Effects of Economic Prosperity on Numbers of Threatened Species

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Abstract: *We used data from over 100 countries to investigate the link between numbers of threatened species and per-capita gross national product. We corrected for factors that might otherwise confound such a relationship. Our study was motivated by the continuing debate over the relationship between environmental degradation and per-capita income. Proponents of the environmental Kuznets-curve hypothesis argue that although environmental degradation may increase initially, increases in per-capita income will eventually result in greater environmental quality. Theoretical objections and the lack of widespread empirical evidence recently have thrown doubt on the existence of such a pattern. Treating threat to biodiversity as one potential indicator of environmental degradation, we divided threatened species into seven taxonomic groups (plants, mammals, birds, amphibians, reptiles, fishes, and invertebrates) and analyzed each group separately. Count-data regression analysis indicated that the number of threatened species was related to per-capita gross national product in five of seven taxonomic groups. Birds were the only taxonomic group in which numbers of threatened species decreased throughout the range of developed countries' per-capita gross national product. Plants, amphibians, reptiles, and invertebrates showed increasing numbers of threatened species throughout this same range. If these relationships hold, increasing numbers of species from several taxonomic groups are likely to be threatened with extinction as countries increase in prosperity. A key challenge is to understand the interactions among consumer preferences, biology, and institutions that lead to the relationship observed for birds and to see whether this knowledge can be applied to conservation of other taxa.*

Efectos de la Prosperidad Económica sobre los Números de Especies Amenazadas

Resumen: *Utilizamos datos de más de 100 países para investigar la relación entre números de especies amenazadas y el producto interno bruto per cápita. Hicimos ajustes para factores que pudieran confundir tal relación. Nuestro estudio fue motivado por el continuo debate sobre la relación entre la degradación ambiental y el ingreso per cápita. Proponentes de la hipótesis de la curva ambiental de Kuznets argumentan que, aunque la degradación ambiental puede aumentar inicialmente, el incremento en el ingreso per cápita eventualmente resultará en una mejor calidad ambiental. Recientemente, objeciones teóricas y la carencia de evidencia empírica generalizada hacen dudar de la existencia de ese patrón. Tratando la amenaza a la biodiversidad como un potencial indicador de la degradación ambiental, dividimos a las especies amenazadas en siete grupos taxonómicos (plantas, mamíferos, aves, anfibios, reptiles, peces e invertebrados) y analizamos cada uno por separado. El análisis de regresión de los datos de conteo indicó que el número de especies amenazadas se relacionó con el producto interno bruto per cápita en 5 de los 7 grupos taxonómicos. Las aves fueron el único grupo en el que el número de especies amenazadas decreció a lo largo del rango del producto interno bruto per cápita de los países desarrollados. Las plantas, anfibios, reptiles e invertebrados mostraron un incremento en el número de especies amenazadas en este mismo rango. Si estas relaciones persisten, es posible que aumente el número de especies, de varios grupos taxonómicos, amenazadas de extinción a me-*

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dida que los países incrementen su prosperidad. Constituye un reto clave entender las interacciones entre la preferencia de los consumidores y los factores biológicos e institucionales que conducen a la relación observada en las aves, y ver si este conocimiento puede aplicarse en la conservación de otros taxones.

Introduction

Evidence suggests that the current global extinction spasm is resulting in the extermination of species at a rate 100 to 1000 times greater than in prehuman times (Pimm et al. 1995). The main drivers of this event are hypothesized to be anthropogenic in origin (Sala et al. 2000). Hypotheses concerning the nature of the relationship between biodiversity and various ecosystem services essential for human societies suggest that, even from a utilitarian point of view, continuing to drive vast numbers of species to extinction may be an unwise course of action (Costanza et al. 1997; Daily 1997; Chapin et al. 2000; Tilman 2000). The cultural, aesthetic, and ethical reasons for avoiding a massive extinction of much of the earth's biodiversity have also been well documented (Ehrlich & Ehrlich 1992; Gowdy 1997; Ludwig 2000). So why do species continue to be driven to extinction? A widely held view among those in the environmental sciences is that "economic growth"—an increasing global population that desires an increasing per-capita level of consumption—fuels excessive land conversion, resource exploitation, and climate change (Sisk et al. 1994). The results of economic growth are thought to be incompatible with the conservation of biodiversity, so reduction of per-capita consumption (along with reduced population growth rates) is often a key recommendation in global conservation strategies (Mangel et al. 1996).

