

Who Cares about Biodiversity? Optimal Conservation and Transboundary Biodiversity Externalities

Charles Perrings & George Halkos

Environmental and Resource Economics

The Official Journal of the European Association of Environmental and Resource Economists

ISSN 0924-6460
Volume 52
Number 4

Environ Resource Econ (2012)
52:585-608
DOI 10.1007/s10640-012-9544-8



Your article is protected by copyright and all rights are held exclusively by Springer Science+Business Media B.V.. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.

Who Cares about Biodiversity? Optimal Conservation and Transboundary Biodiversity Externalities

Charles Perrings · George Halkos

Accepted: 1 February 2012 / Published online: 26 February 2012
© Springer Science+Business Media B.V. 2012

Abstract The Convention on Biological Diversity's (2010) target to reduce the rate of biodiversity loss was achieved by very few countries. Why? We use the theory of conservation implicit in the Hotelling model of non-renewable resource pricing to analyze the problem, distinguishing between the benefits to countries where conservation takes place, and to other countries. We estimate models for three taxonomic groups, and find that while individual countries value conservation within their borders, in poor countries this effect is dominated by the negative impact of income growth. International concessional financial contributions to conservation in poor countries are found to be statistically insignificant. We conclude that countries care about the biodiversity within their national borders, but only when development priorities permit, and only when it becomes scarce enough that its value grows more rapidly than the return on alternative assets. There is little evidence that high income countries yet care sufficiently about biodiversity in the places where it is most threatened to affect conservation outcomes there.

Keywords Biodiversity · Hotelling-conservation · Transboundary externality

JEL Classification Q21

1 Who Pays for Biodiversity Conservation

In 2002 the Convention on Biological Diversity set a target for member states to reduce the rate of biodiversity loss by 2010. The evidence indicates that few countries came close to meeting that target (Perrings et al. 2010). Most indicators suggest that biodiversity continued

C. Perrings (✉)
School of Life Sciences, Arizona State University, PO Box 874501, Tempe, AZ 85287, USA
e-mail: Charles.Perrings@asu.edu

G. Halkos
Department of Economics, University of Thessaly, 43 Korai str., 38333 Volos, Greece
e-mail: halkos@uth.gr

to decline at or above historic rates over the whole period 2002–2010, and that the proximate drivers of biodiversity loss—habitat conversion to meet the food needs of a growing population, changes in environmental conditions due to emissions to soils, water and air, and the dispersal of invasive species—continued to increase in intensity (Hoffmann et al. 2010). At the same time, however, the collective policy response to the problem strengthened. There were increases in the extent of protected areas, the area of ‘sustainably managed’ forests, the number of countries signing international agreements on invasive alien species or introducing national legislation to control them, and the level of biodiversity-related aid (Butchart et al. 2010). The continued decline in the biodiversity state indicators implies that even though the policy response was positive, it was not enough to reduce the rate of biodiversity loss. In this paper we ask what determines the value of species conservation at different temporal and spatial scales, and how this affects national conservation effort.

In their discussion of the value of biodiversity, Brock and Xepapadeas identified a number of distinct benefits of biodiversity conservation: an array of ecosystem services that benefit people at different spatial and temporal scales (Brock and Xepapadeas 2003). Some benefits, like the maintenance of the information contained in the global gene pool, are pure public goods offering long-term benefits at a global scale. Others, like the protection of pollinators, the control of soil erosion, or the regulation of productivity in grasslands, are impure public goods offering more immediate benefits at a much more local scale (Perrings and Gadgil 2003). It follows that the optimal level of biodiversity conservation might be expected to differ depending on the spatial and temporal scale at which the problem is analyzed, and depending on which groups are involved in conservation decisions. The structure of property rights established by national law and by the multilateral biodiversity-related agreements¹ have significant implications for the nature and extent of the externalities involved in national conservation decisions, and so for difference in the privately and socially optimal level of conservation (Brock and Xepapadeas 2003). But even if we leave the question of externalities to one side, we would expect to find differences in the socially optimal level of conservation in different countries. Differences in national income, species richness, threats to biodiversity and conservation infrastructure are all likely to be associated with differences in national conservation effort.

Whether or not countries are signatories to the biodiversity-related conventions, and whether or not they have supporting national legislation in place, effort is best measured by the resources committed to conservation. An analysis of the effectiveness of the United States Endangered Species Act (ESA), for example, found that even for this flagship of national conservation legislation, the act of listing a species under the legislation does nothing to enhance species recovery unless accompanied by the commitment of significant public resources (Ferraro et al. 2007). The gap between formal conservation commitments and conservation outcomes is much wider elsewhere. We note that conservation effort is cost effective if it achieves a conservation target at minimum cost, and efficient if it matches the benefits and costs of conservation at the margin.

The evidence of the last four decades is that biodiversity conservation has been especially challenging in the poorest countries. This is partly because the cost of conservation has been displaced on to people for whom conservation is not their first priority. There are certainly instances where conservation efforts have yielded tangible benefits to local populations (see,

¹ Six international conventions are argued to have a primary focus on biodiversity issues: the Convention on Biological Diversity (year of entry into force: 1993), the Convention on Conservation of Migratory Species, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (1975), the International Treaty on Plant Genetic Resources for Food and Agriculture (2004), the Ramsar Convention on Wetlands (1971) and the World Heritage Convention (1972).

for example, [Naidoo et al. 2011](#)). Yet over all very few conservation projects in developing countries have had positive impacts on rural incomes ([Wells and Brandon 1992](#); [IUCN 2002](#); [Tallis et al. 2008](#)). Conservation through the designation of protected areas has often adversely affected the people displaced in the process ([Adams et al. 2004](#)). In the absence of enforcement of the protected areas, this has not only reduced local incomes, but has also compromised the integrity of the conservation effort ([Bruner et al. 2001](#)). While 'Pro-poor' Integrated Conservation and Development Projects (ICDPs) have partly addressed the problem by including compensation for those who have lost access to resources due to the formation of protected areas, they too have had mixed results ([Wells et al. 2004](#); [Tallis et al. 2008](#)).

More recently, attention has focused on the development of direct conservation incentives to landholders in the form of Payments for Ecosystem Services (PES) ([Ferraro and Kiss 2007](#); [Wunder and Wertz-Kanounnikoff 2009](#); [Rands et al. 2010](#)). Both pro-poor ICDPs and PES schemes recognize that the local trade-offs involved in conservation programs need to be addressed directly if local conservation is to be effective. That is, local conservation depends on the existence of mechanisms to translate global willingness to pay for conservation into local incentives. In the absence of such incentives biodiversity conservation is unlikely to have high priority in the poorest countries.

2 The Relation between Income and Biodiversity Conservation

Ever since the Brundtland Commission asserted that poverty and environmental degradation are positively correlated ([World Commission on Environment and Development 1987](#)) the relation between income and biodiversity loss has been closely investigated. The evidence is that there is a persistently high and positive spatial correlation between species richness, biodiversity threats and poverty ([Fisher and Christopher 2007](#); [Sachs et al. 2009](#)).² A substantial empirical literature has investigated the relationship between some measure of biodiversity change and per capita income, using both cross-sectional and time series data. The same approach has been used to investigate a number of indicators of environmental quality. For some indicators, such as fecal coliform in water where the costs are born here and now, the relation has been found to be monotonically decreasing—i.e. environmental quality improves as incomes rise no matter what the level of income. For others, such as CO₂ emissions where the costs are distributed globally and occur largely in the future, it has been found to be monotonically increasing. But for many more indicators, environmental quality has been found to deteriorate as per capita incomes rise at low levels of income, but to improve at higher levels of income—yielding an inverted 'U' shaped relation between income and environmental quality: the so-called Environmental Kuznets Curve ([Cole et al. 1997](#); [Cole 2003](#); [Halkos 2003](#); [Stern 2004](#)).

Technically, for some index of environmental quality to rise (or fall) with income, the marginal rate of substitution between environmental quality and consumption of other goods and services must fall (or rise) more rapidly than the marginal rate of transformation between them as income increases ([Lieb 2002](#); [Chimeli and Braden 2005](#); [Khanna and Plassmann 2007](#)). What this means is that as incomes rise, peoples' willingness to trade off a degraded

² Sachs et al. (2009) argue that policies that tackle the root causes of biodiversity loss and poverty can be complementary—citing the policies to reduce population pressure as an example. However, they acknowledge that there are difficult trade-offs involved. Policies that stimulate income growth by enhancing agricultural productivity also increase pressure on remaining wildlife refugia, and on species that have the status of crop pests or predators.

environment for consumption must fall (or rise) more rapidly than their capacity to maintain environmental quality without sacrificing consumption. Most explanations of the phenomenon have therefore focused on the factors affecting peoples' willingness to trade off consumption and environmental change, and the technical possibilities for the mitigation of environmental damage.

The problem we discuss in this paper is the relation between the spatial and temporal distribution of the costs and benefits of conservation, and the tradeoffs that people are willing to make. Some examples of environmental change impose immediate local costs, others impose costs that affect people far removed in space and time (Arrow et al. 1995). The turning point in national environmental effort tends to vary directly with the opportunity cost of damage mitigation, and inversely with the discounted damage cost of environmental change. The lower the opportunity cost of mitigation, and the higher the discounted damage cost of environmental change, the lower the income level at which environmental change is mitigated (Khanna and Plassmann 2004). Moreover, since the internalization of environmental externalities generally relies on political institutions, and since these tend to be most responsive to local concerns, externalities that involve immediate local costs will tend to be addressed before externalities generating costs that occur in the future at distant locations (Barbier 1997).

