

# A Cross-National Analysis of How Economic Inequality Predicts Biodiversity Loss

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**Abstract:** *We used socioeconomic models that included economic inequality to predict biodiversity loss, measured as the proportion of threatened plant and vertebrate species, across 50 countries. Our main goal was to evaluate whether economic inequality, measured as the Gini index of income distribution, improved the explanatory power of our statistical models. We compared four models that included the following: only population density, economic footprint (i.e., the size of the economy relative to the country area), economic footprint and income inequality (Gini index), and an index of environmental governance. We also tested the environmental Kuznets curve hypothesis, but it was not supported by the data. Statistical comparisons of the models revealed that the model including both economic footprint and inequality was the best predictor of threatened species. It significantly outperformed population density alone and the environmental governance model according to the Akaike information criterion. Inequality was a significant predictor of biodiversity loss and significantly improved the fit of our models. These results confirm that socioeconomic inequality is an important factor to consider when predicting rates of anthropogenic biodiversity loss.*

**Keywords:** biodiversity loss, economy, income distribution, IUCN Red List, social-ecological systems

Análisis Transnacional de Cómo la Inequidad Económica Predice la Pérdida de Biodiversidad

**Resumen:** *Utilizamos modelos socioeconómicos que incluyeron la inequidad económica para predecir la pérdida de biodiversidad, medida como la proporción de especies amenazadas de plantas y vertebrados, en 50 países. Nuestra principal meta fue evaluar si la inequidad económica, medida como el índice Gini de distribución del ingreso, mejoraba el poder predictivo de nuestros modelos estadísticos. Comparamos cuatro modelos que incluyeron lo siguiente: solo densidad poblacional, huella económica (i.e., el tamaño de la economía en relación con la superficie del país); huella económica e inequidad de ingresos (índice Gini) y un índice de gobernabilidad ambiental. También probamos la hipótesis de la curva ambiental de Kuznets, pero no fue sustentada por los datos. Las comparaciones estadísticas de los modelos revelaron que el modelo que incluyó la huella ecológica y la inequidad fue el mejor pronosticador de especies amenazadas. Superó significativamente el funcionamiento de la densidad poblacional sola y la gobernabilidad ambiental de acuerdo con el criterio de información de Akaike. La inequidad fue un pronosticador significativo de la pérdida de biodiversidad y mejoró significativamente el ajuste de nuestros modelos. Los resultados confirman que la inequidad socioeconómica es un factor importante a considerar cuando se pronostican tasas de pérdida antropogénica de biodiversidad.*

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Paper submitted August 31, 2008; revised manuscript accepted December 16, 2008.

**Palabras Clave:** distribución de ingresos, economía, Lista Roja IUCN, pérdida de biodiversidad, sistemas sociales-ecológicos

## Introduction

Global species loss is occurring 100 to 1000 times faster than the background rate (May & Lawton 1995), primarily due to the effects of habitat degradation, overexploitation, introduction of invasive species, and pollution (MA 2005*a*). Given the importance of biodiversity to human well-being and the irreversibility of its loss, the depletion of biodiversity is one of the most important environmental threats that humanity faces (Chapin et al. 2000; Tilman 2000; MA 2005*a*).

The impact humanity has on biodiversity is largely determined by the social and economic activities of societies. For example, the transformation of primary forest into agricultural land, which is the direct driver of the loss of many species, is caused by a variety of indirect socioeconomic drivers. Market pressures, land tenure arrangements, poverty, and various regulatory frameworks all play a role (Chomitz 2007). Similarly, the dynamics of fishery exploitation depend on international law and negotiation at a large scale, and community management practices, financial resources, and the availability of markets play a significant role at a smaller scale (MA 2005*b*). As can be seen from these examples, an understanding of the connections between socioeconomic factors and environmental outcomes is crucial if effective strategies for managing the environment are to be developed (cf. Vitousek et al. 1997). We compared the ability of several statistical models to predict biodiversity loss. Each model contained different combinations of socioeconomic variables representing different theories regarding the indirect drivers of environmental impact.

Despite the importance of socioeconomic factors as indirect drivers of biodiversity loss, their role has been overlooked until quite recently (Naidoo & Adamowicz 2001; Asafu-Adjaye 2003). This recent empirical work has its origins in a longer tradition of literature examining the relationship between socioeconomic factors and environmental change in general (e.g., Ehrlich & Holdren 1971; World Bank 1992; York et al. 2003). Most of these studies, as well as the two recent studies that examined biodiversity loss specifically, focused primarily on the economy and particularly on its overall size. They generally looked at the relationship between environmental change and gross domestic product (GDP) or GDP per capita. Naidoo and Adamowicz (2001), for example, found that GDP per capita is a significant predictor of the number of species threatened for five out of seven taxonomic groupings, in which higher values were associated with more threatened species in four of those

five cases. Asafu-Adjaye (2003), in a similar vein, found that higher rates of economic growth are associated with greater biodiversity loss. In addition he found that composition of the economy (in this case, the proportion of GDP contributed by agricultural production) is an important determinant of biodiversity loss. In a similar analysis at a smaller scale Taylor and Irwin (2004) used a regional proxy for GDP and found that greater economic activity is associated with higher numbers of introduced exotic plant species in the United States and Canada.