Studies in the environmental economics and environmental policy literature often have come to a very different conclusion regarding the role of economic development and environmental degradation, namely that increasing per-capita income may be the only way environmental problems will be solved (Beckerman 1992). It is thought that as per-capita incomes increase, the demand for environmental quality and the resources available for investment in the environment also rise (World Bank 1992). The relationship between per-capita income and measures of environmental degradation has been the source of much recent investigation. A lively debate has occurred regarding the hypothesis that this relationship is often shaped like an inverted U in that environmental degradation initially rises with increasing per-capita income but at a certain income level subsequently declines. Evidence supporting this hypothesis, termed the environmental Kuznets curve (EKC), has been submitted for various types of air pollutants (Shafik & Bandyopadhyay 1992; Selden & Song 1994; Grossman & Krueger 1995) and deforestation (Antle & Heidebrink 1995; Mather et al. 1999). Others argue that there is no strong theoretical reason to expect the EKC to exist (Arrow et al. 1995; Rothman & de Bruyn 1998) and that previous studies supporting the EKC suffered from methodological and interpretation problems (Stern et al. 1996; de Bruyn et al. 1998). In addition, various other types of functional relationships have been shown to exist between measures of environmental degradation and per-capita income (de Bruyn et al. 1998).

To the extent that environmental quality is reflected in remaining levels of biodiversity, it is possible to examine the relationship between proxies for this variable and per-capita income. Because the majority of the world's biodiversity is concentrated in developing tropical countries (Wilson 1988), predicting the trajectory that biodiversity levels will take as per-capita income of these countries increases has important conservation implications. As part of the effort to catalogue species that have already gone extinct and those that are poised to do so, the World Conservation Union (IUCN) periodically publishes Red Lists of "threatened" animals and plants. These Red Lists, although far from a global species-by-species assessment, are a valuable source of information about the magnitude of the threat to any individual country's biodiversity. Our goal was to examine, after controlling for confounding factors, the relationship between numbers of threatened species and per-capita income at the country level.

The hypothesis that increasing per-capita income results in increased demand for environmental quality assumes that people have adequate knowledge concerning the environmental good in question or that at least enough information is provided to allow for the expression of these preferences. This may not be the case for threatened species, because the academic community itself has only recently recognized the benefits of retaining elevated levels of biodiversity (Chapin et al. 2000). Furthermore, to the extent that preferences may be expressed for threatened species, they may vary with the type of organism threatened. In general, people tend to display preferences for species that are large, highly visible, and capable of displaying various behaviors interpretable as humanlike (Kellert 1985; Metrick & Weitzman 1996). Indeed, several studies of threatened species have shown that conservation efforts have been motivated less by the degree of threat to a particular species and more by whether the species belonged to a particular charismatic taxonomic group (Simon et al. 1995; Metrick & Weitzman 1996).

It is therefore possible that the relationship between numbers of threatened species and per-capita income will vary by taxonomic status. Accordingly, we broadly classified threatened species into several taxonomic groups and analyzed per-capita income relationships separately for each group. One could speculate about the nature of the relationship between income and the number of threatened species in various taxa, but we focused on the "stylized facts" arising from the relationships we examined and the interpretations that arose from these exploratory analyses.

Methods

We used data from a recent report that examined the status of the global environment (World Resources Institute 1999). Data contained in this report are also available free at http://www.wri.org/wri/facts/data_tables.html. This publication contains, among other things, information on biodiversity, land use, and economic activity for 157 countries. The World Resources Institute collates these data from various sources. Information on species endangerment, total species number, endemic species, protected areas, and forest cover comes primarily from the World Conservation Monitoring Centre (WCMC: http://www.wcmc.org.uk), which maintains extensive databases on threatened species and habitats throughout the world, and the IUCN Red Lists of Threatened Animals and Plants (World Conservation Union 1996, 1997). Information on country area and land use is collated from the FAOSTAT Statistics Database of the Food and Agriculture Organization (FOA) of the United Nations (http://apps.fao.org/cgi_bin/nph_db.pl).

