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Research

Social-Ecological Predictors of Global Invasions and Extinctions

Aaron Lotz [1] *and Craig R. Allen* [2]

ABSTRACT. Most assessments of resilience have been focused on local conditions. Studies focused on the relationship between humanity and environmental degradation are rare, and are rarely comprehensive. We investigated multiple social-ecological factors for 100 countries around the globe in relation to the percentage of invasions and extinctions within each country. These 100 countries contain approximately 87% of the world's population, produce 43% of the world's per capita gross domestic product (GDP), and take up 74% of the earth's total land area. We used an information theoretic approach to determine which models were most supported by our data, utilizing an a priori set of plausible models that included a combination of 15 social-ecological variables, each social-ecological factor by itself, and selected social-ecological factors grouped into three broad classes. These variables were per capita GDP, export-import ratio, tourism, undernourishment, energy efficiency, agricultural intensity, rainfall, water stress, wilderness protection, total biodiversity, life expectancy, adult literacy, pesticide regulation, political stability, and female participation in government. Our results indicate that as total biodiversity and total land area increase, the percentage of endangered birds also increases. As the independent variables (agricultural intensity, rainfall, water stress, and total biodiversity) in the ecological class model increase, the percentage of endangered mammals in a country increases. The percentage of invasive birds and mammals in a country increases as per capita GDP increases. As life expectancy increases, the percentage of invasive and endangered birds and mammals increases. Although our analysis does not determine mechanisms, the patterns observed in this study provide insight into the dynamics of a complex, global, social-ecological system.

Key Words: *biodiversity; endangered species conservation; extinctions; invasions; invasive species management; social-ecological systems*

INTRODUCTION

Multiple forces, exacerbated by human activity, interact to cause the decline of many species (Wilson 2002). Humanity's global influence is orders of magnitude greater than that of any other species, primarily because of the large human population size, anthropogenic CO_2 production, biomass consumption, energy use, and geographical range size (Fowler and Hobbs 2003). The debate as to what aspects of humanity are most responsible for environmental degradation has been ongoing since the 1970s (Commoner et al. 1971, Ehrlich and Holdren 1971). Regardless of particular mechanisms, current governance regimes have been largely unable to mitigate the decline of the Earth's supporting services (United Nations Environment Programme 2007).

One of the unresolved problems at the forefront of global environmental concerns is the increase in biological invasions and extinctions. Tens of thousands of invasive plants and animal species are established; however, predicting their success and impact on ecosystems has proven elusive. There are few generalities in the field of invasion ecology (reviewed in Martin 2011) and even fewer studies with demonstrable evidence of negative impacts of invasive species at a national scale (studies of plants were reviewed in Powell et al. 2011). Invasive species can alter populations, communities, and ecosystems via predation, hybridization, niche displacement, competitive exclusion, and possibly extinction (Mooney and Cleland 2001). The decline of native species may follow invasions, allowing more invasive species to become established and affecting ecosystem processes at varying scales (Williamson 1996, Vitousek et al. 1997, Forys and Allen 2002).

Biodiversity had been increasing for the past 600 million years until very recently (Signor 1990), yet studies indicate a recent global decline in biodiversity and an increase in pressures on biodiversity (Butchart et al. 2010). Changes in biodiversity because of human actions have been more profound in the last 50 years than in the whole of prior recorded human history; 52% of cycads, 32% of amphibians, 25% of conifers, 23% of mammals, and 12% of bird species are currently threatened with extinction (Millennium Ecosystem Assessment 2005). According to the International Union for the Conservation of Nature's (IUCN) Invasive Species Specialist Group (ISSG), 1159 species have possibly gone extinct and 22% of vertebrates, 41% of invertebrates, and 70% of plants are endangered (Vié et al. 2009). The integrity of ecosystems declines with the loss of native species (Noss 1995, Sanders et al. 2003) and may affect the delivery of ecosystem services (Ehrlich and Ehrlich 1992). Extinction rates are 100 to 1000 times their prehuman levels (Pimm et al. 1995, United Nations Environment Programme 2007). This potential loss of native species diversity may disrupt the numerous ecological processes that inherently shape landscape structure, such as

[1]University of California, Davis, [2]Nebraska Cooperative Fish and Wildlife Research Unit

predator-prey dynamics, dispersal, foraging behavior, functional group composition, and the very resilience of ecosystems (Peterson et al. 1998).