## Inequality and Biodiversity Loss

Studies of how economic concerns contribute to species loss have not analyzed the consequences of the distribution of economic wealth. Nevertheless, extensive empirical evidence demonstrates that inequality has a negative effect on other social outcomes and institutions (e.g., Ronzio et al. 2004; Ross et al. 2005; Wilkinson & Pickett 2006). For example, a study of community forestry in Mexico showed that village forest management was correlated with levels of inequality. In a village with an economic structure that was highly unequal, forests were managed poorly because small groups of powerful people manipulated the logging industry for their own benefit, resulting in overexploitation. In more equitable villages, however, community institutions were more effective, resulting in better forest management and likely less biodiversity loss (Klooster 2000).

Researchers propose that social inequality has a significant effect on the environment (e.g., Ostrom 1990; Boyce 1994; Baland et al. 2007). Olson (1965) suggests that small groups with considerable inequality might favor the provision of a public good. The expectation is that when the majority of the wealth is held by a few resource users, it is in their interest to conserve, regardless of what the poorer members of the group do. Some more recent analyses also support this perspective (e.g., Itaya et al. 1997). Nevertheless, others suggest that inequality may hinder conservation, and empirical work shows that inequality can thwart the collective action required for environmental protection (Boyce 1994; Dayton-Johnson & Bardhan 2002; Baland et al. 2007). Although these studies suggest a connection between inequality and environmental degradation, the direction and strength of the relationship with biodiversity were revealed only recently (Mikkelsen et al. 2007).

Mikkelsen et al. (2007) found that greater inequality is associated with the number of threatened species (International Union for Conservation of Nature [IUCN] Red

List data) at the international scale when human population, GDP, and the total number of species are controlled for. The situation is similar in the United States for species of birds: states with higher socioeconomic inequality tend to have a greater proportion of species undergoing population decline (Mikkelsen et al. 2007). Here we used a more recent version of the IUCN Red List. These are the only data on species endangerment that are global in scope; thus, despite some well-known shortcomings (Akçakaya et al. 2006), they are uniquely appropriate for a cross-national comparison of threatened species.

Our work here is a significant extension of the work by Mikkelsen et al. (2007). In particular we partitioned data by taxonomic group and partitioned countries according to their level of development; both of these analyses were additional to Mikkelsen et al. We also tested a broader range of competing models across a greater number of countries than Mikkelsen et al. did. To evaluate this range of models we used a comparison approach, whereby we developed competing models, each based on theoretical expectations of the indirect drivers of environmental change, and assessed which best predicted differing rates of biodiversity loss among countries. To address the role of collinearity among independent variables we also included an analysis based on hierarchical partitioning to evaluate the independent contribution of each variable (Mac Nally 2000).

## Methods

To determine which socioeconomic factors are most likely to be indirect drivers of biodiversity loss we used a model comparison approach. We evaluated the following six models: (1) saturated, includes all variables, (2) stepwise-reduced, stepwise deletion of terms from the saturated model, (3) population density only, (4) economic footprint, simplified version (York et al. 2003) of the IPAT (impact = population  $\times$  affluence  $\times$  technology) framework (Ehrlich & Holdren 1971) that includes population density and GDP per capita (together these provide a measure of total economic activity per unit of land area), (5) economic footprint + inequality and (6) environmental governance, includes the index of environmental governance as only term.

In addition to the variables mentioned above we controlled for the level of species endemism in all models. The economic footprint models were evaluated with and without the square of GDP included in addition to the linear GDP term. This tested for nonlinear responses, particularly the hypothesized—but only weakly supported—environmental Kuznets curve (EKC), which suggests that environmental indicators will deteriorate through the ini-

tial stages of economic growth but will improve in the later stages (Stern 2004).

We used adjusted  $R^2$  and the Akaike information criterion (AIC) from an ordinary least-squares multiple linear regression to compare models for predictive power and parsimony, respectively. When comparing the fit of several models, AIC provides a criterion (penalized log likelihood) with which to find the model that best explains the data with a minimum of free parameters (Akaike 1974; Burnham & Anderson 2004). We also used a correction for small sample sizes when necessary. Countries were not weighted in the analyses (either by country area or by human population). We decided that because each country has a single, independent set of institutions, all countries should be treated equally. For the sake of consistency at the model comparison stage we only included countries that had data for all the variables in the saturated model. The model that performed best according to the corrected AIC was then tested for consistency between development categories as defined by the United Nations Development Programme (UNDP)'s Human Development Reports (UNDP 2006). Because this model included fewer total variables than the full-model comparison, we were able to include more countries in the sample at this stage of analysis.