The particular problem of biodiversity loss has been approached in three ways in this literature. One uses deforestation as a proxy for biodiversity loss, appealing to the species area relationship to explain the link between changes in forest area and biodiversity loss. The evidence for any well-defined relation between income and biodiversity loss using this metric is extremely weak (Dietz and Adger 2003; Mills and Waite 2009). A second uses the National Biodiversity Risk Assessment Index (NABRAI) developed by Reyers et al (1998). This combines indices of pressure, state and response. Once again, it has failed to find evidence for a statistically significant relation between biodiversity loss and income (Mozumder et al. 2006). A third has focused on the direct measures of threat contained in the IUCN's red list, and finds a statistically significant relation between the natural log of per capita income and the number of threatened species that is linear in the case of plants, 'U' shaped in the case of amphibians, reptiles, fishes and invertebrates, and inverted 'U' shaped in the case of birds (Naidoo and Adamowicz 2001).

We have already observed that the spatial and temporal distribution of the costs of biodiversity change depends on local conditions. The local benefits yielded by biodiversity conservation are generally less sensitive to species richness or endemism than the global benefits. They are also more closely connected to the productivity of managed agricultural or forest systems (Perrings and Gadgil 2003). Biodiversity conservation in agricultural systems, for example, implies protection of enough interspecific and intraspecific diversity to underwrite the productivity of the system. It also involves a number of quite localized services (such as flood control and water supply, waste assimilation, recycling of nutrients, conservation and regeneration of soils and pollination of crops) and disservices (such as predation by insects, animals and birds and zoonotic diseases) (Jackson et al. 2007). The importance of these localized services/disservices to people is a function of their dependence on agriculture, forestry or fisheries. Since the proportion of the population that directly depends on agriculture, forestry and fisheries is generally highest in poor countries, the localized consequences of biodiversity conservation (both positive and negative) are generally expected to be greatest in those countries (Perrings 2007). The value of local conservation efforts accordingly reflects both private and public benefits and costs, and the public benefits and costs may well differ at different scales and at different income levels.

To understand why the rate of biodiversity loss has not slowed, we consider two possible explanations. One is that increasingly levels of stress on biodiversity are, in some sense, 'globally optimal' for very poor countries: that the most urgent and important objective in those countries is not to protect biodiversity, but to improve indicators of wellbeing such as income, infant mortality, education or life expectancy. The other is that increasing levels of stress on biodiversity are not globally optimal for the poorest countries, but that the mechanisms available for the global community to support local conservation efforts in those countries are ineffective. By this explanation the global community would prefer to increase levels of local conservation effort but are unable to do so. Using the theory of conservation implicit in the Hotelling model of non-renewable resource pricing (Hotelling 1931), we identify the conditions in which globally valued biodiversity conservation will be locally optimal. We then estimate the implied model of conservation outcomes. We find that while the value attached by local communities to biodiversity conservation is increasing in income, in poor countries this effect is dominated by the negative impacts of economic growth. At the same time we find that international investment in biodiversity conservation (measured by biodiversity-related development assistance) has no statistically significant impact on conservation in poor countries. Increasing national affluence is positively correlated with national conservation efforts, but it is not a driver of international conservation.

3 Optimal Conservation

Hotelling investigated the conditions in which the owner of a non-renewable resource, such as a mineral deposit, would be indifferent between extracting the resource or leaving it in place. The arbitrage condition in the non-renewable resource case is that the value of the resource in situ is expected to grow at the same rate as the return on alternative assets. The condition extends naturally to the case of renewable resources, in which the growth in value of the resource in situ reflects not just a change in its price, but also a change in its physical magnitude. By the same reasoning, the condition provides us with a general theory of conservation. For any environmental asset, it will be optimal to conserve that asset if and only if the value of the asset in the conserved state is expected to grow at a rate at least equal to the rate of return on the asset when converted to an alternative state.

The generalized Hotelling conservation problem is the following. Define the unconverted land available to country i at time t to be, $L^i(t)$. Its value to society may lie in the fact that it is habitat for a set of species that underpin the production of a range of ecosystem services (Naeem et al. 2009).³ The social problem is to choose the rate at which $L^i(t)$ is converted, $a^i(t)$, so as to maximize an index of wellbeing that depends both on unconverted land, and the flow of benefits that result from converting land into other assets. The problem has the following general form:

$$\text{Max}_{a^i(t)} = \int_{t=0}^{\infty} U^i(a^i(t), L^i(t))e^{-\delta t} dt \quad (1)$$

³ For the provisioning and regulating services the dimension of biodiversity that matters most is diversity within and between functional groups of species. For example, the diversity of traits between rice or corn varieties matters more in agriculture than the genetic distance between grass species in croplands. For particular cultural services, genetic distance may matter more.

subject to

$$dL^i/dt = -a^i(t). \tag{2}$$

We suppose that utility is additive separable in its arguments, and that $a^i(t)$, land converted at time t , is the basis for wealth accumulation from habitat conversion. We denote this by $V^i(t)$:

$$V^i(t) = \int_t^\infty U^i(a^i(\tau), L^i(\tau))e^{-\delta(\tau-t)}d\tau \tag{3}$$

That is, wealth from habitat conversion is equal to the discounted stream of benefits it yields, δ being a discount rate that corresponds to the return on assets created out of habitat conversion.

The solution to this problem requires the following conditions to be satisfied:

$$U_{a^i}^i = \lambda^i(t) \tag{4}$$

$$d\lambda^i/dt = \delta U_{a^i}^i - U_{L^i}^i \tag{5}$$

$$\frac{da^i}{dt} = \frac{U_{a^i a^i}^i}{U_{a^i a^i}^i} \left(\delta - \frac{U^i}{U_{a^i}^i} \right) \tag{6}$$

where $\lambda^i(t)$ is the user cost (the shadow value) of habitat conversion; $U_{a^i}^i, U_{L^i}^i$ are measures of the marginal utility of a change in $a^i(t)$ and $L^i(t)$ respectively; and da^i/dt is the rate of change in land conversion/conservation. Condition (4) requires that the marginal utility of converted habitat should be equal to the user cost of that habitat along an optimal conversion/conservation path. Condition (5) requires that marginal utility of unconverted habitat be equal to the difference between the rate of return on converted habitat and the rate of growth in its user cost. If $U_{L^i}^i = 0$, implying that unconverted habitat has no social value, the condition requires that the rate of growth in the user cost of converted habitat is equal to the marginal return on converted assets, i.e. $d\lambda^i/dt = \delta U_{a^i}^i$.

Equation (6) gives the conditions under which the rate of land conversion will be increasing or decreasing. We make the following observations about this condition. The creation of assets out of habitat conversion (investment) and the production of goods for consumption are both embedded in $U^i(a^i(t))$. While social utility would be expected to bear the usual relation to consumption, its relation to habitat conversion reflects the productivity of asset-generating processes. The first derivative is positive, the second derivative may be positive or negative, depending on whether there are increasing or diminishing returns. Figure 1 illustrates the case where $U^i(a^i(t))$ is logistic, i.e. where $U_{a^i a^i}^i$ is positive at low values of $a^i(t)$ and negative at high values of $a^i(t)$. We would expect the inflection point in such cases to be sensitive to current levels of land conversion.

Away from the steady state, i.e. where $\delta \neq \frac{U^i}{U_{a^i}^i}$, the direction of the rate of change in land conversion will depend both on the difference, $\delta - \frac{U^i}{U_{a^i}^i}$, and on $U_{a^i a^i}^i$. If there are increasing returns, $U_{a^i a^i}^i > 0$, the rate of conversion will be decreasing (increasing) if the discount rate is less than (greater than) the marginal rate of substitution between converted and unconverted habitat. If there are diminishing returns, $U_{a^i a^i}^i < 0$, the rate of conversion will be increasing (decreasing) if the discount rate is less than (greater than) the marginal rate of substitution between converted and unconverted habitat.