Studies have recognized the need to couple human and environmental systems (Turner et al. 2003, Fischer et al. 2012) and have noted the convergence of environmental and financial markets (Sandor et al. 2002), the importance of social-cultural dynamics in natural resource management (Stratford and Davidson 2002), and the tremendous impact of humans on the environment in comparison to other species (Fowler and Hobbs 2003). Numerous studies have focused on only one aspect of the social-ecological relationship, for example carbon emissions (Kratena 2004), water (Postel 2003), and human population growth (Struglia and Winter 2002). Three recent projects have attempted to focus on and integrate multiple social-ecological factors at a national scale, with an emphasis on their roles in an ecologically sustainable society, and have created an index of values that can be ranked and compared.

In 2003, the Global Footprint Network was begun in an effort to establish and maintain a sustainable future. As part of that effort, the Ecological Footprint was created. This metric, composed of five levels and six subcategories, calculates natural resources' availability and the amount and distribution of human natural resource use, to track human demands on the biosphere (Ewing et al. 2008). The Socioeconomic Data and Applications Center (SEDAC) of the United States National Aeronautics and Space Administration (NASA) published three indexes: the 2005 Environmental Sustainability Index, or ESI (Esty et al. 2005), the 2006 Environmental Performance Index , or EPI (Esty et al. 2006), and the 2008 EPI (Esty et al. 2008). Each index was developed to explore the relationships, at a national scale, among multiple social-ecological factors and their effect on a country's environmental performance and sustainability. In 2004, the Environmental Vulnerability Index (EVI) was created by the South Pacific Applied Geoscience Commission (SOPAC) and the United Nations Environment Programme to provide a rapid and standardized method of assessing a country's vulnerability to negative impacts on sustainable development (Kaly et al. 2004).

These indices demonstrated that economic, demographic, environmental, and societal variables are not mutually exclusive, but are highly integrated and have profound impacts on a country's sustainability. The indices create a single condensed quantity based on multiple multidimensional variables (Ebert and Welsch 2004). There is a clear need for better models that can help elucidate the complex interactions between humans and their environment (Balmford et al. 2005). We utilize a unique set of social-ecological factors to explore the relationships of the factors with the percentage of endangered and invasive birds and mammals within 100 countries.

METHODS

We utilized a suite of social-ecological variables to determine which variables or combinations of variables predict the percentage of endangered and invasive birds and mammals for 100 countries. We utilized 15 social-ecological factors that fall into 3 broad groups: economic, ecological, and social/ governance variables. These variables are described below. We also assessed three other factors (total population, latitude, and total land area) and two reference indexes (ESI and EVI).

Variables

Economic variables

1. Per capita GDP. Per capita gross domestic product (GDP), a standard measure of affluence, has been shown to have a curvilinear relationship with environmental impact; this relationship has been termed the environmental Kuznets curve, or EKC (Cavlovic et al. 2000, Stern 2004, Dietz et al. 2007). Species richness of invasive plants (Liu et al. 2005) and all invasive taxonomic groups combined (Lin et al. 2007) are both positively correlated with increased per capita GDP.
2. Export-import ratio. International trade positively affects a country's income (Frankel and Romer 1999); therefore, limiting trade limits a country's income and subsequently diminishes opportunities for biological invasions. In fact, a closed international trade policy helped Eastern European bloc countries limit invasive bird species introductions during the Cold War (Chiron et al. 2010).
3. Tourism. Based on tourist arrivals per capita (mass tourism) and tourism expenditures per GDP (individual tourism), Freytag and Vietze (2010) suggest that nature is an influential factor in individual tourism demand. Tourism in a country is positively correlated with its degree of biodiversity, and a high degree of endangered biodiversity is negatively correlated with tourism (Freytag and Vietze 2009).
4. Undernourishment. Malnutrition reduces the economic performance of people and promotes unsustainable farming practices that can lead to more poverty, political instability, violence, and environmental degradation (Gonzalez 2004, 2006, Chapman et al. 2006). Smith et al. (2010) suggest that on a global scale, regions with high levels of undernourishment have weaker governance, which results in a failure of governments to regulate overfishing, bycatch, and the environmental impacts of aquaculture.