Consistent with IUCN classification, we considered the number of threatened species in a country to be the sum of all species in the critically endangered, endangered, and vulnerable categories. Threatened species were divided into seven groups: plants, mammals, birds, amphibians, reptiles, fish, and invertebrates. Analyses were performed separately for each group. Criteria for consideration of threatened species status by the IUCN varied by taxonomic group. For marine species, only those that return to land to breed or nest are assigned to a country record. Threatened cetaceans were not assigned to particular countries, except for inshore or coastal species. Only vascular plants were considered by the IUCN when it developed the list of threatened plant species. For birds, threatened species were listed for countries included within their breeding or wintering range. Threatened marine turtles were excluded from reptile totals, and most threatened marine fishes were similarly excluded from fish totals. For invertebrates, no distinction appeared to have been made in the WCMC database between countries that had no threatened species and countries for which no estimate existed. For this group, therefore, we used only those countries that had at least one threatened species. All known bird and mammal species were assessed for the 1996 Red List of Threatened Animals (World Conservation Union 1996), whereas coverage for the other taxonomic groups, in particular invertebrates, was less complete.

In developing regression models for the effects of per-capita income on threatened species, we also included variables that account for country-specific differences in ecology, level of human activity, and geography. The variables included those that potentially influence species endangerment through sheer species numbers or species-area relationships ("covariates"), land-use practices, and economic well-being (Table 1). Covariates included the total number of species (by taxonomic group) that occurred in a country, the number of endemic species that occurred in a country (by taxonomic group), and country area. Most cetaceans were excluded by the WCMC from total mammal species lists. Only breeding birds were considered by the WCMC when it compiled total bird species lists. Only flowering plants were listed in total plant species lists. Data were unavailable for invertebrates. Number of endemic species refers to the number of species that occur exclusively within one country's borders. For plants, all vascular plants were included by the WCMC. Data were unavailable for fish and invertebrates.

We included three land-use variables that we thought would have important influences on numbers of threatened species. The first was the percentage of a country under domestication, which is a crude indicator of the degree to which national landscapes have been modified by agricultural use. It is defined as the sum of the FAO's land-use categories of cropland and permanent pasture. It does not include developed lands or plantation forests. The second land-use variable was percentage of original forest cover remaining in a country, where original forest cover refers to the area of land that would have been covered by closed forest about 8000 years ago (assuming current climatic conditions), before large-scale disturbance by human society began. These were WCMC estimates based on global and regional biogeographic maps. Remaining forest is current forest area measured at some point within the last 10 years, depending on the country. The final land-use variable was percentage of a country in IUCN protected areas, where IUCN protected area is the sum of natural areas at least 1000 ha in size in IUCN management categories I–V (generally described as scientific reserves, national/provincial parks, natural monuments, wildlife sanctuaries/managed nature reserves, and protected landscapes).

Finally, we included two economic variables in our analyses. We used per-capita gross national product (GNP) as a proxy for per-capita income of a country. Per-capita GNP refers to the total value of the final output of goods and services produced by the domestic economy as well as net income from abroad (1995 U.S. dollars), divided by the population. We also included the square of per-

Table 1. Descriptive statistics for threatened species, covariates, and land-use variables.

Variable	n	*Mean*	*Median*	*SD*	*Minimum*	*Maximum*
Threatened plant spp.	150	157.2	24.5	318.63	0	1845
Total plant spp.	126	6120.8	3337.5	8109.65	234	55000
Endemic plant spp.	98	1515.5	226.5	3297.09	1	18000
Threatened mammal spp.	157	16.0	11	17.19	1	128
Total mammal spp.	140	153.4	128	105.38	3	450
Endemic mammal spp.	145	12.2	1	31.62	0	206
Threatened bird spp.	157	15.1	9	18.88	0	104
Total bird spp.	144	407.4	297.5	313.20	20	1695
Endemic bird spp.	153	15.3	0	50.04	0	393
Threatened amphibian spp.	154	0.8	0	3.06	0	25
Total amphibian spp.	108	68.4	26.5	101.03	0	585
Endemic amphibian spp.	149	21.4	1	51.67	0	366
Threatened reptile spp.	154	4.6	3	5.72	0	37
Total reptile spp.	111	122.0	72	141.90	0	748
Endemic reptile spp.	147	27.3	2	73.67	0	628
Threatened fish spp.	157	5.7	1	14.05	0	123
Total fish spp.	77	140.7	79	169.67	3	822
Threatened invertebrate spp.	131	17.3	5	58.13	1	594
Country area (ha)	157	82773.9	23034	204467	61	1688850
Percent country domesticated	157	41.5	43	21.62	1	86
Percent country in protected areas	152	7.6	5.5	7.61	0	43.1
Percent original forest cover remaining	148	29.8	20	29.17	0	100
Per-capita GNP (U.S. dollars 1995)	144	5309.58	1365	8806.36	80	40630

capita GNP as a quadratic variable in the analysis, to allow a range of possible nonlinear functional responses.