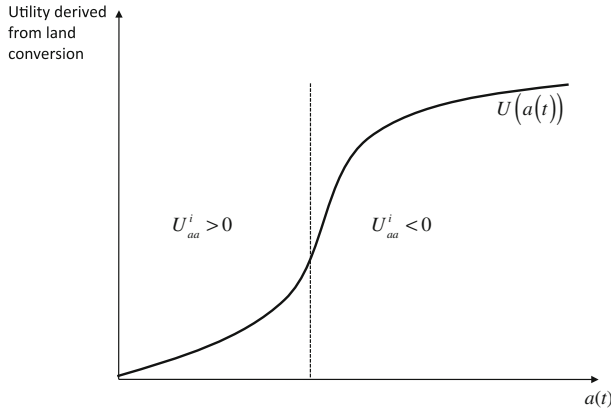


Fig. 1 Utility derived from land conversion. Conversion, $a(t)$, is the source of production, investment and consumption. The utility it yields reflects the indirect effects of scale economies in production, as well as the direct effects of consumption. The figure illustrates the case where scale economies in the early stages of growth imply that the social utility of land conversion increases at an increasing rate

The Hotelling conservation principle implies that conservation will be an optimal strategy only if the rate of growth in the growth in value of the conserved asset is greater than the rate of return on converted assets. Note that the current value Hamiltonian for problem (1),

$$\tilde{H}(a^i(t), L^i(t), \lambda^i(t), t) = U^i(a^i(t), L^i(t)) - \lambda^i(t)a^i(t) \tag{7}$$

measures the (sustainable) flow of benefits yielded along an optimal path. From the Hamilton–Jacobi–Bellman equation we know that this is equal to the interest on accumulated inclusive wealth⁴, $\delta V^i(t)$, where wealth, as defined in Eq. (3), is the discounted stream of future benefits from both conversion and retained habitat (Hartwick 2000). Hotelling conservation requires that

$$\frac{dV^i(t)}{dt} = \delta V^i(t) \tag{8}$$

and hence that

$$\frac{d\tilde{H}(a^i(t), L^i(t), \lambda^i(t), t)}{dt} = \delta^2 V^i(t) \tag{9}$$

which yields

$$-a^i(t)U^i_{a^i} = \delta V^i(t) \tag{10}$$

Using (4)–(7) to obtain an expression for $a^i(t)$, and substituting into (10), we find that

$$U^i(a^i(t), L^i(t)) = 2\delta V^i(t) \tag{11}$$

To go beyond this we need to impose some structure on $U^i(a^i(t), L^i(t))$. We hypothesize that $U^i(a^i(t))$ is quadratic in income, $Y^i(t)$, and that $U^i(L^i(t))$ depends upon both the species conserved through the $L^i(t)$, $S^i(L^i(t))$, and on the international transfers associated with $L^i(t)$, $B(L^i(t))$. Specifically, we suppose that $U^i(a^i(t)) = a^i(t)(Y^i(t) + \frac{1}{2}Y^i(t)^2)$ and that

⁴ Inclusive wealth is the term used for the sum of produced, natural and human capital (Dasgupta 2001).

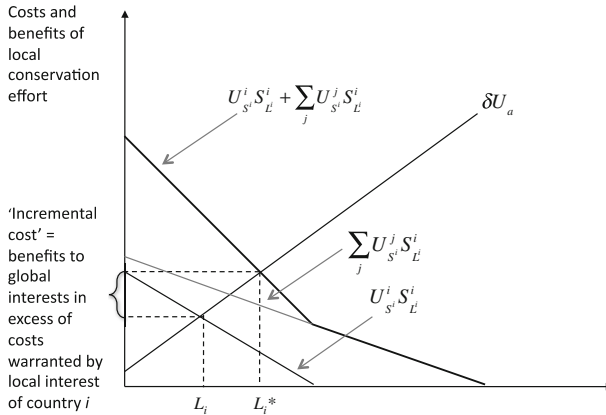


Fig. 2 Local and global benefits of conservation

$U^i(L^i(t)) = S^i(L^i(t)) + L^i(t)dB^i(t)$. Using these functional forms, the arbitrage condition provides us with an equation to be estimated:

$$-S^i(L^i(t)) = a^i(t) \left(Y^i(t) + \frac{1}{2} Y^i(t)^2 \right) + L^i(t)dB^i(t) - \lambda^i(t)a^i(t) \tag{12}$$

$B^i(L^i(t))$ in (12) represents transfers from other countries. We assume a ‘global’ social utility function of the form

$$U^{i,-i}(a^i(t), L^i(t)) = U^i(a^i(t), L^i(t)) + \sum_j U^j(a^i(t), L^i(t)) \tag{13}$$

in which U^i denotes utility of the i th country yielded by conservation in that country, and $\sum_j U^j$ denotes the utility gained in the rest of the world from conservation in the i th country. If the interest of the j th country in conservation activity in country i is

$$U^j(t) = U^j(L^i(t)) \tag{14}$$

when unconverted habitat is at $L^i(t)$, then the marginal social utility of a change in unconverted habitat in country i is the sum of the marginal social utility of conservation to that country and the marginal social utility of conservation to the rest of the world.

$$U_{L^i}^{i,-i} = U_{S^i}^i S_{L^i}^i + \sum_j U_{L^i}^j \tag{15}$$

The greater is the value of local conservation to the rest of the world, the greater the globally optimal level of local conservation—illustrated in Fig. 2.

From (5), the rate of change in the user cost of converted habitat, $\lambda^i(t)$, will be positive only if $U_{L^i}^i < \delta U_{a^i}^i$. It captures the net effect of benefits and costs that differ depending on the temporal and spatial scale at which they are evaluated. The marginal utility of unconverted habitat may be negative for some people and positive for others. For example, local conservation may increase local crop predation so harming farmers, but may simultaneously benefit the global community through the protection of the global gene pool. Where there is an array of benefits and costs associated with local conservation, the marginal value that drives conservation decisions will depend on whether the international beneficiaries of local

Table 1 Threatened mammal, bird and plant species 2007, descriptive statistics

	Mammals	Birds	Plants
Mean	22.19417	22.44660	92.30097
Median	15.00000	13.00000	19.00000
Maximum	146.0000	122.0000	1838.000
Minimum	1.000000	1.000000	1.000000
SD	21.54296	24.71751	209.9056
Skewness	2.729766	2.069702	6.014394
Kurtosis	13.37866	7.161705	48.22320
Jarque–Bera	590.2029	147.8670	9398.019
Probability	0.000000	0.000000	0.000000
Observations	103	103	103

conservation express a willingness to pay for local conservation. The term $B^i(t)$ on the right hand side of (12) is the direct benefit to the i th country of international willingness to pay for local conservation efforts.

4 Data and Methods

Our proxy for the ‘national’ utility of the impact of land conversion on threatened species in the i th country is the number of species in that country that are recorded in the IUCN’s red list of endangered species for three taxonomic groups: mammals, birds and plants, $S^i(t)$. The red list can be thought about as an index of the stress acknowledged as being caused by land conversion. It is not yet a good measure of the change in acknowledged stress, since it has yet to generate a consistent time series of threat indicators. Because of revisions in the basis on which estimates are made it is not currently possible to calculate a rate of change in the number of threatened species. Estimates for different years are not comparable. The number of threatened bird and mammal species recorded in the red list is, however, correlated with species richness and with single country endemic species. These, along with anthropogenic stress, are the principle elements in the designation of ‘biodiversity hotspots’ (Caro 2010). Data on known species in these groups derive from the United Nations Environment Programme World Conservation Monitoring Centre UNEP-WCMC Species Database.⁵ Data on threatened species in these groups derive from International Union for Conservation of Nature and Natural Resources, 2002 Red List of Threatened Species, IUCN, Gland, Switzerland.⁶ Table 1 presents the descriptive statistics for each taxonomic group.

As our proxy for the international willingness to pay for national conservation efforts, $B^i(t)$, we used the change in biodiversity-related overseas development assistance (ODA). Specifically, we used the incremental change in biodiversity-related development aid over the period 2004–2007. The data for this derive from the OECD. ODA includes flows of official financing aimed at promoting the welfare of developing countries and which are concessional

⁵ <http://www.unep-wcmc.org>.

⁶ <http://www.redlist.org/info/tables>.

(having a grant element >25%). We consider disbursements by bilateral donors. Biodiversity-related ODA is concessional finance that targets at least one of the three objectives of the Convention on Biological Diversity: the conservation of biodiversity, sustainable use of its components (ecosystems, species or genetic resources), or fair and equitable sharing of the benefits of genetic resources.

Our measure of income, $Y^i(t)$, is per capita gross national income (GNI) in international prices (i.e. on a purchasing power parity basis). The measure is not perfect. Like GDP, it is based on market transactions only, and so excludes non-market income, but unlike GDP it includes the impact of remittances and other cross border flows. This makes it particularly appropriate for cross-country comparisons involving international income transfers. Population pressure is accounted for by a measure of population density, $P^i(t)$. Elevated population density and growth have been shown to be common drivers of the anthropogenic stress that characterizes biodiversity hotspots (Cincotta et al. 2000). Our measure of the extent of habitat conserved for endangered species, $L^i(t)$, is the percentage of land under some form of protection. Protected areas comprise totally or partially protected areas of at least 1,000 ha that are designated by national authorities as scientific reserves with limited public access, national parks, natural monuments, nature reserves or wildlife sanctuaries, and protected landscapes. The data for GNI, population and protected areas all derive from the World Resources Institute online database.⁷

The effect of latitude and climatic type on species richness is controlled for by including a dummy variable capturing the Koppen–Geiger equatorial climates, G , (Kottek et al. 2006). While bioclimatic envelope models do not provide a complete explanation for species distribution in that they omit abiotic factors and species interactions, at large scales they do perform satisfactorily (Pearson and Dawson 2003; Willis and Bhagwat 2009).