5. Energy efficiency. Energy efficiency is a measure of technology. As technology improves, humans become more energy efficient. Environmental impacts therefore can be potentially reduced via "refinement of production" or superindustrialization (Mol 1995).

Ecological variables

1. Agricultural intensity. An increase in agricultural energy efficiency could reduce the withdrawal of freshwater, which would in turn lessen the impact on the environment (Kates and Parris 2003) and lead to improvements in the supply of ecosystem services (Carpenter et al. 2006).

2. Rainfall. Mean annual precipitation is positively correlated with the number of threatened bird and mammal species in a global country-by-country analysis (McKee et al. 2003) and is positively correlated with the overall density of endangered species within the United States at the state level (Dobson et al. 1997).

3. Water stress. Running-water ecosystems, which may be the most impacted ecosystems on the planet, may be rapidly degrading because of damming, diversion, and extraction (Malmqvist and Rundle 2002). On a state-by-state analysis in the United States, human water use was positively correlated with the density of endangered reptiles (Dobson et al. 1997).

4. Wilderness protection. Wilderness protection is an essential factor in the preservation and conservation of the remaining biodiversity worldwide; such protection has been shown to be effective (DeFries et al. 2005, reviewed in Fischer et al. 2006). Well-managed protected wilderness areas, via strict control and restoration measures, can help reduce, slow, or even halt the potential spread of invasive plant species (Randall 2000).

5. Total biodiversity. In areas of high species richness, there may be relatively low proportions of threatened species. However, in hotspots that contain a high proportion of threatened species, there is also higher overall species richness (Orme et al. 2005). McKee et al. (2003) observed a positive correlation between the number of threatened bird and mammal species and species richness.

Social/governance

1. Life expectancy. Life expectancy is a complex metric that has many direct and indirect components; it has been used in other studies to determine the extent to which human well-being could increase without an accompanying increase in environmental deterioration (Dietz et al. 2007).

2. Adult literacy. Adult literacy results in better access to information, which in turn suggests that better decisions would be made concerning the environment. In a comparison of approximately 140 countries, a higher adult literacy rate correlated with less pollution in the cases of sulfur dioxide, heavy particles, dissolved oxygen, fecal coliform pollution, and correlated with better sanitation (Torras and Boyce 1998).

3. Pesticide regulation. Pesticide use has led to declines in amphibians (Sparling et al. 2001) and birds (Anthony et al. 1993), and to the decimation of pollination systems (Kearns et al. 1998), and has had numerous other deleterious effects (reviewed in Pimentel et al. 1992). The enactment and implementation of pesticide regulations can control direct, human-caused mortality of endangered species (Miller et al. 2002).

4. Political stability. Environmental degradation can lead to social collapse, famine, disputes within and between nations, and war, and these events can lead to environmental degradation (McNeely 2000, Nelson et al. 2006). Political stability is essential to the success of ecological restoration projects, which are typically undertaken to increase species richness in degraded ecosystems. It has been asserted that the persistence of these conservation projects is negatively correlated with the degree and frequency of political unrest (Soulé 1991).

5. Female participation in national government. Since the turn of the 20th century, women have been political champions of the environmental protection and conservation movement (reviewed in Kleehammer 2011). Women are more concerned about the pain and suffering of animals, e.g., more opposed to hunting, predator control, and trapping; they are more involved in protest efforts and constitute the majority membership of humane societies and animal-welfare organizations (Kellert and Berry 1987).