Because the response variables were not continuous but rather counts (non-negative integers), we used count-data regression (Cameron & Trivedi 1998) instead of ordinary least-squares regression in our analyses. Specifically, we used a negative-binomial regression model, which has the following form:

$$\text{prob}(Y = y_i, \varepsilon_i) = \frac{e^{-\mu_i(\varepsilon_i)}[\mu_i(\varepsilon_i)]^{y_i}}{y_i!}, y_i = 0, 1, 2, \ldots, \quad (1)$$

and

$$\ln\mu_i(\varepsilon_i) = x_i\beta' + \varepsilon_i \quad (2)$$

where Y is a random variable, y_i is the number of occurrences of threatened species, μ_i is the mean intensity parameter, x_i is the vector of independent regressors, β' is the vector of regressor coefficients, and e^{ε_i} is the gamma distribution with mean 1.0 and variance α, a measure of the dispersion of the data.

We used negative binomial models because the dispersion parameter was statistically significant in all models, indicating that a Poisson count-data model would not be appropriate (Cameron & Trivedi 1998). We first attempted to fit models using the untransformed independent variables listed above. The fit of these models was poor, however, as indicated by extremely low deviance R^2 and chi-square values, and by asymmetry and outlying observations in plots of residuals versus fitted values (Cameron & Trivedi 1998). Inspection of the independent variables revealed highly skewed distributions. We therefore log-transformed all the independent variables (with the exception of the $[\log(\text{GNP})]^2$ variable) and used these transformed variables in subsequent analyses.

Initially, we estimated models with all six noneconomic explanatory variables and the two per-capita GNP variables. We subsequently removed all noneconomic variables for which the coefficient was not significantly different from 0 (as defined by a p value of >0.05) and reestimated reduced models. Examination of the residual plots for these models revealed outlying observations for several taxa. In particular, the United States and Australia were outliers for four and three of the seven taxa, respectively. Both of these countries are wealthy industrialized nations that seem to have invested more into documenting the natural history of their fauna and flora than other countries in the analysis (with the possible exception of Great Britain). Accordingly, to remove any potential bias due to these countries, we removed them from the statistical analyses. Outliers in models for amphibians (South Africa, Japan), fishes (Mexico), and invertebrates (South Africa) were also removed. The results of analyses with and without these outlier countries were qualitatively similar in most cases.

Finally, to allow nonlinear responses in the noneconomic variables, we repeated the analytical procedures described above while adding to the models the squared terms of each of the original covariate and land-use variables. An extension to these analyses would be to use a systems approach to estimate the regression coefficients (Srivastava & Giles 1987); this would be challenging, however, given the number of equations and the count nature of the data.

We interpreted the functional response of numbers of threatened species to the log of per-capita GNP by examining the sign and magnitude of the coefficients on both economic variables. The quadratic functional form we employed allows for nonlinearity in the relationships between income and threatened species. The environmental Kuznets-curve hypothesis would be supported by positive linear and negative quadratic terms, but other relationships, including increasing numbers of threatened species as income increases, can be captured by this functional form.

Results

Results from three regression analyses—all countries, outliers removed, nonlinear effects of noneconomic variables—were similar in terms of the responses of threatened species to the log of per-capita GNP (Table 2). When all countries were included in the analysis, income variables were significant predictors in all taxonomic groups except for mammals. The number of threatened plants increased linearly with increasing log(GNP). The number of threatened amphibians, reptiles, fishes, and invertebrates all had a negative log (GNP) term and a positive quadratic term, indicating a general U-shaped functional relationship. The number of threatened bird species exhibited an inverted-U (EKC) relationship with increasing log(GNP). When outlying observations were removed, the results were much the same, the only difference being that numbers of threatened fish species were no longer affected by either of the income variables.

