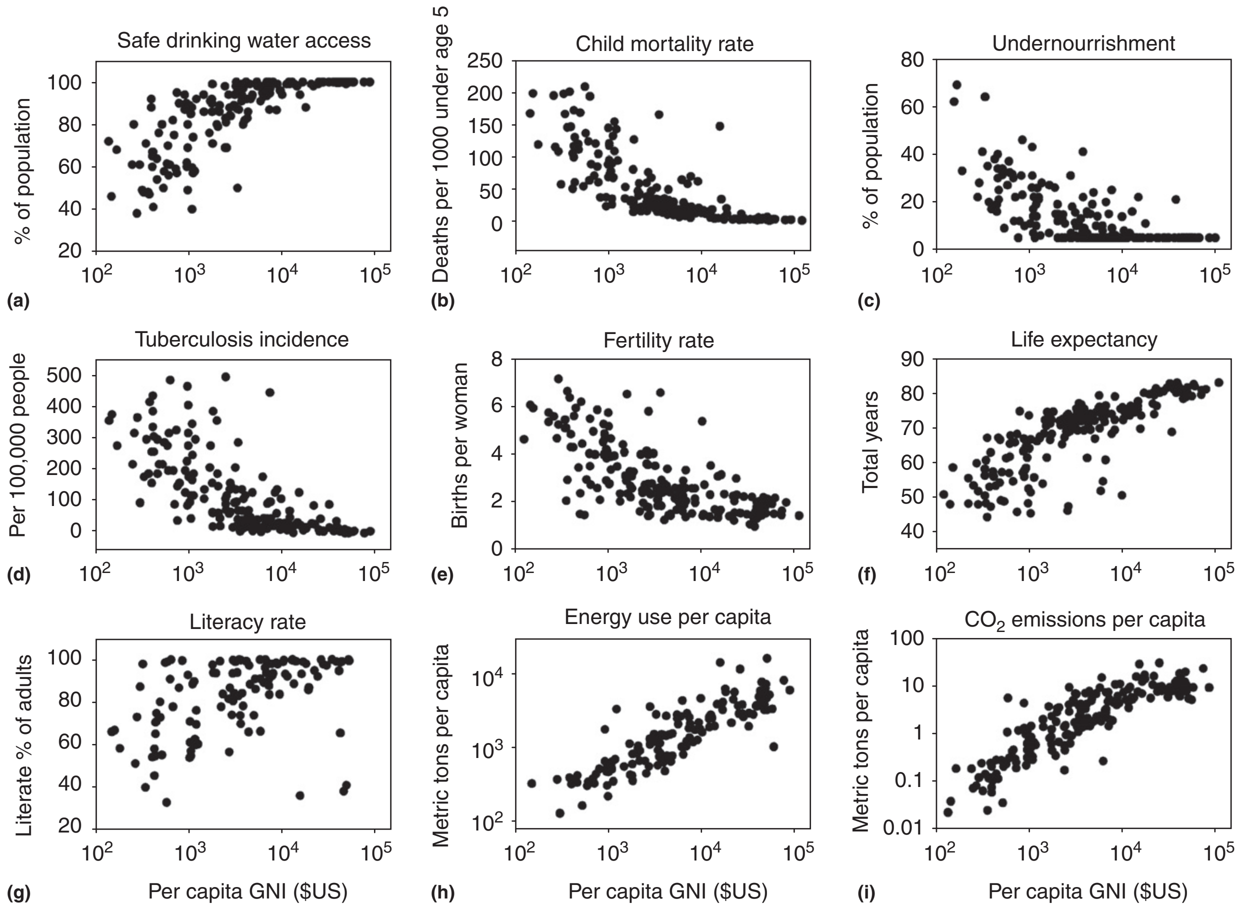

Figure 3 Indicators of human well-being and consumption rates are associated with monetary wealth. Wealthier nations have higher access to safe drinking water (a), lower child mortality rates (b), lower fractions of their populations undernourished (c), and lower rates of tuberculosis (d), an indication of disease risk. Wealthier nations also have lower fertility rates (e) and higher life expectancy (f), and higher literacy rates (g), an indication of demographic transitions. At the same time, consumption rates of energy (per capita) (h) and emissions of CO_2 (i) increase with wealth, indicating that gains in well-being come at a cost for the global environment. Data from the World Bank.

incentivization, greed, or negligence, governments and extractive industries often prioritize short-term economic gains above long-term sustainability. Even where environmental protection policies exist, higher levels of government may have little capacity to enforce them, and the potential economic gains from destructive exploitation negate incentives to attempt enforcement.