Data collection

Each country's latitude was obtained from the United States Central Intelligence Agency's World Factbook (Central Intelligence Agency 2008). Total population and GDP per capita for each country were reported in the 2008 EPI and values represented the year 2005 (Esty et al. 2008). Total land area was reported in the 2008 EPI (Esty et al. 2008). Exports were divided by imports to create an export-import ratio. Export and import data were obtained from the United Nations Food and Agriculture Organization (FAO) and represented the year 2004 (Food and Agriculture Organization 2006*a*). The numbers of international tourist arrivals per country were obtained by accessing the United Nations World Tourism Organization (2009) database. Undernourishment data, the percentage of the population that were malnourished between

2001 and 2003, were obtained from the FAO (Food and Agriculture Organization 2006*b*). Energy efficiency, or total primary energy consumption, was calculated by tabulating the consumption of petroleum; dry natural gas; coal; and net hydroelectric, nuclear, geothermal, solar, wind, wood, and waste electric power, and net electricity imports, which are electricity imports minus electricity exports (Esty et al. 2006).

Agricultural intensity was measured as the percentage of cropland area that is in agriculture-dominated landscapes. High agricultural intensity was defined as having more than 60% of a country's lands cultivated. Low intensity was defined as having at least 40% of the land uncultivated (Esty et al. 2008). Annual rainfall data were reported by the FAO and represent annual rainfall for the year 2002 (Food and Agriculture Organization 2006*c*). Average rainfall between 1971 and 2000 was not different than rainfall in 2002 (Mann-Whitney, Wilcoxon rank-sum $U = 4871.5$, $P = 0.943$). Water stress was defined as the percentage of national territory with water withdrawals exceeding 40% of available water (Esty et al. 2008). Wilderness protection was defined as the amount of land classified by the United Nations Statistics Division as protected, "an area of land and/or sea especially dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, and managed through legal or other effective means", divided by the total land area of a country (United Nations Statistics Division 2009). Total biodiversity includes known mammals, birds, reptiles, plants, amphibians, and fishes in each country as of 2004 (World Resources Institute 2005).

Life expectancy data were obtained from the CIA World Factbook and were calculated as the overall life expectancy at birth regardless of gender (Central Intelligence Agency 2008). Adult literacy, or the percentage aged 15 and above between 1995 and 2005 that were literate, were obtained from the Human Development Report of the United Nations Development Programme (2007). Pesticide regulation was indicated by the legislative status of countries under the Rotterdam and Stockholm conventions and to what degree they followed through on the convention bylaws (Esty et al. 2008). Political stability within a country measured the likelihood that the government would be destabilized or overthrown by unconstitutional or violent means (Kaufmann et al. 2008). Female participation in government represents the proportion of seats held by women in the national parliament as of 2007 (Millennium Development Goals Database 2009).

For the purpose of this study, endangered birds and mammals included those species that were classified by the International Union for Conservation of Nature Red List of Threatened Species as vulnerable, endangered, critically endangered, extinct in the wild, and extinct (International Union for Conservation of Nature 2008). Invasive birds were determined using Birdlife International's world bird database, Avibase (http://avibase.bsc-eoc.org/). Invasive mammals were determined using J. L. Long's definitive book on introduced mammals of the world (Long 2004). The total numbers of birds and mammals in each country were determined using the IUCN database (International Union for Conservation of Nature 2008).

Data analysis

An a priori set of models was created that included a combination of all social-ecological factors, each social-ecological factor by itself, and selected social-ecological factors grouped into three broad classes: economic factors, ecological factors, and social/governance factors. The economic factors were (1) per capita GDP, (2) export-import ratio, (3) tourism, (4) undernourishment, and (5) energy efficiency. The ecological factors were (1) agricultural intensity, (2) rainfall, (3) water stress, (4) wilderness protection, and (5) total biodiversity. The social/governance factors were (1) life expectancy, (2) adult literacy, (3) pesticide regulation, (4) political stability, and (5) female participation in national government.