The analysis including squared terms of noneconomic variables produced slightly different relationships between threatened species and log(GNP). One of the main differences was that in this analysis, mammals showed an inverted-U relationship with increasing log(GNP), which is consistent with the environmental Kuznets curve. In contrast to the other two analyses, fish and invertebrates showed a positive linear relationship between numbers of threatened species and log(GNP).

Of the 21 regression models in the three different analyses, only two, both of them with threatened mammal species as the dependent variables, had as many as three noneconomic independent variables. Covariates (i.e., total species, endemic species, or country area) were significant in 17 of the 21 models. As expected, these were all positively related to numbers of threatened species. Land-use variables were significant in only 5 models. The number of threatened amphibians decreased with increasing percentage of protected country area (two analyses). The number of threatened invertebrate species increased with the percentage of a country's land under domestication (in two models).

Although deviance R^2s were higher in the models including all countries than in those where outliers were removed, examination of residual plots showed that models with outliers removed had superior fits. With the exception of plants and reptiles, where the deviance R^2s were about equal, models that had allowed for nonlinearity in noneconomic variables had lower deviance R^2s than the models where outliers were removed. This is most likely due to the fact that fewer noneconomic variables were included in the reduced models. We consider the results of the analysis that excluded outlying countries and that did not consider nonlinearity in the noneconomic variables to be the most robust and therefore focus our discussion on these results (Fig. 1).

Discussion

One could conclude from our results that if the trends we documented are stable through time, the future prospects for global biodiversity are grim. It has been estimated that at least 50% of the world's biodiversity is contained in the world's moist tropical forests (Wilson 1988), most of which occur in developing countries. The goal of most development policies, particularly those of the World Bank (World Bank 1992), is to increase the per-capita income of developing countries (roughly defined as low-income and middle-income economies that have an average per-capita GNP of less than $9385 [U.S. dollars 1995]: World Bank 1997) so that they reach the level of industrialized nation levels. Our analyses show that within the range of developed country per-capita GNP, threatened plants, amphibians, reptiles, and invertebrates all increase with increasing per-capita GNP (Fig. 1). If these relationships hold, it appears that much of the world's biodiversity will be threatened with extinction should countries reach levels of consumption and economic activity equal to those of developed nations. But for bird species (and in some cases for mammals) there appears to be evidence of increasing preference for environmental quality as income increases. The challenge is to understand why this relationship exists in the case of birds and to assess whether knowledge of these mechanisms could be used to help conserve species in other taxa.

Three factors may interact to produce the types of relationships we have observed between per-capita income and numbers of threatened species: income elasticity, institutional designs, and biological characteristics. Income elasticity refers to the percent change in the demand for a particular good with a unit percent change in income. The EKC relationship may arise from environmental quality being a luxury good, meaning that as income increases the demand for environmental quality increases at a greater rate. Explanation of our results consistent with income elasticity as the driving fac-

Table 2. Results of three count-data regression analyses for the effects of per-capita income, after controlling for confounding factors, on threatened species of each taxonomic group.*