Such biodiversity loss can reinforce and increase poverty. When natural capital is converted into financial or manufactured capital, social, and political inequities often contribute to outcomes of increased poverty. Poor people living in proximity to biodiverse areas tend to accrue relatively fewer benefits, and often bear a greater burden of costs, from commercial resource exploitation. Poor people are disempowered politically, economically, and in some cases face cultural prejudice. As a result, they tend to receive the minimum compensation that larger polities can feasibly offer, ranging from forced land appropriation and resettlement, to conversion to an industrial wage labor force with reduced local authority and autonomy.

Local people also lose ecosystem services, such as wild and semiwild food sources, soil erosion control, water purification and recharge, pollinator services, and cultural values associated with biodiverse areas. Since poor rural populations rely more directly on those services, their loss exacerbates the challenges of poverty and decreases options for improving livelihoods. The poor become even poorer as they try to cope with land loss, meager wages, and the disappearance of the safety net of ecosystem services. Under such pressures, poor people must often resort to destructive resource use themselves in order to survive. Biodiversity loss and increased poverty are therefore both linked to social inequity in economic development. Certain development sectors, such as oil extraction in Africa and Latin America, forest conversion for soy production in Amazonia, and timber extraction in southeast Asia, have come to epitomize these dynamics.

International trade, global markets, and aid relations profoundly influence development trajectories in biodiverse regions. Many developed nations place higher political priority on environmental protection within their own territories, with the result that wealthier nations now import huge proportions of natural resources from developing countries. When donor aid is coupled to restructuring developing economies to prioritize exports, inequities at an international scale can disempower developing countries to conserve natural resources. This model of economic development is meant to increase wealth for developing countries. However, due to weak governance capacity, corruption, and pre-existing inequities within those countries, they can instead lead to greater wealth inequality and create poverty traps for the most vulnerable segments of society. The enticement of quick profits for countries in dire financial straits may generate perverse incentives for governments to tolerate or even prioritize practices that threaten biodiversity and perpetuate poverty. Coupled political inequities, between developed and developing countries, as well as within countries, can derail efforts for sustainable development and biodiversity conservation.

These outcomes of global trade are becoming more widely acknowledged. In response, developing countries are demanding more attention – and compensation – be paid for the environmental burdens relegated to the developing world (Roberts and Parks, 2009). This is spurring an important current trend in sustainable development – to dismantle perverse incentives and create local, equitable economic benefits for maintaining biodiversity. Formulating win–win situations is feasible in theory, yet is difficult to achieve in practice. There are now hundreds of thousands of coupled conservation-poverty alleviation projects worldwide, which vary in their relative emphasis on conservation or poverty reduction, and in their strategies for overcoming inequities and perverse incentives (Adams *et al.*, 2004).

There are successful and failed examples in every kind of project linking biodiversity conservation and poverty alleviation: community based natural resource management, integrated conservation and development programs, payments for ecosystem services, sustainable biodiversity utilization, and the recently burgeoning enterprise of cash payments for intact ecosystems for carbon dioxide sequestration (so-called REDD, Reducing Emissions for Deforestation and Forest Degradation, programs). Given the case-specificity in every project, there is consensus on only a few common attributes of projects that yield greater successes. In general, successful programs are carefully designed to account for the specific nature of linkages and feedbacks between poverty and biodiversity in any given case. And equity is recurringly important. Conservation-poverty initiatives require collective action and regulation. If the governance and benefits are not perceived as equitable and legitimate, there tends to be a breakdown of trust, cooperation, and compliance, and project failure ensues (Ostrom, 1990).

Conservation-poverty programs also vary in their approaches to evaluate changes in human well-being and poverty reduction. The inclusive wealth framework is proposed to integrate the values of biodiversity as well as other forms of wealth, into an aggregate assessment of well-being. It is important to note, however, that in the context of assessing poverty reduction, the framework has limitations. As noted, sociopolitical and economic inequality are major drivers of biodiversity loss and persistence of poverty. Inclusive wealth is based on aggregate summations for a given economic unit, and currently does not account for inequities that exist within that unit. Incorporating metrics of economic inequality, such as the Gini coefficient, would add consideration of the status of the poorest as an additional factor in gauging societal well-being. It would also address the concern that empirically, economic inequality is a strong predictor of biodiversity loss (Mikkelson *et al.*, 2007; Holland *et al.*, 2009).