Our proxy for the user cost of conservation, $C(t) \doteq \lambda^i(t)a^i(t)$, is a measure of the change in the opportunity cost of habitat protection: Δ GNI per hectare of land outside of protected areas multiplied by the area of protected land. This is a measure of local willingness to pay for local conservation effort. Specifically, we used the incremental change in GNI over the period 2004–2007 per hectare of non-protected land. Our sample consists of the 103 developed and developing countries for which there exist observations on these factors.⁸ Area, population density and protected areas were calculated from data at the World Resources Institute's on-line database.⁹

We estimated three sets of models, each set comprising models for the three taxonomic groups evaluated. The first comprised a set of linear models on log–log transformed data using ordinary least squares (OLS). The estimated equations corresponding to (12) were of the form:

⁷ http://earthtrends.wri.org/searchable_db/index.php?theme=7. The database is no longer being maintained.

⁸ Algeria, Angola, Argentina, Armenia, Australia, Bangladesh, Benin, Bolivia, Bosnia and Herz., Brazil, Burkina Faso, Burundi, Cambodia, Cameroon, Canada, Chad, Chile, China, Colombia, Congo Rep., Costa Rica, Cote d'Ivoire, Croatia, Cuba, Denmark, Dominican Rep., Ecuador, Egypt, El Salvador, Eritrea, Ethiopia, Finland, France, Gabon, Gambia, Germany, Ghana, Greece, Guatemala, Guinea, Guinea-Bissau, Honduras, Hungary, India, Indonesia, Iran, Ireland, Italy, Jamaica, Japan, Kazakhstan, Kenya, Kyrgyzstan, Lao, Lesotho, Madagascar, Malawi, Malaysia, Mali, Mauritius, Mexico, Morocco, Mozambique, Namibia, Nepal, New Zealand, Nicaragua, Niger, Nigeria, Norway, Oman, Pakistan, Panama, Papua New Guinea, Paraguay, Peru, Philippines, Poland, Portugal, Romania, Russian Federation, Rwanda, Saudi Arabia, Senegal, Sierra Leone, Singapore, Slovakia, South Africa, Spain, Sri Lanka, Sudan, Sweden, Switzerland, Tajikistan, Tanzania United Rep, Thailand, Togo, Trinidad and Tobago, Turkey, Turkmenistan, Uganda, Ukraine, United Kingdom, United States, Uruguay, Uzbekistan, Venezuela, Vietnam, Yemen Rep., Zambia.

⁹ http://earthtrends.wri.org/searchable_db/index.php?theme=7.

$$\ln S_k^i(t) = \beta_0 + \beta_1 \ln Y^i(t) + \beta_2 \ln Y^i(t)^2 + \beta_3 \ln L^i(t) + \beta_4 (\ln C^i(t) - \ln C^i(0)) + \beta_5 \left(\sum_j \ln B^{ji}(t) - \sum_j \ln B^{ji}(0) \right) + \beta_6 \ln P^i(t) + \beta_7 G^i + \varepsilon \quad (16)$$

where $S_k^i(t)$ is the number of threatened species in taxonomic group k in country i at the end of the reference period; $Y^i(t)$ is per capita gross national income; $H^i(t)$ is protected areas; $(C^i(t) - C^i(0))$ is the change in the local opportunity cost of habitat conservation over the reference period, a function of growth in per capita gross national income; $(\sum_j B^{ji}(t) - \sum_j B^{ji}(0))$ is the change in biodiversity-related development assistance from the rest of the world over the reference period; $P^i(t)$ is population density; and G is climate, a fixed effect. By specifying $S_k^i(t)$ to be a non-linear function of income, we implicitly test the hypothesis that the marginal benefits of conservation are sensitive to the level of income.

A second model was estimated because of the concern that the number of endangered species may be simultaneously determined with the area under protection, and hence that the OLS estimates may be susceptible to endogeneity.¹⁰ To address this possibility we estimated a set of Two Stage Least Squares models, in which the i th equation was the form:

$$\ln S_k^i(t) = \beta_0 + \beta_1 \ln Y^i(t) + \beta_2 \ln Y^i(t)^2 + \beta_3 \ln L^i(S_{-k}^i(t), F^i(t), t) + \beta_4 (\ln C^i(t) - \ln C^i(0)) + \beta_5 \left(\sum_j \ln B^{ji}(t) - \sum_j \ln B^{ji}(0) \right) + \beta_6 \ln P^i(t) + \beta_7 G^i + \varepsilon \quad (17)$$

All variables are as described for (16), except that $S_{-k}^i(t)$ in the first stage estimation of $L^i(S_{-k}^i(t), F^i(t), t)$ denotes the number of threatened species in all taxonomic groups other than group k , and $F^i(t)$ is a measure of the responsiveness of government to local pressure, an index of democracy. The data on democracy derive from the Polity IV dataset.¹¹

A third set of models was estimated because of the asymmetric distribution of the response variable and its potential non-linearity in relation to non-income variables (Table 1). Specifically, we found large differences between the mean and the median, and evidence of both skewness and kurtosis. In fact kurtosis >3, indicating long fat tails at high levels of threat and short thin tails at low levels of threat—a leptokurtic distribution. In all cases, tests of normality were rejected (using the P values of the Anderson–Darling test). Since this raises the possibility of biased estimates, we also estimated a set of conditional quantile regression models (Koenker and Basset 1978; Koenker 2005) for each taxonomic group. We assumed a linear specification for the conditional quantile of the independent variable S_i , given the values of the matrix X . The τ th quantile takes the form

$$Q(\tau|x^i\beta(\tau)) = x^i\beta(\tau), \text{ with } \beta(\tau) = \arg \min_{\beta(\tau)} \left\{ \sum_i \rho_\tau \left(S^i - x^i\beta(\tau) \right) \right\}. \quad (18)$$

Using the Kernel density estimator due to Jones (1992) and Bushinsky (1995) we estimated simultaneous-quantile regression models for the 10th, 20th, . . . , 90th quantiles, bootstrapped

¹⁰ There is also a possibility that international conservation aid and the number of endangered species are determined simultaneously. However, tests of the endogeneity of international conservation aid using the Durbin–Wu–Hausman test rejected the null hypothesis that the variable is exogenous in all three specifications.

¹¹ <http://www.systemicpeace.org/polity/polity4.htm>.

with 1,000 replicates. This allowed us to compare estimates over the whole distribution of threat status with the OLS estimates of the mean effect.

5 Results

The results of the OLS model are reported in Table 2, along with the results of diagnostic tests for heteroskedasticity (White), normality (Jarque–Bera), and specification (polynomial Reset), none of which reveal problems with the results. The first result to note concerns the relation between threatened species and income. Once we control for climate, population density (pressure), and the proportion of land area under protection, the relation between per capita income and species under threat is quadratic for all taxa. This differs from findings by Naidoo and Adamowicz (2001), although we remark that the threatened species data used in their study were different from (and not comparable to) the data used here. The turning

Table 2 OLS regression analysis results

	Log mammals	Log birds	Log plants
(Constant)	−12.7816 [0.0000]	−24.0217 [0.0000]	−35.1497 [0.0000]
<i>G</i> (climate)	0.4446 [0.0006]	0.6086 [0.0003]	1.7798 [0.0000]
<i>L</i> (log protected areas)	0.5196 [0.0000]	0.5089 [0.0000]	0.8759 [0.0000]
λa (log opport. cost of <i>L</i>)	−0.4425 [0.0000]	−0.4220 [0.0000]	−0.4045 [0.0003]
<i>P</i> (log population density)	0.3027 [0.0004]	0.2636 [0.0172]	0.6650 [0.0028]
<i>Y</i> (log GNI per capita)	2.5142 [0.0000]	5.1375 [0.0000]	8.0152 [0.0000]
Y^2 (log GNI per capita ²)	−0.1287 [0.0002]	−0.2750 [0.0000]	−0.4545 [0.0000]
<i>B</i> (log biodiversity aid)	0.0474 [0.4959]	−0.0379 [0.6033]	0.1448 [0.2067]
R ² -adj	0.61	0.49	0.45
White	35.3540 [0.3576]	34.4543 [0.3981]	9.3839 [0.2263]
Jarque–Bera	1.7204 [0.4231]	2.3896 [0.3028]	0.2121 [0.8994]
RESET (quadratic)	0.7162 [0.3996]	1.5693 [0.2134]	3.3993 [0.0684]
RESET (cubic)	0.8121 [0.4471]	0.7772 [0.4626]	1.9328 [0.1505]
Turning point	17455	11388	6750

P values in brackets. Standard-errors used are White Heteroskedasticity-consistent

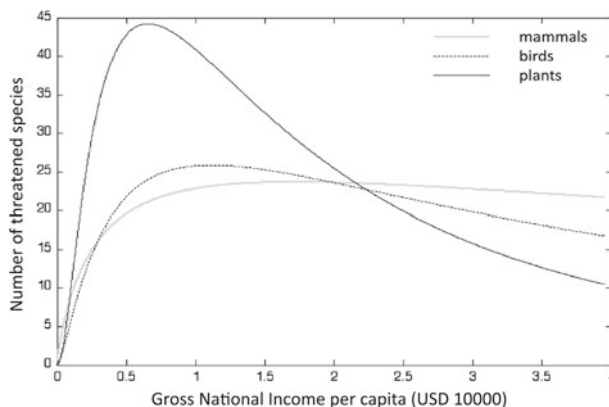


Fig. 3 Threatened species and per capita income. There is a quadratic relation between threatened species and GNI for all taxonomic groups, but both the turning point and the strength of the effect of income growth differ between taxonomic groups

points differ between taxonomic groups but all models provide a reasonable fit to the data and satisfy a range of diagnostic tests. If all countries in the sample are ranked by per capita income, the turning points occur at around the 74th percentile of countries in the sample for mammals, at around the 67th percentile for plants, and around the 52nd percentile for birds. The direct implication of this is that among low-income countries, income growth is expected to have a negative impact on biodiversity, and that this effect is significantly more persistent for mammals than for either birds or plants.