We conducted separate analyses using the aforementioned variables for five dependent variables: (1) the number of endangered mammals divided by the total number of mammals within a country, (2) the number of endangered birds divided by the total number of birds within a country, (3) the number of invasive mammals divided by the total number of mammals within a country, (4) the number of invasive birds divided by the total number of birds within a country, and (5) the number of both endangered and invasive birds and mammals divided by the total number of birds and mammals in each country. Endangered and invasive birds and mammals were chosen as dependent variables because they are considered to be two indicators of what Aldo Leopold termed "land sickness" (Leopold 1941, Leopold et al. 1999, Rapport 2007). Other indicators include soil erosion and increase of pathogens. The combination of both endangered and invasive birds and mammals provides a partial measure of a country's ecosystem health. The Environmental Sustainability Index (ESI) and Environmental Vulnerability Index (EVI) were used as reference indexes in these analyses. The Environmental Performance Index (EPI) was not used as one of the reference indexes because it was correlated with both the ESI (Pearson's correlation coefficient = 0.434) and with its predecessor, the EVI (Pearson's correlation coefficient = 0.544). The ecological footprint was not used as a reference index because it does not account for local impacts (Dietz et al. 2007).

An information theoretic approach (Burnham and Anderson 2002, Johnson and Omland 2004) was used to determine which models were best supported by the data, based on Akaike

Information Criteria, or AIC (Akaike 1973). Model selection is appropriate for simultaneously weighing the evidence for multiple a priori hypotheses. Instead of using an arbitrary probability threshold, i.e., null hypothesis testing, we evaluated the relative support in the observed data for each model. Models were ranked using Akaike weights, to provide a quantitative measure of relative support for each competing hypothesis. Four models included more than one social-ecological factor, our three broad classes of models and the universal model that included all social-ecological factors. We also chose AIC because the probability of an overfit model is less than the probabilities of type I or type II errors encountered in hypothesis testing (Burnham and Anderson 2002).

For each model, AIC_c was calculated. The difference in AIC_c for that model relative to the best-fitting model with the minimum AIC_c (termed ΔAIC_c) was calculated, and the Akaike weight (w_i) was also calculated. The best fit was defined as that with the lowest AIC_c and highest Akaike weight. Models that differed by less than two AIC units have substantial support in terms of explaining the data (Burnham and Anderson 2002). Evidence ratios were also calculated for each model (Burnham and Anderson 2002). Colinearity among explanatory variables was investigated using correlation matrices. Although associations were apparent, they were not sufficient to preclude their inclusion into the modeling process. All data were log transformed, when appropriate, so that all variables would be on the same scale. All analyses were performed in SAS version 9.1 (SAS Institute 1999).

RESULTS

There were sufficient data to analyze 100 countries, which contained approximately 87% of the world's population, had 43% of global GDP per capita, and had 74% of the Earth's total land area. Africa is represented by 26 countries, Asia is represented by 29 countries, Europe is represented by 22 countries, North and Central America are represented by 12 countries, and South America and Oceania are represented by 11 countries. Ireland (0.21%), Togo (0.30%), the United Kingdom (0.33%), Guinea-Bissau (0.41%), and Norway (0.43%) had the smallest percentages of endangered birds. New Zealand (24%), the Philippines (11.3%), the United States (9.2%), Indonesia (7.2%), and Japan (7.1%) had the highest percentages of endangered birds. Sweden (1.38%), Finland (1.61%), Trinidad and Tobago (1.75%), Switzerland (2.38%), and Nicaragua (2.46%) had the smallest percentages of endangered mammals. Cuba (30.77%), the Dominican Republic (28.57%), Indonesia (27.46%), Sri Lanka (25.64%), and India (23.30%) had the highest percentages of endangered mammals.