We used hierarchical partitioning to address collinearity in our data set and assess the independent explanatory power of each variable. This statistical method analyzes all possible models in a multiple regression to identify the contribution of each variable to the total variance, both independently and in conjunction with the other variables, to infer the causal impact of each variable (Chevan & Sutherland 1991; Mac Nally 2000; Quinn & Keough 2002).

We applied the hierarchical partitioning approach with the 'hier.part' package (Walsh & Mac Nally 2008) in R (R-Project 2008). The same model format was used as in the model comparison, with identical variable transformations. We assumed Gaussian errors and calculated goodness of fit with  $R^2$ . The statistical significance of the independent effect of each variable was determined by a randomization approach ( $n = 1000$ ) that produced  $Z$  scores (Mac Nally 2002).

## Data Sources

To measure the status of biodiversity in each country we looked at the proportion of plant and vertebrate species that were threatened in 2007, as defined by the IUCN (2007). For most of this analysis we looked at combined data for plants and vertebrates; however, we also applied our best-performing model to data partitioned between plants and five animal classes. Data on the total number of plant and vertebrate species known and threatened in each country were obtained from the World Resources Institute's EarthTrends database (WRI 2007). Using

the proportion of species threatened, we implicitly controlled for the total number of species known, which varies between countries by more than two orders of magnitude and is related to the number of species threatened. The IUCN defines threat to individual species at a global level, meaning that the threat status for species with wide ranges will be the same for all of the countries they overlap, even though those countries may be managing the species very differently. This challenges one of the assumptions of our analysis, namely, that the socioeconomic variables we measured at the country level have an impact on the threat status of species at the same scale. That assumption may not be entirely true, but there is no reason to expect this issue will bias the results in any particular direction.

All else being equal, the risk of global threat of extinction for a species is greater for highly endemic species than for those that are widespread. It is, therefore, important to control for levels of endemism when comparing the numbers of threatened species among countries. Endemism data for plants are unavailable for many countries; however, endemism data for vertebrates alone are relatively complete. Controlling for endemism with data from all plants and vertebrates combined restricted the number of countries with data for all variables in our target-year range to 40, in contrast to the 50 countries available for the sample when we used endemism data for vertebrates only. In addition to improving the sample size an index of endemism based on vertebrates has more explanatory power with respect to the proportion of species that are threatened (adjusted  $R^2 = 0.33$ ,  $p < 10^{-16}$ ) than does an index of endemism based on both plants and vertebrates (adjusted  $R^2 = 0.15$ ,  $p < 10^{-6}$ ). We, therefore, used an index of endemism based on vertebrates for the rest of the analyses. The correlation between this index of vertebrate endemism and an equivalent one generated for plants was high (Pearson's correlation = 0.76;  $p < 0.001$ ).

### Socioeconomic Data

Gross domestic product (GDP) per capita was used as an indicator of the intensity of economic activity in a country. Instead of raw GDP per capita, we used data that were normalized for purchasing power. This corrected for differences in cost of living and exchange rates between countries and thus provided a better estimate of economic activity in the country in question. We obtained GDP data from the WRI's EarthTrends database for all years between 1975 and 1999 (WRI 2007). To achieve larger sample sizes we averaged GDP over 5-year periods (Fig. 1) because in any given year many countries are missing data.

We measured environmental governance with an index calculated by the Yale Center for Environmental Law and Policy (YCELP 2005). This index is a composite of

several variables, including general governance indicators (such as corruption and the level of democracy) and factors more specific to the environment (such as knowledge creation in environmental science and the number of IUCN member organizations). One deficiency of the environmental governance data is that they are not available over the same time scale as the GDP data: only recent (2005) values are available (Fig. 1).

Inequality was measured with the Gini index, which ranges (theoretically) from 0 to 100, where 0 is perfect equality and 100 is perfect inequality (Milanovic 2005). In practice, national Gini indices between 1995 and 1999 ranged from a high of 59 (Brazil) to a low of 23 (Slovakia). We used the Standardized Income Distribution Database (SIDD) as our source for the Gini index (SIDD 2005). This is a relatively new database that has corrected data inconsistencies that were a problem for previous studies of inequality (Babones & Alvarez-Rivadulla 2007). In a similar fashion to the treatment of GDP data, we averaged Gini values over 5-year periods to improve the sample size. The SIDD contains interpolated estimates of inequality for years and countries that do not have original data available. Because of concerns regarding the reliability of these interpolations we used only original data (Fig. 1).