Although there is much to debate and development in the study of biodiversity, poverty, and equity, there are likewise some key common trends that are critical to understanding the challenge of sustaining biodiversity. Biodiversity loss is largely driven by grossly disproportionate consumption in wealthy nations and in urban environments, and the resource exploitation and land conversion in developing countries necessary to support that consumption. There is geographic colocation of poor people and areas of high biodiversity, and those are also the regions where biodiversity loss is most rapid. The dynamics of biodiversity loss and poverty feedback on one another, which creates both situations of entrenched poverty as well as opportunities to potentially engineer win–win situations. Around the world, there are a panoply of efforts to achieve such win–win outcomes, yet there is weak consensus as to the best ways to do so, or how to evaluate success. Environmental economics, political ecology, sustainability science, and conservation biology are among the host of academic disciplines striving to generate knowledge that can facilitate efforts to simultaneously sustain biodiversity and ecosystem services while alleviating poverty.

Diversity, Resilience, and Sustainability

Evaluating natural capital assets and their likely responses to decreases in resource use and consumption within the inclusive wealth framework are complicated by the fact that Earth system may not respond to change in easily predicted ways. A fundamental question that emerges is how stable are ecosystems and Earth systems in response to perturbation. Ecologists have long been interested in the temporal stability of structure and function of ecosystems, but have defined stability in two distinct ways. The first, termed engineering resilience by Gunderson (2000) defines resistance in terms of the sensitivity of ecosystems to disturbance (i.e., the magnitude of change in response to disturbance of some size) and resilience as the rapidity with which the system recovers to its predisturbance state. In many though by no means all cases (see article from Quijas and Balvanera, *Links between biodiversity and ecosystem services*), more diverse ecological communities are both less sensitive to change, and recover more rapidly to predisturbance values. Ecosystems that are more stable by these metrics might allow for ecosystem services to be obtained with greater regularity and predictability, and thus be of greater value. The shortcoming of studies based on resistance and engineering resilience (sensu Gunderson) is the presumption that ecosystems have a single equilibrium to which they ultimately return. The growing evidence that many ecosystems have more than one equilibrium (i.e., they possess alternative stable states) has more profound implications for relationships between diversity and sustainability.

The notion that ecosystems may shift abruptly between alternative stable states arose first from theoretical models but has since been demonstrated rigorously in natural systems. Some of the most convincing examples of such 'critical transitions' are found in shallow temperate lakes, which can switch rapidly from an oligotrophic clear water system to a eutrophic pea-green soup after nutrient additions pass a threshold (or 'tipping point') (Scheffer *et al.*, 2001). Importantly, reversing such a transition is extremely difficult, because positive feedbacks are reoriented to favor the new equilibrium. Another prominent example of such ecosystem behavior is the transition between woodlands and grasslands in arid and semiarid regions. Feedbacks among fire, herbivory, and the ability of plants to capture runoff all influence such landscapes. The same concepts of feedbacks, thresholds, and critical transitions have been applied to the apparently sudden collapse of human societies such as those in Central America, Easter Island, and elsewhere, generally due to collapse of environmental conditions. The existence of thresholds at the ecosystem scale also raises the notion that there may be planetary boundaries for critical factors, such as ocean acidification levels, atmospheric CO_2 concentrations, temperatures, species extinction levels, and so forth, beyond which Earth systems may switch into alternative states unfavorable to human well-being (Rockström *et al.*, 2010).

The capacity of an ecosystem to absorb external shocks without undergoing such transitions between stable states has been termed 'ecological resilience,' which is the second way ecologists have measured stability. A resilient system, like a ball in a cup, will return to its original equilibrium except in cases of severe disturbance. In a system with low resilience, only a small disturbance may be needed to move past the lip of the cup (the 'basin of attraction') and into another state. Human activities and other external drivers can reduce resilience and increase the probability of state shifts by weakening the interactions that reinforce the original state. Management of ecosystems with alternative stable states requires managing for resilience.