There were 25 countries that did not have any reported invasive bird species, and 13 of those countries did not have invasive mammals. India (0.08%), Sudan (0.10%), Thailand (0.10%), Colombia (0.11%), and Nepal (0.11%) had the smallest percentages of invasive birds of those countries with invasive bird populations. New Zealand (11.73%), Jamaica (4.60%), the United States (4.37%), Australia (3.52%), and the Dominican Republic (3.46%) had the highest percentages of invasive birds. There were 25 countries that did not have any reported invasive mammal species, and 14 of those countries did not have invasive birds. Bolivia (0.28%), Panama (0.41%), Kenya (0.53%), Nepal (0.55%), and Venezuela (0.55%) had the smallest percentages of invasive mammals. New Zealand (70.46%), the United Kingdom (47.30%), Sweden (16.67%), Cuba (15.39%), and Germany (14.85%) had the highest percentages of invasive mammals.

Endangered birds and mammals

The percentage of endangered birds in a country was best predicted by two models. One included only the variable total biodiversity (w_i = 0.44) and another model included only the variable total land area (w_i = 0.28); see Table 1. As total biodiversity and total land area increased, the percentage of endangered birds in a country increased (Table 2). The island nation of New Zealand is an extreme outlier (Figs. 1 and 2). The percentage of endangered mammals in a country was best predicted by the ecological class model (w_i = 0.94), which included the variables agricultural intensity, rainfall, water stress, wilderness protection, and total biodiversity (Table 3). All variables had a positive relationship except wilderness protection, which was negatively correlated with the percentage of endangered mammals (Table 4).

Table 1. A comparison of support for the top 10 models of social-ecological factors and the proportion of endangered birds in 100 different countries. Models were ranked by Akaike's information criteria (AIC), and parameter abbreviations are as follows: ΔAIC_c is the difference between AIC_c values from each model, and w_i is the Akaike weight. Bold values indicate variables in the best model.

Model	AIC_c	ΔAIC_c	w_i	Evidence ratio
Total biodiversity	214.134	0.000	0.442	1.00
Total land area	215.078	0.944	0.275	1.60
Life expectancy	217.431	3.297	0.085	5.20
Total population	218.575	4.441	0.047	9.21
Agricultural intensity + annual rainfall + water stress + wilderness protection + total biodiversity	219.538	5.404	0.029	14.91
Adult literacy	220.463	6.329	0.018	23.68
Undernourishment	220.698	6.564	0.017	26.63
Pesticide regulation	221.104	6.970	0.013	32.62
Water stress	221.433	7.299	0.011	38.46
Null	221.844	7.709	0.009	47.22

Table 2. Parameter estimates for variables selected in the two best models of social-ecological factors and the proportion of endangered birds in 100 different countries.

Variable	Estimate	Standard error
Intercept	2.41576	0.38245
Total biodiversity	0.09117	0.02864
Intercept	2.77852	0.3239
Total land area	0.04528	0.015

Table 3. A comparison of support for the top 10 models of social-ecological factors and the proportion of endangered mammals in 100 different countries. Models were ranked by Akaike's information criteria (AIC), and parameter abbreviations are as follows: ΔAIC_c is the difference between AIC_c values from each model, and w_i is the Akaike weight. Bold values indicate variables in the best model.

Model	AIC_c	ΔAIC_c	w_i	Evidence ratio
Agricultural intensity + annual rainfall + water stress + wilderness protection + total biodiversity	353.704	0.000	0.938	1.00
Life expectancy + adult literacy + pesticide regulation + political stability + female participation in government	361.023	7.319	0.024	38.84
Total biodiversity	363.402	8.731	0.012	78.67
Water stress	364.166	9.495	0.008	115.27
Political stability	365.664	10.993	0.004	243.79
Total population	365.962	11.291	0.003	282.96
Environmental Sustainability Index	366.407	11.736	0.003	353.47
Latitude	367.070	12.399	0.002	492.41
Life expectancy	368.364	13.694	0.001	940.40
Environmental Vulnerability Index	368.877	14.206	0.001	1215.37

Invasive birds and mammals

The percentage of invasive birds in a country was best predicted by a model that included only the variable GDP per capita (w_i = 0.88; see Table 5). As GDP per capita increases, the percentage of invasive birds increases (Table 6, Fig. 3). The percentage of invasive mammals in a country was best predicted by a model that included only the variable GDP per capita (w_i = 0.84), as shown in Table 7. As GDP per capita increases, the percentage of invasive mammals increases (Table 8). The island nations of New Zealand and the United Kingdom were extreme outliers (Fig. 4).