### Time Lag between Human Activity and Effect on Biodiversity

The effects of human activity on biodiversity are not immediate; rather, species populations will respond to anthropogenic impacts after a delay. The length of this time lag depends on both the species and the impact in question. Mikkelsen et al. (2007) found that socioeconomic data for 1989 were most strongly related to species indicators for 2004. In this paper we addressed multiple potential time lags by analyzing data from all 5-year periods between 1975 and 1999. We compared results between the time periods for simple models with only the variables for which time series data were available (population density, GDP, and inequality). To avoid a sampling effect this comparison included only countries that had data for all three variables and all five time periods. When adjusted  $R^2$  values were compared among the models from different time periods, the 1980–1984 time period showed the best predictive power (adjusted  $R^2 = 0.35$ ). Throughout we present results from the period 1980–1984.

## Results

Initially we ran models that included both the linear (Gini) and the quadratic (Gini<sup>2</sup>) inequality term. This tested for the U-shaped relationship between inequality and conservation proposed by Baland and Platteau (1999). In all cases the quadratic Gini was not significant, so we left it out of the models presented here. Similarly, initial models also included the quadratic form of GDP to

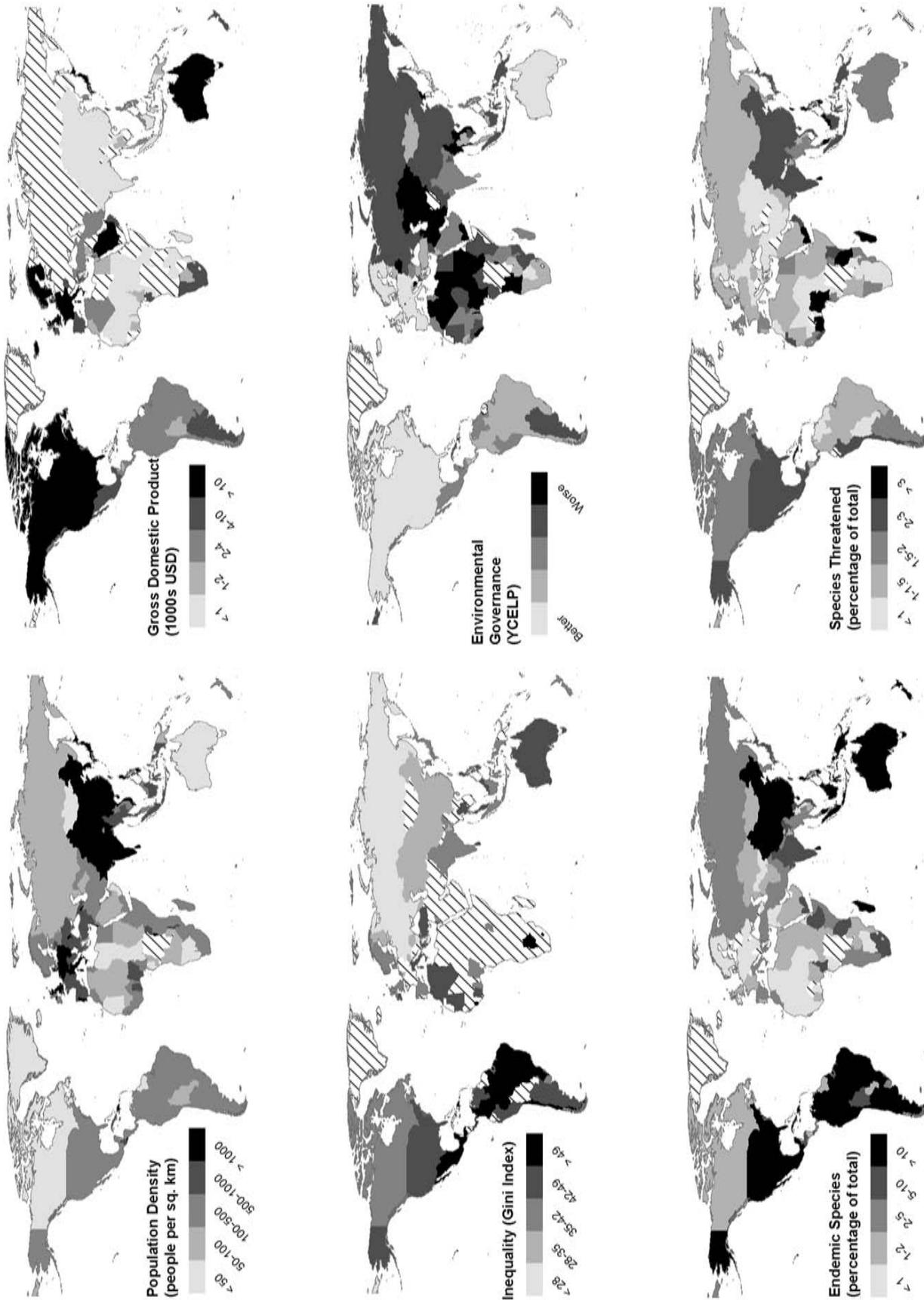


Figure 1. Data used in the analysis of socioeconomic predictors of biodiversity loss, with missing data represented by diagonal hatching. The measure of environmental governance is a unitless index developed by the Yale Center for Environmental Law and Policy (YCELP 2005), whereas the units for other terms are given in the figure. Population density, gross domestic product, and inequality are all from the time period 1980–1984. Environmental governance data are from 2005, data on proportion of endemic species threatened are from 2006, and data on proportion of species threatened are from 2007.

test for the presence of a U-shaped relationship between GDP and species threatened, as predicted by the EKC hypothesis (World Bank 1992; Stern 2004). Nevertheless, the quadratic term was not significant in any of the models examined, so the EKC models were discarded in favor of models with linear GDP.