For plants, while the negative impact of income growth in poor countries is sharply increasing, the turning point occurs at a relatively low level of per capita income, USD7873 (58th percentile), and thereafter improves rapidly. For mammals and birds, the negative impact of income growth among poor countries increases less rapidly but persists over a much wider range of incomes. The differences between the taxonomic groups are illustrated in Fig. 3, which graphs the relation between threatened species in each group and per capita gross national income.

The second result to note concerns the effect of our proxies for the local commitment to conservation in each country (the growth in the opportunity cost of protected areas). There is a positive and significant relation between the proportion of the country under protected status and the number of species under threat, and this holds for all taxa. At the same time there is a negative and significant relation between growth in the opportunity cost of protected areas and the number of species under threat. This also holds for all taxa. Both findings are consistent with the observed positive policy responses to biodiversity threats (Butchart et al. 2010). We note, however, that the negative effect of the opportunity cost of protected areas is much weaker than the positive effect of income growth. While the formation of protected areas might slow the rate of increase in the number of threatened species in low-income countries, it is not enough to reverse it.

The third result to note concerns our proxy for international willingness to pay for the local conservation of threatened biodiversity—international biodiversity-related development assistance. This turns out to have no significant effect on threatened species for any taxonomic group. Biodiversity related development assistance is neither driven by nor drives the number of species under threat. We return to this result later.

Table 3 Two Stage Least Squares analysis results

	Log mammals	Log birds	Log plants
(Constant)	-15.60486 [0.0000]	-27.10984 [0.0000]	-39.2388 [0.0000]
G (climate)	0.2921 [0.1555]	0.4418 [0.0761]	1.5590 [0.0010]
L (log protected areas)	1.1467 [0.0000]	1.1949 [0.0000]	1.7841 [0.0000]
λa (log oport. cost of L)	-0.6442 [0.0000]	-0.6427 [0.0000]	-0.6968 [0.0000]
P (log population density)	0.8714 [0.0000]	0.8857 [0.0002]	1.4887 [0.0001]
Y (log GNI per capita)	2.9063 [0.0007]	5.5665 [0.0000]	8.5831 [0.0000]
Y^2 (log GNI per capita ²)	-0.1375 [0.0052]	-0.2846 [0.0000]	-0.4672 [0.0000]
B (log biodiversity aid)	-0.1652 [0.1950]	-0.2705 [0.0193]	-0.1631 [0.3931]
R^2 -adj	0.25	0.20	0.30
Durbin-Wu-Hausman	11.96 [0.0005]	16.61 [0.0000]	9.94 [0.016]
C test (other taxa)	2.55 [0.2795]	0.2939 [0.8633]	1.01 [0.6050]
Cragg-Donald F stat	12.70 > 9.08 [10%]	21.63 > 13.91 [5%]	20.80 > 13.91 [5%]
White	50.8117 [0.0245]	48.4787 [0.0402]	47.6178 [0.0479]
Jarque-Bera	3.9298 [0.1402]	0.2470 [0.8838]	1.5770 [0.4545]
RESET (quadratic)	0.5765 [0.4496]	0.0439 [0.8345]	0.2382 [0.6266]
RESET (cubic)	0.1948 [0.8233]	0.0410 [0.9598]	0.2355 [0.7907]
Turning point	38997	17666	9757

P values in brackets. Standard-errors used are White Heteroskedasticity-consistent

The results of the simultaneous equation model estimated by Two Stage Least Squares are reported in Table 3. The size of protected areas in this model was instrumented on the number of threatened species belonging to other taxonomic groups, together with the level of democracy in each country. We hypothesize that the numbers of threatened species in any one taxonomic group influences the number of threatened species in other taxonomic groups through the effect they have on the size of the area committed to species protection, and that this effect will be greater the more responsive (democratic) the government is. This is supported by the instrument orthogonality C test for other taxonomic groups, reported in

Table 3. We found the null hypothesis—that the set of instruments is exogenous—was not rejected in all specifications. It is also intuitive that democratic status should not directly affect the number of endangered species. The Cragg–Donald F statistic showed that the set of instruments was not weak at conventional significance levels in all three specifications.

The two things to note about the results in Table 3 is that the qualitative features of the OLS estimates are all unchanged. The effect of protected areas is increased in the Two Stage Least Squares models, but the overall goodness of fit of the models declines. So while they offer some evidence of endogeneity, they do not indicate that this significantly compromises the OLS estimates.

The third set of models was estimated because the descriptive statistics indicated both skewness and kurtosis—significant mass in the tails at high threat levels and very low mass at low threat levels (Table 1). Estimation of these quantile regression models enabled us to test the sensitivity of the OLS results to the degree of threat facing different taxonomic groups. The results are summarized in Tables 4, 5 and Fig. 4a–c. Table 4 reports the Non-parametric quantile regression results, and Table 5 the corresponding diagnostics.

Figure 4a–c reports the estimated coefficients on each of the Independent variables for the 10th, . . . , 90th quantiles. The figure reports coefficients on the independent variables in the conditional quantile regression models for all taxonomic groups. Quantile estimates and 95% confidence interval (grey band) are superimposed on the OLS estimates and 95% confidence interval (black lines).

Consider the relation between threatened species and GNI. For mammals, the relation between the number of species under threat and GNI is consistent across risk levels. The estimated quantile coefficients track the OLS coefficient well, and all lie within the 95% confidence interval for the OLS estimate. For birds and plants, however, the relation looks different at low levels of threat, than it does at high levels of threat.

For birds, the adverse impact of income growth on threatened species is much stronger at low levels of threat than at high levels of threat, while the positive impacts of income are much weaker. For plants the difference is more extreme, and in the opposite direction. The adverse impact of income growth on threatened species is considerably weaker at low levels of threat than at high levels of threat (and may not even be negative), while the positive impacts of income are much stronger.

For the relation between threatened species and growth in biodiversity-related development assistance, our proxy for the growth in international willingness to pay for domestic conservation, the OLS and quantile results are consistent, but the results are not significant either for the OLS or for any of the quantile regression models.

The relation between threatened species and our proxies for the growth in national willingness to pay for conservation, the growth in the local opportunity cost of maintaining protected areas, is much less consistent. The estimates of the effect of these measures on the conditional mean number of threatened mammals significantly misrepresents their effect on the lower and upper tails of the distribution of threatened mammals. The effect of the growth in opportunity cost of protected areas is negatively related to the number of threatened mammals for all quantiles, but that effect is very much stronger at low levels of threat, and much weaker at high levels of threat. The OLS estimates are, however, more reasonable proxies for the quantile estimates for the other two taxonomic groups.

Table 4 Non-parametric quantile regression results

Variables	Quantiles	Log mammals	Log birds	Log plants
(Constant)	10th	-12.8805 [0.0001]	-34.75148 [0.000]	-11.2647 [0.522]
	50th	-14.31828 [0.0000]	-21.03334 [0.001]	-36.00027 [0.0000]
	90th	-10.76856 [0.004]	-19.26214 [0.0000]	-31.93409 [0.010]
<i>G</i> (climate)	10th	.3684734 [0.024]	-.02653 [0.944]	1.51767 [0.023]
	50th	.4512324 [0.007]	.7600864 [0.001]	1.414105 [0.034]
	90th	.8095906 [0.010]	1.112992 [0.0000]	2.45618 [0.000]
<i>L</i> (log protected areas)	10th	.6375413 [0.000]	.5358798 [0.003]	.5944576 [0.043]
	50th	.5584006 [0.000]	.5171211 [0.000]	1.030499 [0.001]
	90th	.3606271 [0.055]	.4642601 [0.000]	.3881951 [0.468]
λa (log oport. cost of <i>L</i>)	10th	-.5355577 [0.0000]	-.3841981 [0.006]	-.3262162 [0.142]
	50th	-.4396711 [0.0000]	-.4214772 [0.0000]	-.5492949 [0.001]
	90th	-.3017391 [0.0000]	-.3369366 [0.0000]	-.3314465 [0.074]
<i>P</i> (log population density)	10th	.3574645 [0.000]	.3917975 [0.075]	.3927497 [0.234]
	50th	.4199113 [0.004]	.2244283 [0.171]	.8269944 [0.016]
	90th	.1689962 [0.399]	.2180607 [0.046]	.190317 [0.720]
<i>Y</i> (log GNI per capita)	10th	2.10455 [0.012]	7.569406 [0.000]	2.059128 [0.605]
	50th	2.871711 [0.002]	4.585486 [0.003]	7.862376 [0.000]
	90th	2.44603 [0.004]	4.38539 [0.000]	7.386899 [0.008]
Y^2 (log GNI per capita ²)	10th	-.0936182 [0.044]	-.4145127 [0.000]	-.117117 [0.604]
	50th	-.1510963 [0.005]	-.2491508 [0.006]	-.438199 [0.000]
	90th	-.1272563 [0.010]	-.233675 [0.000]	-.4057924 [0.011]