The concept of alternative stable states is important to the integration of biodiversity and sustainability in several respects: First, at the local and global scale, biodiversity may itself be subject to catastrophic declines as the human influences on ecosystems intensify. Rather than a linear decline with resource use (**Figure 4(a)**), biodiversity may exhibit threshold responses where minor stressors have little or no impact on biodiversity, but major stressors lead to severe losses (**Figure 4(b)**). In other words, there is no guarantee that diversity responds in a smooth fashion to environmental pressures – in fact, most evidence points to the contrary. The ongoing mass extinction associated with humans may represent the crossing of such a threshold. At the global scale, loss of species diversity is effectively permanent and irreversible, due to the contingent nature of evolutionary processes and the sheer length of time required for new species to evolve. But even at the local scale, loss of foundation species may effectively prevent reestablishment of original diversity levels after removal of stressors – meaning that biodiversity may exhibit alternative stable states within individual ecosystems (**Figure 4(c)**).

The response of ecosystem processes (and thus ecosystem service provision) to biodiversity can also be nonlinear. Rather than linear decreases (**Figure 4(d)**), relationships between species diversity and ecosystem functions such as productivity exhibit little change initially, followed by increasing large declines at low species number (**Figure 4(e)**; Cardinale *et al.*, 2011). In general, such relationships reflect redundancy among species' functional roles within ecosystems. How often feedbacks between ecosystem function and biodiversity are strong enough to generate alternative stable states (**Figure 4(f)**) is unknown.

Whether considering the response of biodiversity to environmental change, or the response of ecosystem services to biodiversity, nonlinear relationships have important implications for sustainability. Obtaining ecosystem services generally requires human institutions and infrastructure tailored for that purpose. Thus transitions to alternative states often incur significant costs due to the loss of services, even if the potential services from the new state are equal to those of the old. The risk of such losses is magnified by the fact that the location of thresholds and the potential loss of ecosystem services associated with a state transition are often difficult to determine ahead of time (Scheffer *et al.*, 2009). Global measures of sustainability such as inclusive wealth must

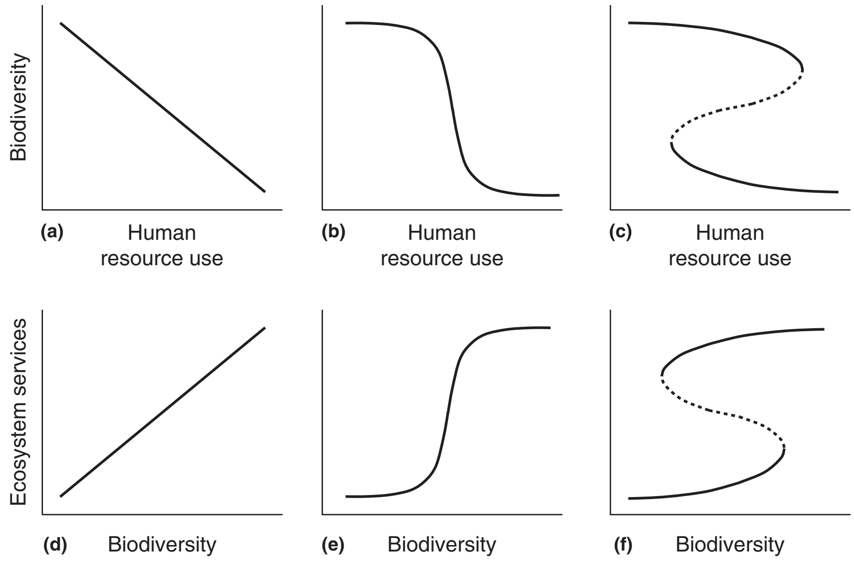

Figure 4 Potential relationships between human resource use and biodiversity (top row), and between biodiversity and ecosystem service provision (bottom row). Panels (a), (b), and (c) show linear, threshold, and hysteretic responses, respectively, of biodiversity to human resource use. Panels (d), (e), and (f) show linear, threshold, and hysteretic responses, respectively, of ecosystem service provision to biodiversity. Although the rate and costs of biodiversity loss are often assumed to be linear (a, d), some evidence suggests that these relationships exhibit sharp breaks at some level of human resource use (b) or biodiversity (e). A third possibility is that these relationships have alternative states (c, f), so that loss of biodiversity or the services that depend on them may not recover even when the underlying stressor (resource use or biodiversity loss) is ameliorated. Note that it would be possible for these relationships to exhibit one form when considered globally, and others when considered at the scale of individual ecosystems.

account for such risks if they are to guide or inform a sustainability transition.