Among the 50 countries with sufficient data in the 1980–1984 time period, the fully saturated model explained 48.6% of the total variance (adjusted  $R^2$ ) in the proportion of plant and vertebrate species threatened (Table 1). These countries represented 48.7% of the world's land area and 70.9% of its human population. Of the variables included, only the proportion of vertebrate species endemic to the country stood out as significant. Endemism had a positive coefficient, meaning that higher levels of endemism were related to a greater proportion of threatened species.

The use of AIC in a stepwise simplification of the saturated model resulted in a model that included only GDP, inequality, and endemism. These remaining terms were all significant at the  $p < 0.05$  level. The regression coefficients for all remaining variables were of the same sign and, as in the saturated model, wealthier economies and more equitable ones both tended to be associated with fewer threatened species. This simplified model had an equivalent adjusted  $R^2$  to the fully saturated model (0.486). It also had the best (lowest) corrected AIC score of all 6 models, with a 47.7% probability of being the best fitting model, according to the Akaike weight (Table 1). The Gini index had a positive coefficient, meaning that greater inequality was associated with a greater proportion of species threatened (Fig. 2).

The population density model performed the worst of the six models. The population density term itself was not significant, and the adjusted  $R^2$  was only 0.364 (Table 1).

The economic footprint model retained three of the seven variables in the saturated model and explained

43.9% of the variance in the proportion of species threatened. Of the three variables included, GDP per capita and endemism were significant, whereas population density was not. In the case of all four variables the direction of their effect was the same as in the saturated model (Table 1).

The economic footprint + inequality model had the second-best corrected AIC after the stepwise-reduced saturated model and had a 33.6% probability of being the best fitting model (Table 1). Summing the Akaike weights of the models containing inequality yielded an 81.3% probability that one of them was the best model. Adding the Gini index increased the adjusted  $R^2$  from 0.439 to 0.492. Three of the four terms in the model were significant; the exception was population density. No coefficients changed sign compared with the saturated model (Table 1).

The final model introduced a new variable: environmental governance. This term was not significant at the  $\alpha = 0.05$  level, and the model as a whole performed poorly relative to the others in terms of the corrected AIC and the adjusted  $R^2$  (Table 1). The sign of the coefficient was expected—that better environmental governance was associated with a lower proportion of species threatened—however, this relationship was weak.

When we used the best-performing model—stepwise-reduced—with data partitioned by level of development, only high- and medium-development categories could be compared because there were insufficient data on low-development countries. The coefficients for each term at the model comparison stage were consistent across all development categories (Table 2). The strength of the model as judged by the adjusted  $R^2$  value was greatest for the high-development category and declined with the level of human development. Neither GDP nor inequality was significant when countries were split by development category.

**Table 1.** Comparison of models predicting the proportion of plant and vertebrate species threatened (log).<sup>a</sup>

| Independent variable                       | Model <sup>b</sup>   |                                 |                       |                                  |                                            |                                        |
|--------------------------------------------|----------------------|---------------------------------|-----------------------|----------------------------------|--------------------------------------------|----------------------------------------|
|                                            | saturated<br>$\beta$ | stepwise-<br>reduced<br>$\beta$ | population<br>$\beta$ | economic<br>footprint<br>$\beta$ | econ. footprint +<br>inequality<br>$\beta$ | environmental<br>governance<br>$\beta$ |
| GDP per capita (log)                       | -0.258*              | -0.215**                        | -                     | -0.186**                         | -0.191**                                   | -                                      |
| Population density (log)                   | 0.059                | -                               | 0.097                 | 0.051                            | 0.070                                      | -                                      |
| Inequality (Gini index)                    | 0.020*               | 0.019*                          | -                     | -                                | 0.021*                                     | -                                      |
| Environmental governance                   | 0.113                | -                               | -                     | -                                | -                                          | -0.202                                 |
| Proportion of vertebrates<br>endemic (log) | 0.249**              | 0.225**                         | 0.385***              | 0.331***                         | 0.243**                                    | 0.317***                               |
| Constant                                   | -2.09                | -2.46                           | -2.87                 | -1.53                            | -2.61                                      | -3.06                                  |
| Adjusted $R^2$                             | 0.486                | 0.486                           | 0.364                 | 0.439                            | 0.492                                      | 0.378                                  |
| Corrected AIC                              | 68.7                 | 66.0                            | 75.5                  | 70.4                             | 66.7                                       | 74.3                                   |
| Akaike weight                              | 0.124                | 0.477                           | 0.004                 | 0.052                            | 0.336                                      | 0.008                                  |

<sup>a</sup>All evaluated with the same set of 50 countries.