Independent variable	*Plants*	*Mammals*	*Birds*	*Amphibians*	*Reptiles*	*Fish*	*Invertebrates*
All countries							
log(no. spp.)	ns	0.2744	ns	ns	0.8504	0.779	—
log(no. endemic spp.)	0.5330	0.3297	0.3703	0.7398	ns	—	—
log(country area)	ns	0.7857	0.1428	ns	ns	ns	0.2694
log(percent area domesticated)	ns	ns	ns	ns	ns	ns	0.4492
log(percent area protected)	ns	ns	ns	−0.4038	ns	ns	ns
log(percent original forest left)	ns	ns	ns	ns	ns	ns	ns
log(GNP per capita)	0.2898	ns	0.2445	−1.1570	−0.6262	−0.7039	−0.9484
[log(GNP per capita)]^2	ns	ns	−0.0214	0.1162	0.0460	0.0574	0.0877
n	90	127	141	134	101	74	120
chi-square	13223.82	61.31	285.75	14.10	32.47	529.32	1483.56
deviance R^2	0.61	0.84	0.74	0.74	0.67	0.50	0.70
p	<0.00001	<0.00001	<0.00001	0.0002	<0.00001	<0.00001	<0.00001
Outliers removed							
log(no. spp.)	ns	0.2843	ns	ns	0.8230	0.7097	—
log(no. endemic spp.)	0.5221	0.3326	0.3757	0.7206	ns	—	—
log(country area)	ns	0.0835	0.1455	ns	ns	ns	0.2097
log(percent area domesticated)	ns	ns	ns	ns	ns	ns	0.3751
log(percent area protected)	ns	ns	ns	−0.5115	ns	ns	ns
log(percent original forest left)	ns	ns	ns	ns	ns	ns	ns
log(GNP per capita)	0.3226	ns	0.2319	−1.0089	−0.5664	ns	−0.6489
[log(GNP per capita)]^2	ns	ns	−0.0203	0.1025	0.0404	ns	0.0619
n	88	125	139	130	99	72	118
chi-square	12381.20	59.61	263.66	67.09	31.81	487.00	1038.1
deviance R^2	0.52	0.84	0.74	0.65	0.61	0.26	0.26
p	<0.00001	<0.00001	<0.00001	0.05	<0.00001	<0.00001	<0.00001
Nonlinearity in noneconomic variables							
log(no. spp.)	ns	ns	ns	ns	1.7577	ns	ns
[log(no. spp.)]^2	ns	ns	ns	ns	ns	ns	ns
log(no. endemic spp.)	0.5221	0.2832	ns	0.7132	ns	ns	ns
[log(no. endemic spp.)]^2	ns	ns	ns	ns	ns	ns	ns
log(country area)	ns	ns	ns	ns	ns	ns	ns
[log(country area)]^2	ns	ns	ns	ns	ns	ns	ns
log(percent area domesticated)	ns	ns	ns	ns	ns	ns	ns
[log(percent area domesticated)]^2	ns	ns	ns	ns	ns	ns	ns
log(percent area protected)	ns	ns	ns	ns	ns	ns	ns
[log(percent area protected)]^2	ns	ns	ns	ns	ns	ns	ns
log(percent original forest left)	ns	0.3283	ns	ns	ns	ns	ns
[log(percent original forest left)]^2	ns	−0.0653	ns	ns	ns	ns	ns
log(GNP per capita)	0.3226	0.5860	0.6207	−1.0691	−1.2277	0.3751	0.3584
[log(GNP per capita)]^2	ns	−0.0453	−0.0485	0.1007	0.0826	ns	ns
n	88	131	136	132	99	141	117
chi-square	12381.2	99.83	314.41	4.57	31.86	14.95	237.13
deviance R^2	0.52	0.79	0.14	0.41	0.62	0.02	0.14
p	<0.00001	<0.00001	<0.00001	0.03	<0.00001	<0.00001	<0.00001

**Analyses were all countries included, outliers removed, and nonlinearity in covariates and land-use variables. Variables with coefficients not statistically different from 0 ($p < 0.05$) in initial full models, and therefore removed from subsequent reduced models, are indicated by "ns." Significant coefficients on variables included in final reduced models are given. Full results for all preliminary models are available from the authors upon request.*

tor requires that increasing preferences for the preservation of birds as income rises be greater than that for other taxonomic groups, because birds were the only group to show a negative relationship between numbers of threatened species and per-capita GNP. In fact, an income elasticity explanation suggests that preservation of bird species is a luxury good, while preservation of other species is not.

We could not find empirical evidence for the relationship between income and preferences for species conservation but there is evidence to suggest that in wealthy countries birds receive greater conservation attention than other taxonomic groups, regardless of relative degrees of threat (Simon et al. 1995). Of the 10 endangered species in the United States on which the most money has been spent, seven are bird species, including the top three species: Bald Eagle (*Haliaeetus leucocephalus*), Northern Spotted Owl (*Strix occidentalis caurina*), and Florida Scrub Jay (*Aphelocoma coerulescens*). These seven bird species account for 40% of the total amount