Table 4 Continued

<i>B</i> (log biodiversity aid)	10th	-.0526909 [0.611]	-.0276123 [0.881]	.339639 [0.174]
	50th	.0277295 [0.824]	-.0135547 [0.921]	.0585939 [0.755]
	90th	.0604733 [0.622]	-.0809924 [0.507]	-.1316665 [0.602]

Table 5 Non-parametric quantile regression diagnostics

Test/specification	Mammals	Birds	Plants
Koenker–Bassett	30.46 [0.0066]	28.14 [0.0137]	20.81 [0.1066]
Newey and Powell	9.10 [0.3340]	10.60 [0.2256]	6.86 [0.5520]
RESET (quadratic)	0.18 [0.6755]	0.039 [0.8433]	0.72 [0.3969]
RESET (cubic)	0.47 [0.7939]	0.176 [0.9159]	1.05 [0.5921]
Pseudo R ² (0.5)	0.3736	0.3132	0.3456

6 Discussion

The question we pose in the title to this paper—“Who cares about biodiversity?”—is a question about the global value of conservation versus the local value of conversion at particular locations. The theory of conservation implicit in the Hotelling principle implies that if the mechanisms exist to translate global willingness to pay into local incentives, then conservation should be the preferred option wherever the global value of conserved habitat is growing faster than the local rate of return on converted assets. Since biodiversity conservation in a particular country yields distinct benefits to people both in that country and elsewhere, we identify two main measures of the value of conservation. One is indirect. It is the growth in the opportunity cost of maintaining land in protected areas. The second is more direct. It is the growth in the value of international biodiversity-related development assistance. This is a measure of the change in the value of local conservation to other countries.

Our findings are striking in three respects. First, the quadratic relation between threatened species and GNI per capita that exists for all taxonomic groups indicates that, over some income ranges and some levels of biodiversity, conversion appears to be socially efficient. The tradeoff occurs over the widest range of per capita incomes in the case of mammals, and over the smallest range of per capita incomes in the case of plants. This may reflect differences in adaptability between ‘mobile’ and ‘immobile’ species, although we have not tested for this. The social efficiency of habitat conversion at low levels of income should not be surprising, but it has not been shown in earlier studies. The mechanisms are already familiar, and are similar in all cases. The activities responsible for income growth in the poorest

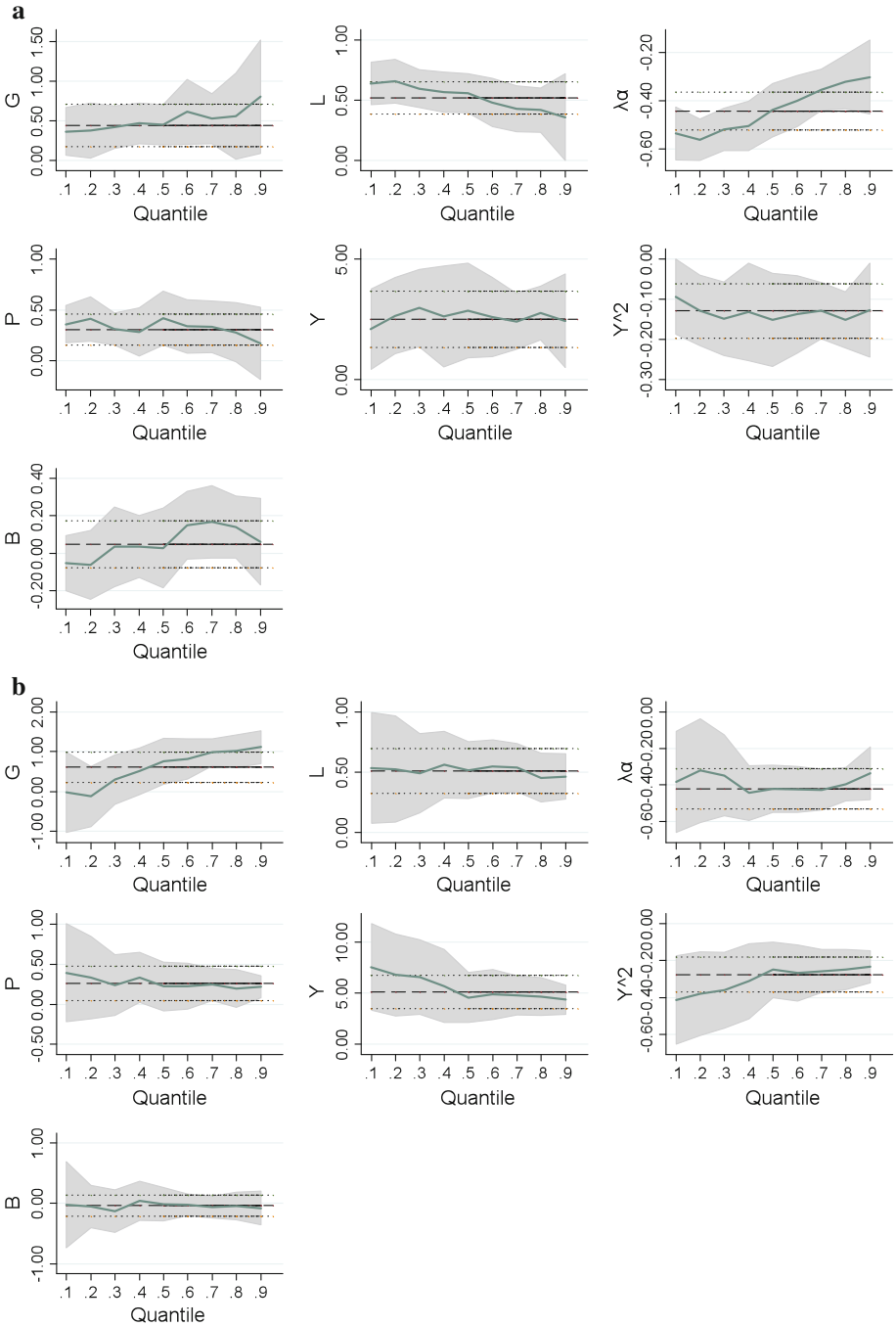


Fig. 4 **a** Mammals: quantile regression coefficients, **b** birds: quantile regression coefficients, **c** plants: quantile regression coefficients G climate, L log protected areas, $\lambda\alpha$ log opportunity cost of L , P log population density, Y log GNI per capita, Y^2 log GNI per capita squared, B log change in biodiversity related development assistance

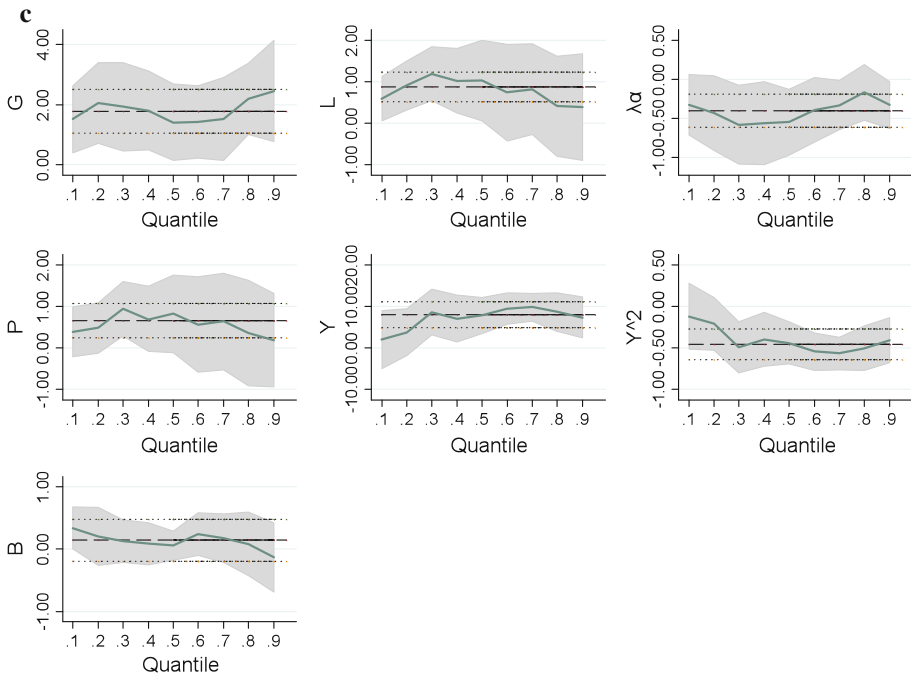


Fig. 4 continued

countries are also responsible for increasing stress on terrestrial species. These involve conversion of existing habitat to agriculture; the direct harvesting of many wild living resources; the diversion of water for human consumption; and the increase in the pollution burden on terrestrial systems and the introduction of novel pests and pathogens (Millennium Ecosystem Assessment 2005; World Bank 2006; Jones et al. 2008).