<sup>b</sup>Significance: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .

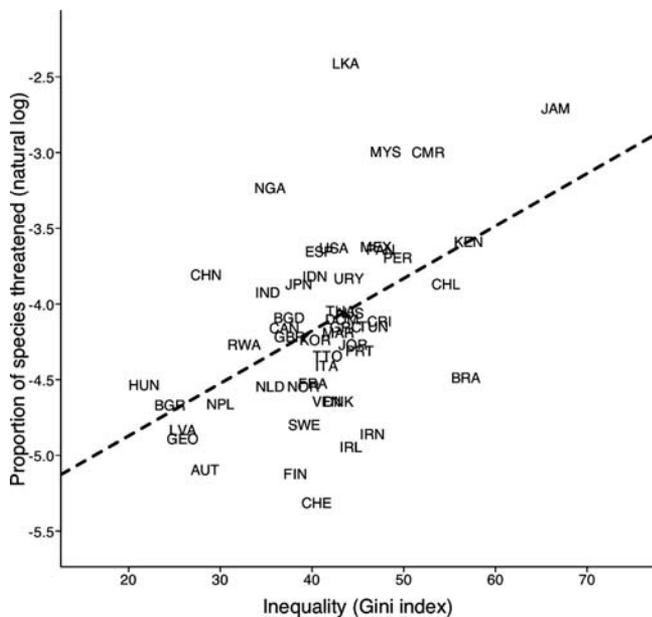


Figure 2. Correlation between the Gini index and the proportion of species threatened (dashed line, best fit of that relationship). Countries indicated by the three-letter codes assigned by the International Organization for Standardization (ISO).

The results of hierarchical partitioning further supported our model analyses by consistently identifying three variables—the proportion of endemic species, inequality, and the size of the economy—as important predictors of the proportion of species threatened for both time periods ( $p < 0.01$ ). This accounted for collinearity and showed the independent importance of each of these three variables (Fig. 3). In our models the total independent contribution accounted for over 60% of the total explained variance.

Analyzing our data by taxonomic group revealed different patterns among taxa (Table 3). As mentioned above, we tested different taxa with the stepwise-reduced model. Partitioning the data resulted in never significant

GDP per capita and inequality terms for all five classes of vertebrates (mammals, birds, reptiles, amphibians, and fish). Nevertheless, inequality was significantly and positively associated with the proportion of threatened plant species ( $\beta = 0.018$ ,  $p < 0.05$ ), whereas GDP per capita was significantly negatively associated with threatened plant species ( $\beta = -0.204$ ,  $p < 0.01$ ). Model fit was lower than that for the combined data for all taxonomic groups except amphibians (adjusted  $R^2 = 0.532$ ). The same analysis with the hierarchical partitioning approach returned similar results, with one important difference: the inequality term was also significantly and positively associated with threatened species for amphibians (Table 3). The GDP per capita term was significant for mammals and plants. Nevertheless, the amount of variance explained by the independent variables dropped below 50% for all the taxa except plants and amphibians.

## Discussion

Patterns of biodiversity loss are complex, and no single statistical model can predict them perfectly. Nevertheless, our analysis shows that much of the variation seen between countries can be explained by a few socioeconomic variables, among which inequality is a key factor. Two models, population density and environmental governance, performed poorly relative to others. The poor performance of the former suggests that population numbers alone are not a particularly good indicator of the environmental impact of a society, as some authors have suggested (Boserup 1965; Ehrlich 1968). A broadened conception of environmental impact that includes the economic characteristics of a society seems more effective at predicting biodiversity loss than population alone. The poor performance of the environmental governance model was an interesting finding and may indicate that although governance has an effect, it is small relative to the impact of the economy. This conclusion should be drawn with caution, however. An aggregate measure such as the

Table 2. Comparison among development categories of the prediction by the stepwise-reduced model of the proportion of plant and vertebrate species threatened (log)<sup>a</sup>.

| Independent variable                    | All countries <sup>b</sup><br>$\beta$ | Countries with high human development <sup>b</sup><br>$\beta$ | Countries with medium human development <sup>b</sup><br>$\beta$ |
|-----------------------------------------|---------------------------------------|---------------------------------------------------------------|-----------------------------------------------------------------|
| GDP per capita (log)                    | -0.199**                              | -0.232                                                        | -0.395                                                          |
| Inequality (Gini index)                 | 0.025*                                | 0.019                                                         | 0.038                                                           |
| Proportion of vertebrates endemic (log) | 0.235**                               | 0.300**                                                       | 0.208                                                           |
| Constant                                | -2.70                                 | -1.91                                                         | -2.01                                                           |
| Adjusted $R^2$                          | 0.428                                 | 0.477                                                         | 0.222                                                           |
| $n$                                     | 53                                    | 30                                                            | 19                                                              |

<sup>a</sup>Insufficient data in the low-development category prevented its inclusion here.