One important implication of the inclusive wealth framework is that of intergenerational equity – the needs of the present balanced against those of future generations. Threshold relationships between biodiversity and ecosystem services (and among many other components of ecological systems) exacerbate the tension between maximizing current provision of ecosystem services and maintaining the capacity of ecosystem to provide services indefinitely, particularly when the potential for alternative states is considered. Available evidence suggests that maintaining diverse ecological communities is an important component of managing for resilient ecosystems and ensuring the future provision of ecosystem services.

Trends

Biodiversity Trends – The Millennium Ecosystem Assessment (2005) reports that extinction rates are 100 to almost 1000 times the background level of extinction based on the fossil record. Two thirds of the world's ecosystem services that depend on biodiversity are declining. These alarming trends led scientists to consider the current epoch of humanity the 'Sixth Extinction' (Leakey and Lewin, 1995). The largest driver of biodiversity loss is habitat change. On land, such changes occur through land use changes. Both globally and particularly in heavily indebted poor countries, conversion of land to agriculture (**Figure 5(e)**) has been on the rise in the last half century. Such trends occurred much earlier in many wealthier regions of the globe. Land conversions and land degradation also degrade or destroy ecosystems and the services they provide to humans. Increasing need for fuelwood and land for agriculture, together with industrial logging, have resulted in global losses of forest at a rate of 16 million hectares per year during the 1990s. World deforestation, mainly the conversion of tropical forests to agricultural land, has decreased over the past decade (2000–2010) to approximately 13 million hectares of forests per year but continues at an alarmingly high rate in many countries (Global Forest Resources Assessment, 2010).

In coastal and ocean ecosystems, habitat change is driven by loss of coral reefs through ocean acidification, pollution, climate change, species invasions, overexploitation, and damage to sea floors due to trawling. In coastal ecosystems, Worm *et al.* (2006) report dramatic declines in populations of ecologically and economically important species: In fishery taxa that have maintained viable population sizes over the last 1000 years, 40% have collapsed (their populations have dropped below 10% of their maximum population size) since 1800. More than half of the world's coral reefs face changes in species composition, obliteration, and other major ecosystem effects. In open ocean ecosystems, the situation is even more dire: 80% of fish and invertebrate taxa in our global fisheries have collapsed in the last 50 years. These collapses have resulted in major losses of ecosystem services (fisheries, nursery habitat, and filter function) and with concomitant increases in risks (such as beach closures, harmful algal blooms, fish kills, oxygen depletion, coastal flooding, and species invasions).

Covering less than 1% of the Earth's surface, freshwater ecosystems have lost the largest proportion of species and habitat when compared with other ecosystems on land or with the oceans. Physical modification or water withdrawal from