Second, there is a significant negative relation between growth in the local opportunity cost of protected areas and our measure of conservation outcomes. The number of threatened species declines as the opportunity cost of protected areas increases. This is consistent with the notion that the value attaching to biodiversity conservation is increasing in incomes. For mammals, we have already observed that the relation strengthens with the number of species under threat. However, we have also noted that the positive effect of this is dominated over certain income ranges by the negative impacts of income growth. So while there is evidence that people's willingness to carry the cost of habitat protection is increasing in income, in poorer countries that effect is swamped by the negative effects of the activities that lead to income growth.

We illustrate this in Fig. 5, which shows the net impact of the two effects of income growth. Each curve is a measure of the difference between the positive impact of income growth on willingness to commit resources to protected areas and the negative impact of income growth on the various biodiversity stressors. As in Fig. 3 there is a significant difference between the species groups, with plants being associated with a much stronger positive impact of income growth than birds or mammals.

Third, the commitment of international funds for local conservation activities has no significant effect on threatened species. This is more surprising. The main international mechanism

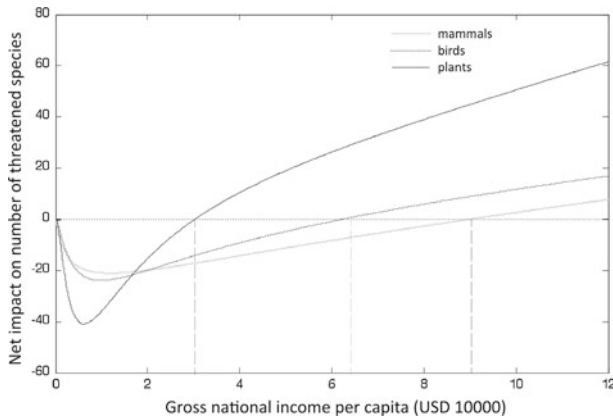


Fig. 5 Net impact of income growth on threatened species. The point at which income growth is associated with a net improvement in the number of threatened species differs between taxonomic groups. Although the negative impact of income growth in low income countries is stronger for plants than for birds and mammals, the income growth required before the net effect on threatened species is positive (i.e. the number of threatened species falls) is much lower

for making payments for biodiversity-related development assistance, the Global Environment Facility, was established precisely to cover the global interest in local conservation. The concept of incremental cost, which in principle determines payments made by the GEF, is a measure of the difference between the cost a country would be prepared to bear in the provision of an environmental public good and the cost of meeting global demand for the same public good (Pearce 2003, 2005). The fact that the GEF is widely regarded by scientists as underfunded is an indication that donor countries have a lower estimate of the incremental cost of local conservation than the scientific community.

It is possible (a) that the way disbursements are made does not reflect that principle, (b) that disbursements made for biodiversity protection are ineffective, or (c) that the measure itself is weak. We were, however, unable to find any measure of international biodiversity-related development assistance that bears a statistically significant relation to the number of threatened species. We infer that international willingness to pay for biodiversity conservation as measured by biodiversity-related ODA is uncorrelated to the perceived threat to biodiversity. This is consistent with the results of studies of the effectiveness of ODA-financed conservation projects discussed earlier. If the willingness of other countries to pay for local conservation effort does not increase with the local level of threat, then the fate of local biodiversity depends on the rate of change in that country's own willingness to pay for conservation relative to the local return on habitat conversion. This would then imply that biodiversity loss in those countries is globally optimal, in the sense that the international externalities of local habitat loss are not sufficient to change local conservation decisions. The second of the Convention on Biological Diversity's Aichi targets requires that 'biodiversity values have been integrated into national and local development and poverty reduction strategies and planning processes' (Convention on Biological Diversity 2010). However, this would only change conservation outcomes in poor countries if conservation conferred recognized benefits on other countries. One of the potential advantages of the increasing focus on ecosystem services is that it will clarify the benefits of conservation to users at different geographical scales (Perrings et al. 2011). Indeed, the introduction of systems of payments for ecosystem services such as the Reducing Emissions from Deforestation

and Forest Degradation (REDD) scheme may generate additional resources for biodiversity conservation by expanding biodiversity-related ODA (Dutschke and Angelsen 2008; Blom et al. 2010).

The existence of a turning point for all taxa implies that there is a level of per capita income beyond which the number of threatened species has been observed to decline. We cannot rule out that some of this reflects historic biodiversity loss in higher income countries, but it has been understood for some time that it also reflects the existence of legal, institutional and social conditions in higher income countries that favor conservation. The implication is that growth oriented strategies may yield conservation benefits in the long run, but that this is not to be expected in countries where poverty rates are currently high. This said, we do not have evidence that the problem lies in institutional barriers to biodiversity-related development assistance. Most of the evidence suggests that willingness to commit resources for development assistance of all categories is declining, not increasing. Our findings are consistent with this. To the question “Who cares about biodiversity?” the answer at present is that countries care about the biodiversity within their national borders, but only when development priorities permit, and only when it becomes scarce enough that its value grows more rapidly than the return on alternative assets. There is little evidence that countries yet care sufficiently about biodiversity to affect conservation outcomes in the places where it is most threatened. We note that this analysis covers state expenditures only, and not civil society commitments through non-governmental organizations. Individual members of many societies do contribute to international conservation in that way (see, for example, Brockington and Scholfield 2010), but our findings suggest that their elected representatives do not.

Acknowledgements We thank the editor and three referees for helpful comments

References

- Adams WM, Aveling R, Brockington D, Dickson B, Elliott J, Hutton J, Roe D, Vira B, Wolmer W (2004) Biodiversity conservation and the eradication of poverty. *Science* 306:1146–1149
- Arrow K, Bolin B, Costanza R, Dasgupta P, Folke C, Holling CS, Jansson B-O, Levin S, Maler K-G, Perrings C, Pimentel D (1995) Economic growth, carrying capacity and the environment. *Science* 268:520–521
- Barbier EB (1997) Introduction to the environmental Kuznets curve special issue. *Environ Dev Econ* 2:369–382
- Blom B, Sunderland T, Murdiyasar D (2010) Getting REDD to work locally: lessons learned from integrated conservation and development projects. *Environ Sci Policy* 13:164–172
- Brock WA, Xepapadeas A (2003) Valuing biodiversity from an economic perspective: a unified economic, ecological, and genetic approach. *Am Econ Rev* 93:1597–1614
- Brockington D, Scholfield K (2010) Expenditure by conservation nongovernmental organizations in sub-Saharan Africa. *Conserv Lett* 3:106–113
- Bruner AG, Gullison RE, Rice RE, da Fonseca GAB (2001) Effectiveness of parks in protecting tropical biodiversity. *Science* 291:125–128
- Buchinsky M (1995) Estimating the asymptotic covariance matrix for quantile regression models: a Monte Carlo study. *J Econ* 68:303–338
- Butchart S, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque J-F, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Morcillo MH, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vie J-C, Watson R (2010) Global biodiversity: indicators of recent declines. *Science* 328:1164–1168
- Caro TM (2010) *Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species*. Island Press, Washington, DC