<sup>b</sup>Significance: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .

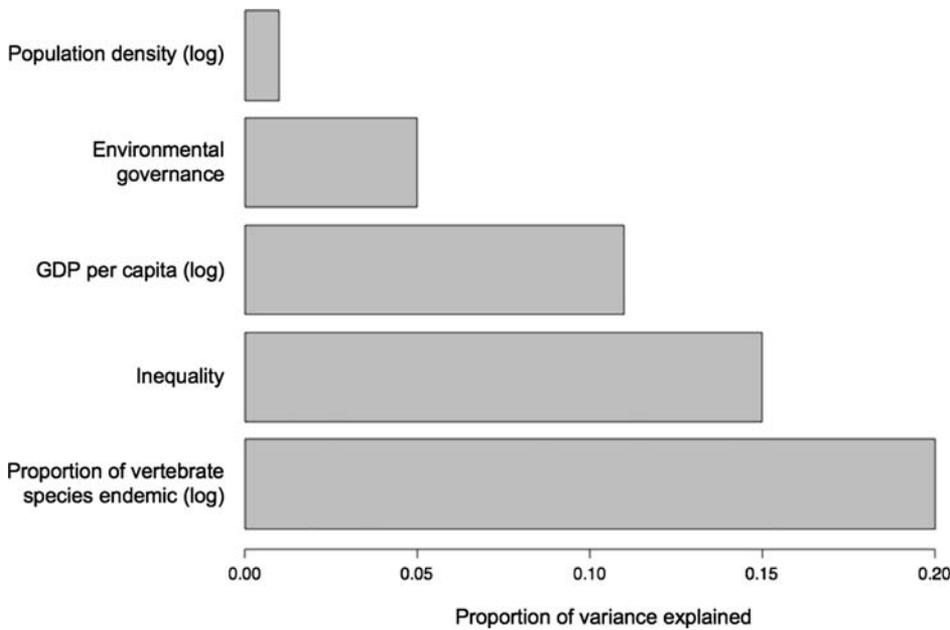


Figure 3. Independent effect of each variable on the proportion of plant and vertebrate species threatened (asterisk [\*], independent effects significant [p < 0.05]; GDP, gross domestic product).

one produced by the YCELP may not sufficiently capture the complexities of environmental governance. Also, because the YCELP data only go back to 2005, they do not account for a time lag between the quality of governance and the biodiversity outcome. Any large changes in environmental governance that occurred prior to 2005 would thus interfere with the detection of a relationship between governance and biodiversity.

**The Role of Affluence and Economy Size**

Similar to York et al. (2003), we found that total size of a country’s economy relative to its population was a significant predictor of environmental indicators. Nevertheless, in their study, they found that ecological footprint increases monotonically with increasing GDP per capita, whereas we found that the proportion of species threatened decreased with increasing GDP per capita. Other researchers found that greater affluence negatively affects biodiversity (Naidoo & Adamowicz 2001; Taylor & Irwin 2004), whereas we found the reverse. These differing results suggest the nature of the relationships between

population size, affluence, total size of the economy, and species loss merit further study.

The predictive power of our models was about half that of the models used by York et al. (2003) when equivalent sets of terms were compared. This is likely because they used a measure of human impact as their dependent variable, whereas we used an outcome (the number of threatened species) of that impact. By proceeding one step further down the causal chain we introduced more variation; however, we also gained a better understanding of the actual outcomes of human impact, which is ultimately where our interest lies.

The two most useful models for explaining the proportion of species threatened were the stepwise-simplified model and the economic footprint + inequality model. The former included GDP per capita, inequality, and the proportion of endemic species, whereas the latter contained the same three variables, with population density added (Tables 1 & 2). The explanatory power of these models with all countries included (adjusted R<sup>2</sup> = 0.486 and 0.492, respectively) was lower than that of the full models developed by Naidoo and Adamowicz (2001),

Table 3. Results of hierarchical partitioning analysis in which values shown are the independent effect of each variable on the proportion of species threatened in each taxonomic group.

| Independent variable                    | Plants and vertebrates | Mammals | Birds | Reptiles | Amphibians | Fish  | Plants |
|-----------------------------------------|------------------------|---------|-------|----------|------------|-------|--------|
| GDP per capita (log)                    | 0.11*                  | 0.08*   | 0.01  | 0.04     | 0.05       | 0.16* | 0.14*  |
| Population density (log)                | 0.01                   | 0.02    | 0.01  | 0.04     | 0.02       | 0.01  | 0.01   |
| Inequality (Gini index)                 | 0.15*                  | 0.02    | 0.03  | 0.01     | 0.07*      | 0.01  | 0.13*  |
| Environmental governance                | 0.05                   | 0.03    | 0.01  | 0.10*    | 0.11*      | 0.09* | 0.05   |
| Proportion of vertebrates endemic (log) | 0.20*                  | 0.21*   | 0.43* | 0.11*    | 0.39*      | 0.01  | 0.18*  |

\*p < 0.05.

which also predicted the proportion of species threatened (deviance  $R^2$  values of between 0.50 and 0.84 for different classes of animals and plants). Our models, however, explained this variation with fewer terms.