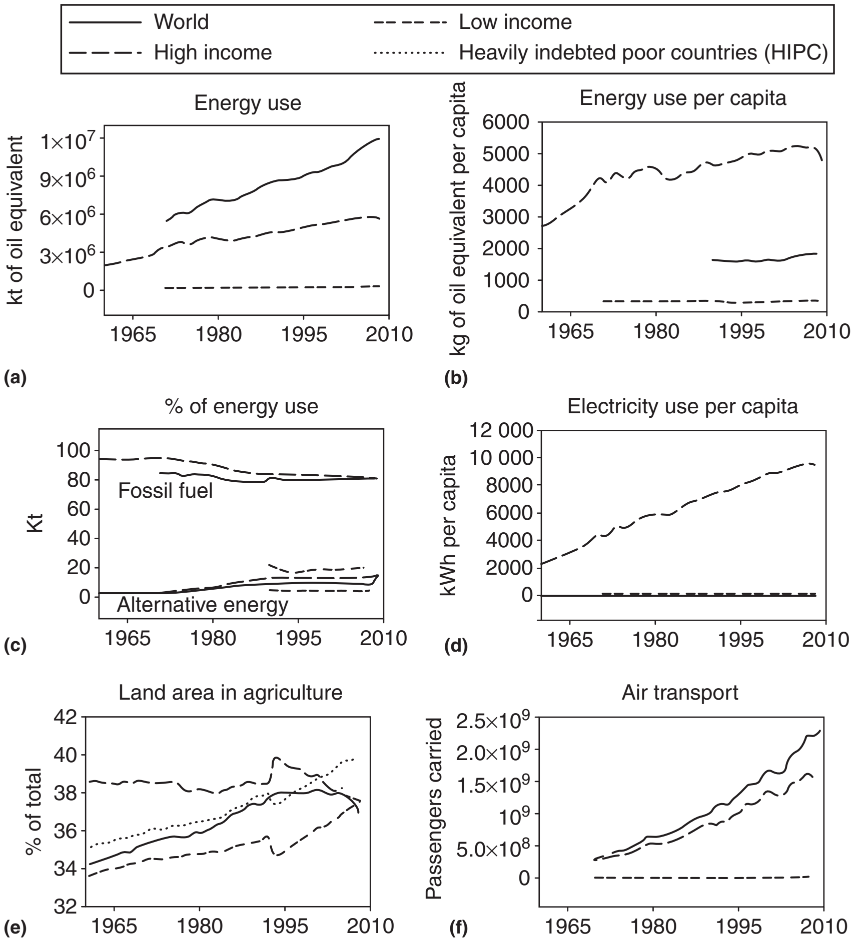

Figure 5 Global trends in total and per capita energy use and land area for agriculture. (a) Total energy use in kt of oil equivalents for the Word, high income nations and low income nations since 1960. High income and World totals continue to rise, whereas low income totals remain very low. (b) Per capita energy consumption has increased fairly steadily in high income nations since 1960 with a slight down-turn in recent years. (c) Fossil fuels still comprise the vast majority of energy consumption in the word, particularly in high income nations. In low income nations, fossil fuel energy use as a percentage of total energy use is much lower. Alternative energy sources, such as wind, solar, and nuclear remain very low percentages of total energy use throughout the world. (d) Electricity use per capita continues to increase steadily in high income nations but is stable in low income nations and for the World. (e) Land are for agriculture as a percentage of total land area has remained fairly stable in high income nations; it continues to increase in low income nations, and it is steadily increasing in heavily indebted poor countries, surpassing that of high income nations. (f) Air transport in terms of passengers carried an indicator of energy use and consumption that is afforded only by the wealthy, has grown steadily since 1970. This trend is driven largely by high income nations. Low income nations show very low and near constant levels. Data from the World Bank.

rivers, continuing overfishing, dam building and river development, and contamination have driven species losses and will continue to place greater threats on freshwater ecosystems. Many estuaries and bays have also deteriorated because of activities associated with land development and fishing pressure, undermining ecosystem services. All the habitat transformations have profound impacts on human well-being. Biodiversity losses affect the livelihood of local communities that depend on diverse ecosystems for food, tourism, and ecosystem stability.

Future projections of species extinction rates based on habitat change current population status of threatened or endangered species indicate that extinction rates will continue to rise to ten times their current rates (MEA, 2005), although the methods for generating such predictions are difficult (He and Hubbell, 2011). Measuring and monitoring for biodiversity loss presents a major challenge given that possibly >85% of species on land and >90% in the ocean have still not been identified or described (Mora *et al.*, 2011).

Trends in health, consumption, and communication – At the same time that biodiversity indicators show increasing cause for alarm in our ability to manage for sustainability, indicators of human well-being continue to show positive trends (**Figure 1(c)** and **1(e)**). But these benefits to human well-being have come at the cost of consumption of nonrenewable resources (**Figure 5(a)–(d)**), homogenization of the biota, emission of climate altering greenhouse gases (**Figure 6(a)** and **6(b)**), and pollutants to human health (**Figure 6(c)** and **6(d)**). Inequities in the distributions of costs and benefits are apparent, as discussed in section Diversity, Resilience, and Sustainability. Indicators such as disease incidence, literacy rate, safe drinking water access, and life expectancy indicate that wealthier nations have higher material well-being in terms of health, education, and access to basic resources (**Figure 3**). Wealthy nations have high per capita energy consumption rates and CO_2 emissions rates (**Figure 3(h)** and **(i)**). As such, wealthy nations appear to be reaping the benefits of consumption but the costs of this consumption is paid for globally. CO_2 emissions per capita have begun to level off in wealthy nations; globally, however, yearly emissions continue to increase as a result of population growth and consumption in fast developing countries. In the past 50 years, total annual nitrous oxide pollution has remained relative constant and particulate matter has markedly declined (**Figure 6(c)** and **(d)**). Electricity use per capita and total energy use of high income countries continues to rise. Air travel in wealthy nations and globally has risen sharply. At the same time, humans are increasingly connected and have the capacity to share ideas, cultural values, and transfer technology rapidly. The exponentially increasing trends in internet use and cell-phone use (**Figure 7(a)** and **(b)**) attest to the increasing global connectedness. The same global interconnectedness that creates pressures on biodiversity may also facilitate mechanisms such as REDD that provide incentives to address climate change while sustaining biodiversity.