- Chimeli AB, Braden JB (2005) Total factor productivity and the environmental Kuznets curve. *J Environ Econ Manag* 49:366–380
- Cincotta RP, Wisniewski J, Engelman R (2000) Human population in the biodiversity hotspots. *Nature* 404:990–992
- Cole MA (2003) Environmental optimists, environmental pessimists and the real state of the world—an article examining the skeptical environmentalist: measuring the real state of the world by Bjorn Lomborg*. *Econ J* 113:F362–F380
- Cole MA, Rayner AJ, Bates JM (1997) The environmental Kuznets curve: an empirical analysis. *Environ Dev Econ* 2:401–416
- Convention on Biological Diversity (2010) Revised and updated strategic plan: technical rationale and suggested milestones and indicators. In: Conference of the parties to the convention on biological diversity, tenth meeting, Nagoya, Japan, 18–29 October. CBD, Montreal
- Dasgupta P (2001) Human well-being and the natural environment. Oxford University Press, Oxford
- Dietz S, Adger N (2003) Economic growth, biodiversity loss and conservation effort. *J Environ Manag* 68:23–35
- Dutschke M, Angelsen A (2008) How do we ensure permanence and assign liability?. In: Angelsen A (ed) *Moving ahead with REDD*. CIFOR, Bogor
- Ferraro P, Kiss A (2007) Direct payments to conserve biodiversity. *Science* 298:1718–1719
- Ferraro PJ, McIntosh C, Ospina M (2007) The effectiveness of the US endangered species act: an econometric analysis using matching methods. *J Environ Econ Manag* 54:245–261
- Fisher B, Christopher T (2007) Poverty and biodiversity: measuring the overlap of human poverty and the biodiversity hotspots. *Ecol Econ* 62:93–101
- Halkos G (2003) Environmental Kuznets curve for sulphur: evidence using GMM and random coefficient panel data models. *Environ Dev Econ* 8:581–601
- Hartwick J (2000) *National accounting and capital*. Edward Elgar, Cheltenham
- Hoffmann M, Hilton-Taylor C, Angulo A, Böhm M, Brooks TM, Butchart SHM, Carpenter KE, Chanson J, Collen B, Cox NA, Darwall WRT, Dulvy NK, Harrison LR, Kataria V, Pollock CM, Quader S, Richman NI, Rodrigues ASL, Tognelli MF, Vié J-C, Aguiar JM, Allen DJ, Allen GR, Amori G, Ananjeva NB, Andreone F, Andrew P, Ortiz ALA, Baillie JEM, Baldi R, Bell BD, Biju SD, Bird JP, Black-Decima P, Blanc JJ, Bolaños F, Bolivar-G W, Burfield IJ, Burton JA, Capper DR, Castro F, Catullo G, Cavanagh RD, Channing A, Chao NL, Chenery AM, Chiozza F, Clausnitzer V, Collar NJ, Collett LC, Collette BB, Fernandez CFC, Craig MT, Crosby MJ, Cumberlidge N, Cuttelod A, Derocher AE, Diesmos AC, Donaldson JS, Duckworth JW, Dutton G, Dutta SK, Emslie RH, Farjon A, Fowler S, Freyhof J, Garshelis DL, Gerlach J, Gower DJ, Grant TD, Hammerson GA, Harris RB, Heaney LR, Hedges SB, Hero J-M, Hughes B, Hussain SA, Icochea MJ, Inger RF, Ishii N, Iskandar DT, Jenkins RKB, Kaneko Y, Kottelat M, Kovacs KM, Kuzmin KM, La Marca KM, Lamoreux KM, Lau KM, Lavilla KM, Leus KM, Lewison KM, Lichtenstein KM, Livingstone KM, Lukoschek KM, Mallon KM, McGowan KM, McIvor KM, Moehlman KM, Molur KM, Alonso KM, Musick KM, Nowell KM, Nussbaum KM, Olech KM, Orlov KM, Papenfuss KM, Parra-Olea KM, Perrin KM, Polidoro KM, Pourkazemi KM, Racey KM, Ragle KM, Ram KM, Rathbun KM, Reynolds KM, Rhodin KM, Richards KM, Rodriguez KM, Ron KM, Rondinini KM, Rylands KM, Sadovyde Mitcheson KM, Sanciangco KM, Sanders KM, Santos-Barrera KM, Schipper KM, Self-Sullivan KM, Shi KM, Shoemaker KM, Short KM, Sillero-Zubiri KM, Silvano KM, Smith KM, Smith KM, Snoeks KM, Stattersfield KM, Symes KM, Taber KM, Talukdar KM, Temple KM, Timmins KM, Tobias KM, Tsytsulina KM, Tweddle KM, Ubeda KM, Valenti KM, Paulvan Dijk KM, Veiga KM, Veloso KM, Wege KM, Wilkinson KM, Williamson KM, Xie KM, Young KM, Akçakaya KM, Bennun KM, Blackburn KM, Boitani KM, Dublin KM, da Fonseca KM, Gascon KM, Lacher KM, Mace KM, Mainka KM, McNeely KM, Mittermeier KM, Reid KM, Rodriguez KM, Rosenberg KM, Samways KM, Smart KM, Stein KM, Stuart KM, (2010) The impact of conservation on the status of the world's vertebrates. *Science* 330:1503–1509
- Hotelling H (1931) The economics of exhaustible resources. *J Polit Econ* 39:137–175
- IUCN (2002) *Beyond rhetoric: putting conservation to work for the poor*. IUCN, Gland
- Jackson LE, Pascual U, Brussaard L, de Ruiter P, Bawa KS (2007) Biodiversity in agricultural landscapes: investing without losing interest. *Agric Ecosyst Environ* 121:193–195
- Jones KE, Patel NG, Levy MA, Storeygard A, Balk D, Gittleman JL, Daszak P (2008) Global trends in emerging infectious diseases. *Nature* 451:990–993
- Jones MC (1992) Estimating densities, quantiles, quantiles densities and density quantiles. *Ann Inst Stat Math* 44:721–727
- Khanna N, Plassmann F (2004) The demand for environmental quality and the environmental Kuznets curve hypothesis. *Ecol Econ* 51:225–236

- Khanna N, Plassmann F (2007) Total factor productivity and the environmental Kuznets curve: a comment and some intuition. *Ecol Econ* 63:54–58
- Koenker R (2005) *Quantile regression*. Cambridge University Press, Cambridge
- Koenker R, Basset G (1978) Regression quantiles. *Econometrica* 46:33–50
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* 15:259–263
- Lieb CM (2002) The environmental Kuznets curve and satiation: a simple static model. *Environ Dev Econ* 7:429–448
- Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: current state and trends: findings of the condition and trends working group*. Island Press, Washington, DC
- Mills JH, Waite TA (2009) Economic prosperity, biodiversity conservation, and the environmental Kuznets curve. *Ecol Econ* 68:2087–2095
- Mozumder P, Berrens RP, Bohara AK (2006) Is there an environmental Kuznets curve for the risk of biodiversity loss?. *J Dev Areas* 39:175–190
- Naeem S, Bunker D, Hector A, Loreau M, Perrings C (2009) The ecological and social implications of changing biodiversity: an overview of a decade of biodiversity and ecosystem functioning research. In: Naeem S, Bunker D, Hector A, Loreau M, Perrings C (eds) *Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective*. Oxford University Press, Oxford, pp 3–13
- Naidoo R, Adamowicz WL (2001) Effects of economic prosperity on numbers of threatened species. *Conserv Biol* 15:1021–1029
- Naidoo R, Stuart-Hill G, Weaver L, Tagg J, Davis A, Davidson A (2011) Effect of diversity of large wildlife species on financial benefits to local communities in northwest Namibia. *Environ Resour Econ* 48:321–335
- Pearce DW (2003) The social cost of carbon and its policy implications. *Oxf Rev Econ Policy* 19:362–384
- Pearce DW (2005) Paradoxes in biodiversity conservation. *World Econ* 6:57–69
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful?. *Glob Ecol Biogeogr* 12:361–371
- Perrings C (2007) Pests, pathogens and poverty: biological invasions and agricultural dependence. In: Kontoleon A, Pascual U, Swanson T (eds) *Biodiversity economics: principles, methods, and applications*. Cambridge University Press, Cambridge, pp 133–165
- Perrings C, Gadgil M (2003) Conserving biodiversity: reconciling local and global public benefits. In: Kaul I, Conceicao P, Le Goulven K, Mendoza RL (eds) *Providing global public goods: managing globalization*. Oxford University Press, Oxford, pp 532–555
- Perrings C, Naeem S, Ahrestani F, Bunker DE, Burkill P, Canziani G, Elmqvist T, Ferrati R, Fuhrman J, Jaksic F, Kawabata Z, Kinzig A, Mace GM, Milano F, Mooney H, Prieur-Richard A-H, Tschirhart J, Weisser W (2010) Ecosystem services for 2020. *Science* 330:323–324
- Perrings C, Naeem S, Ahrestani F, Bunker DE, Burkill P, Canziani G, Elmqvist T, Ferrati R, Fuhrman J, Jaksic F, Kawabata Z, Kinzig A, Mace GM, Milano F, Mooney H, Prieur-Richard A-H, Tschirhart J, Weisser W (2011) Ecosystem services, targets, and indicators for the conservation and sustainable use of biodiversity. *Frontiers Ecol Environ* 9:512–520
- Rands MRW, Adams WM, Bennun L, Butchart SHM, Clements A, Coomes D, Entwistle A, Hodge I, Kapos V, Scharlemann JPW, Sutherland WJ, Vira B (2010) Biodiversity conservation: challenges beyond 2010. *Science* 329:1298–1303
- Reyers B, Van Jaarsveld AS, McGeoch MA, James AN (1998) National biodiversity risk assessment: a composite multivariate and index approach. *Biodivers Conserv* 7:945–965
- Sachs JD, Baillie JEM, Sutherland WJ, Armsworth PR, Ash N, Beddington J, Blackburn TM, Collen B, Gardiner B, Gaston KJ, Godfray HCJ, Green RE, Harvey PH, House B, Knapp S, Kumpel NF, Macdonald DW, Mace GM, Mallet J, Matthews A, May RM, Petchey O, Purvis A, Roe D, Safi K, Turner K, Walpole M, Watson R, Jones KE (2009) Biodiversity conservation and the millennium development goals. *Science* 325:1502–1503
- Stern DI (2004) The rise and fall of the environmental Kuznets curve. *World Dev* 32:1419–1439
- Tallis H, Kareiva P, Marvier M, Chang A (2008) An ecosystem services framework to support both practical conservation and economic development. *Proc Nat Acad Sci* 105:9457–9464
- Wells MP, Brandon K (1992) *People and parks: linking protected areas with local communities*. World Bank, Washington, DC
- Wells MP, McShane TO, Dublin HT, O'Connor S, Redford KH (2004) The future of integrated conservation and development projects: building on what works. In: McShane TO, Wells MP (eds) *Getting biodiversity projects to work: towards more effective conservation and development*. Columbia University Press, New York, pp 397–422
- Willis KJ, Bhagwat SA (2009) Biodiversity and climate change. *Science* 326:806–807

- World Bank (2006) Where is the wealth of nations? Measuring capital for the 21st century. The World Bank, Washington, DC
- World Commission on Environment and Development (1987) Our common future. Island Press, Washington, DC
- Wunder S, Wertz-Kanounnikoff S (2009) Payments for ecosystem services: a new way of conserving biodiversity in forests. *J Sustain For* 28:576–596