The stepwise-reduced model had the most predictive power among countries at higher levels of development. This may be indicative of two things. First, data quality is better in wealthier countries, so it is reasonable to expect that patterns will be easier to detect there. Second, it may be that institutions are more effective at regulating the environment in rich countries than in poor ones, so variables expected to alter the effectiveness of institutions, such as inequality, may have a greater effect in countries at high levels of development (cf. Ostrom 1990, 2001). The strength of the model also varied across taxa, with plants and amphibians generally being the best predicted, and fish and reptiles the least. This may be the result of differences in range sizes among taxa and thus in the degree to which species are affected by activities in particular countries. What determines the variation among taxa in their relative sensitivity to human economic and social activity requires further study.

### The Role of Inequality

The inequality term had a significant positive coefficient in all models in which it was included and had a stronger independent effect on the proportion of threatened species than GDP per capita (Fig. 3). The stepwise-reduced model provided the most conservative regression coefficient for the inequality term (0.019; Table 1). With this value, the 8-point difference in the Gini index between the United Kingdom (Gini = 42) and Spain (Gini = 34) could represent an increase from 2.6% to 3.0% in the proportion of species threatened if Spain saw its inequality increase to the level of the United Kingdom. Alternatively, taking a time-scale approach, the 5-point change in the Gini index in the United States from 1990 to 1997 (from 44 to 49) could eventually be associated with an increase in the proportion of species threatened in the United States from 2.7% (as it is now) to 3.0%, all else being equal.

There are many mechanisms by which inequality may influence biodiversity, and these can be categorized as individual or collective effects. Individual effects are those in which the inequality changes the incentives and behavior of individuals, and collective effects are those that are mediated through environmental management institutions. Institutions, either formal or informal, play an important role in how communities or nations manage their natural resources. Biodiversity, although not always managed directly, is closely linked to the fate of those natural systems. Communally owned resources are not necessarily doomed to overexploitation. Collective decision making and action, when effective, can avoid the "tragedy of the commons" (Ostrom 1990). Greater inequality, however, often interferes with the effectiveness

of these institutions (Boyce 1994; Dietz et al. 2003). Individuals are less likely to have common goals, and the wealthy will be more able to insulate themselves from the problems faced by the rest of the group. As these institutions weaken, so too will the effective management practices that biodiversity ultimately depends on.

The presence of both individual and collective effects is at the core of the theory that environmental degradation should be greatest in intermediate-equality societies and lowest in highly equal and highly unequal societies (Baland & Platteau 1999). In very unequal societies, individuals will have an incentive to conserve the resources they profit from, which would have a beneficial effect on biodiversity (Olson 1965). In contrast, in very equal societies, groups will collectively manage conservation more effectively (Ostrom 1990). This U-shaped relationship, with better conservation at the extremes of inequality, was not supported by our results. The quadratic Gini term was never significant in our models. It may be that countries are generally too large for individual-level conservation decisions to directly benefit the individuals themselves; therefore, this potentially positive effect of inequality may not occur at the scale of countries. In the absence of individual-level effects institutional effects would dominate the pattern, meaning that only a monotonic increase in degradation and biodiversity loss would be seen as inequality increases. This is the pattern demonstrated by our results.

An awareness of economic distribution improves the understanding of the socioeconomic drivers of biodiversity loss. The importance of inequality as a determinant of environmental degradation in general is asserted theoretically by many different disciplines (Ostrom 2001; Dayton-Johnson & Bardhan 2002; Ronzio et al. 2004; Baland et al. 2007). Our study and Mikkelsen et al.'s (2007) study provide clear empirical confirmation of the importance of inequality as a predictor of biodiversity loss in particular. The results of the hierarchical partitioning analysis suggest that there is an independent causal relationship with inequality, although plants and amphibians seem to be most affected. Although the average level of affluence is an important explanatory factor, the inclusion of the Gini index consistently improved our ability to predict the numbers of threatened species. The distribution of the economy is a factor that cannot be ignored as researchers work to understand those processes that drive humanity's impact on biodiversity.

### Acknowledgments

We thank G. Mikkelsen for helpful discussion throughout this research and G. Meffe and four anonymous reviewers for thoughtful comments that greatly improved this manuscript. We thank V. Bahn, S. Breau, J. Cardille, and B. McGill for help and advice. This research was supported

by grants from the National Sciences and Engineering Research Council and the Canada Research Chairs program.

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