Meeting human needs while preserving the Earth's life support systems for future generations will require a worldwide acceleration of today's halting progress in a transition toward sustainability. Whether humanity can take advantage of human capital, knowledge, and technological advances to develop processes and governing mechanisms to achieve sustainability will determine much about the fate of the Earth's biodiversity.

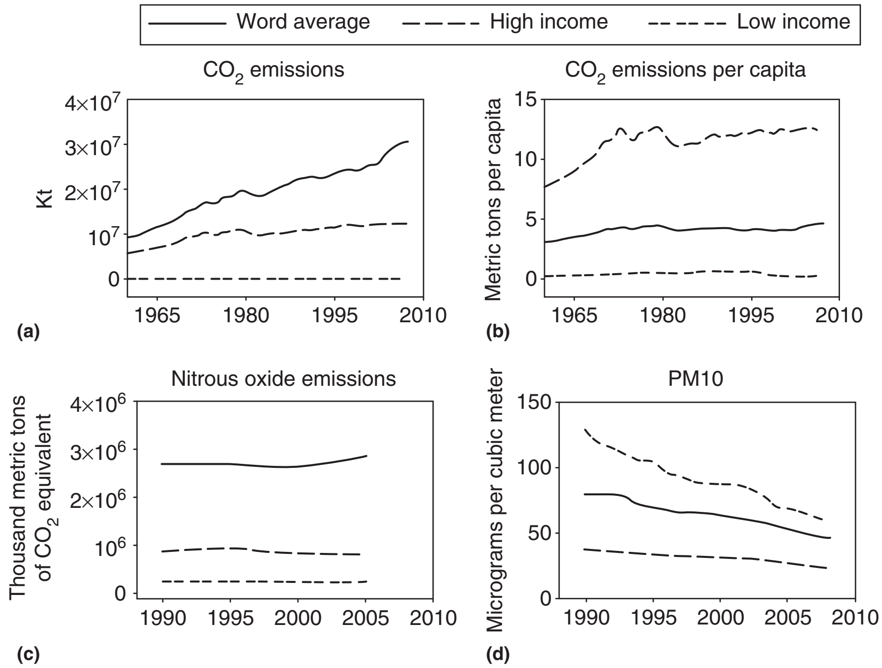

Figure 6 Pollution levels show contrasting trends. Although global CO_2 emissions have risen sharply (a), people in wealthy nations are largely responsible (a, c). Nitrous oxide emissions have stabilized (c) whereas particulate matter has decreased (d). Data from the World Bank.

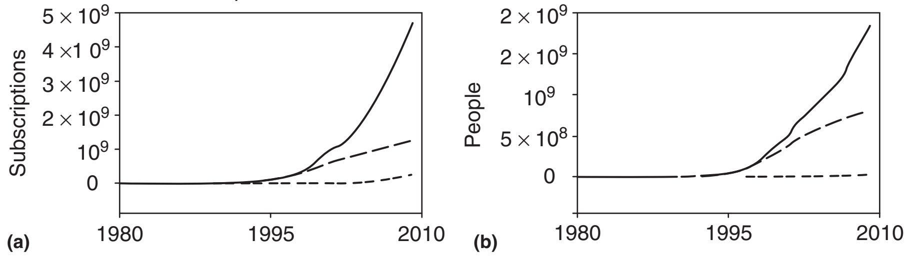

Figure 7 Exponential increase in global cell phone subscriptions (a) and internet users (b) in recent decades provides an indication of the change in communication and access to information that human societies have undergone. Data from the World Bank.

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