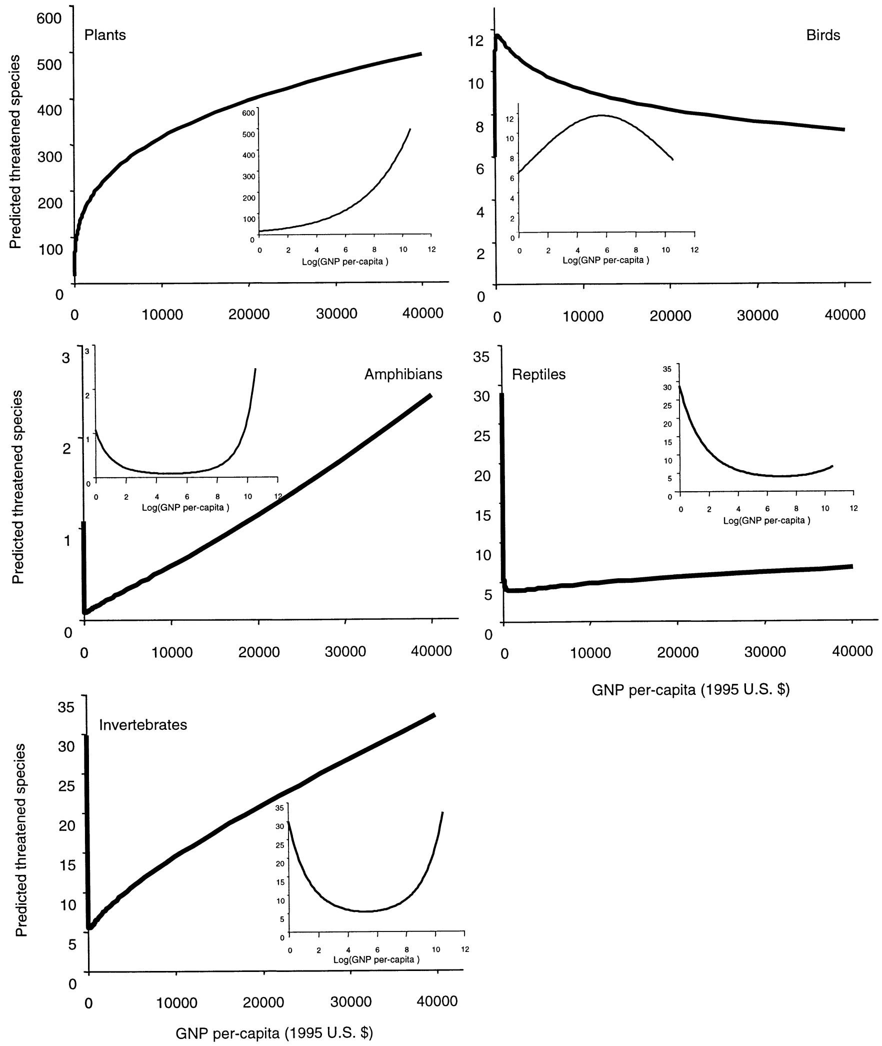

Figure 1. Predicted numbers of threatened species as per-capita GNP increases, based on regression models developed with outlying countries removed. Significant covariate and land-use regressors (Table 2) are held at mean values, so predicted values do not reflect actual model predictions but rather the qualitative functional response across the range of per-capita GNPs of countries included in the analysis. Inset graphs are plotted on a logged per-capita GNP scale; larger graphs are on a linear per-capita GNP scale.

of money spent on endangered species by United States federal and state agencies from 1989 to 1991, $127.6 million (Metrick & Weitzman 1996).

Loomis and White (1996) have summarized data from studies assessing willingness to pay (WTP) for preservation of various threatened species. The average WTP value for avoiding the loss of threatened species was greater for birds than either mammals or fishes. This was true of studies that measured annual WTP values ($31.51 [U.S.$ 1993] for birds vs. $26.67 for mammals and $24.92 for fishes) and those that measured lump-sum payments ($165.41 for birds vs. $79.87 for mammals and $15.19 for fish). In addition, people are generally most inclined to protect species that are large, aesthetically attractive, and most similar to human beings in terms of their capacity for feeling, thought, and pain (Kellert 1985; Metrick & Weitzman 1996). Birds display many of these qualities, whereas plants, amphibians, reptiles, and invertebrates—generally the antithesis of the charismatic megafauna represented by threatened birds—increase in extinction vulnerability with increasing economic prosperity.

Institutional and biological factors are also likely to be important determinants of the relationships we have discussed. For example, the evidence is mixed regarding whether species richness in different taxa coincide in a given geographic area (Dobson et al. 1997; Howard et al. 1998; Lawton et al. 1998; Gaston 2000). Therefore, habitat-protection measures targeted at one species or one group of species may not necessarily conserve biodiversity in general, so it is not surprising from a biological point of view that we have observed different functional responses among taxonomic groups.

Certain institutions may also make conservation of birds less formidable than that of other taxonomic groups. For example, although mammals are often considered charismatic megafauna, we found only weak evidence of a decline in threatened mammal species as per-capita income increased. Many mammals are relatively large and require much larger tracts of undisturbed habitat than birds to maintain viable populations (e.g., Noss et al. 1996). These large pristine areas are becoming increasingly scarce in industrialized countries. In contrast to their aesthetic and cultural values, mammals, particularly large mammals, have also been vulnerable to the expansion of subsistence-oriented human economies for several reasons, including competition for resources, danger as predators, and value as food and clothing (Burghardt & Herzog 1980; Kellert 1985). Therefore, although preferences for mammal conservation may exist among certain segments of society, institutions that promote habitat loss and consumptive use of mammals may prevent effective conservation. Less obvious complications may also be acting to reduce efficiency in the conservation of other taxonomic groups.

Although only threatened bird species declined as per-capita income increased, such a relationship may occur at some point in the future for other taxonomic groups. This depends on the relationship between preference for species protection (as embodied by policy and other measures) and income or development. In the case of threatened plant species, which increased with per-capita GNP, the range of economic development of countries may not encompass the range required to display an EKC relationship—the income range may not yet have reached the "turning point." Whether preferences for conservation of these species will increase with income is uncertain and will depend on the evolution of preferences with income, the increasing relative scarcity of species, the ability of institutions to respond to changing preferences and scarcity, and other factors. In addition, many of the species now listed as threatened will eventually become extinct. Therefore, although listed species may decrease, the number of extant species will not increase but will rather decline. Extinction is irreversible, unlike other environmental responses that have shown EKC relationships with economic prosperity, such as pollutant emissions and forest cover.

Caution in interpreting these results is required because of the nature of the data used in these analyses. Although these data are to our knowledge the best of their kind, several concerns regarding their quality and appropriateness for these types of analyses should be raised. Most studies looking for evidence of Kuznets-curve relationships have used time-series data spanning one or more decades for a set of countries (Selden & Song 1994; Grossman & Krueger 1995; Koop & Tole 1999). Unfortunately, data on biodiversity at the country level simply do not exist over these time scales for most countries.

There is also the issue of discrepancy in knowledge and search effort among the various taxa used in these analyses. Undoubtedly, taxonomic groups such as birds and mammals are much better known than those of plants and invertebrates and therefore are likely to receive greater effort in determining the status of known species and the discovery of new species (McKinney 1999). Discrepancies in knowledge and search effort are also likely to exist among countries. Developing countries clearly have fewer resources than richer countries to devote to biodiversity monitoring. Quantifying the amount of time and resources that individual countries devote to this task would strengthen our arguments.

Finally, our analysis assumes that each country's wealth affects the environmental quality of the country, but concern for endangered species within a country may arise from other (perhaps wealthier) countries, prompting investment in species protection by direct transfer or by indirect means. Such "spillover" effects have been observed in Kuznets curves for transboundary air pollution (G. Hauer & C. F. Runge, unpublished data) but are difficult to assess for endangered species. These spillover effects, and their manifestation in global biodiversity conservation programs, may have significant effects on conservation programs in less wealthy countries.

Conclusions

We examined global, cross-sectional data on economic prosperity, threatened species, and various covariates to investigate the relationship between income and threatened species. The important issue arising from the results is that, for some taxa (birds and, in a limited number of cases, mammals) increasing economic wealth appears to result in increased protection for threatened species, or at least is associated with reductions in threatened species numbers. This is in contrast to the majority of taxa that do not have such a relationship with income. It is important to continue to assess why this relationship holds for bird species and not others, so that this knowledge can be applied to the conservation of other species as incomes increase. Anecdotal evidence suggests that the relationship for bird species may arise because of different preferences (income elasticities) for threatened birds as an indicator of environmental quality. This may suggest that the public's preference for some species is effective in fostering protection for those species, but that preferences for other "small and slimy" species have not yet been recognized. The underlying institutions associated with the conservation of threatened bird species may also be more effective than institutions associated with other taxa. Also, biological factors may result in different levels of effectiveness of conservation efforts. The key issue is to assess the reasons for the relative "success" in the conservation of threatened bird species and to apply such knowledge to conservation of threatened species in other taxa.

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