Table 4. Parameter estimates for variables selected in the best model of social-ecological factors and the proportion of endangered mammals in 100 different countries.

Variable	Estimate	Standard error
Intercept	4.21526	1.82371
Agricultural intensity	0.05029	0.04093
Annual rainfall	0.33938	0.12343
Water stress	0.14313	0.04013
Wilderness protection	-0.07443	0.05017
Total biodiversity	0.10826	0.06668

Table 5. A comparison of support for the top 10 models of social-ecological factors and the proportion of invasive birds in 100 different countries. Models were ranked by Akaike's information criteria (AIC), and parameter abbreviations are as follows: ΔAIC_c is the difference between AIC_c values from each model, and w_i is the Akaike weight. Bold values indicate variables in the best model.

Model	> AIC_c	ΔAIC_c	w_i	Evidence ratio
Per capita GDP	57.040	0.000	0.879	1.00
Per capita GDP + export-import ratio + tourism + undernourishment + energy efficiency	61.762	4.722	0.083	10.60
Life expectancy	64.650	7.610	0.020	44.93
Life expectancy + adult literacy + pesticide regulation + political stability + female participation in government	66.333	9.293	0.008	104.20
Political stability	66.350	9.310	0.008	105.11
Undernourishment	71.228	14.188	0.001	1204.90
Adult literacy	72.777	15.737	0.000	2613.90
Pesticide regulation	74.712	17.672	0.000	6877.77
Latitude	74.965	17.925	0.000	7803.68
Environmental Vulnerability Index	76.748	19.708	0.000	19036.24

Table 6. Parameter estimates for variables selected in the best model of social-ecological factors and the proportion of invasive birds in 100 different countries.

Variable	Estimate	Standard error
Intercept	0.15755	0.18560
Per capita GDP	0.06531	0.01242

Fig. 1. One of the two models best explaining the proportion of endangered birds was the total biodiversity in a country. The proportion of endangered birds ranged from 0.21% to 24.05% and total biodiversity ranged from 380 species to 60,322 species. New Zealand is an extreme outlier.

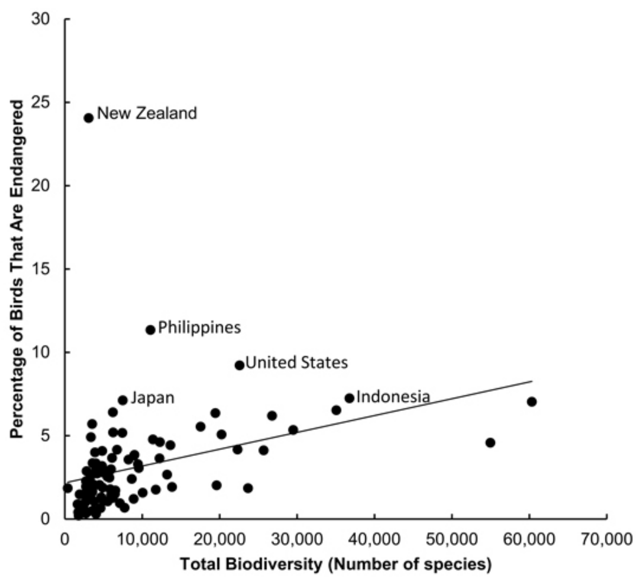

Fig. 2. One of the two models best explaining the proportion of endangered birds was the total land area in a country. The proportion of endangered birds ranged from 0.21% to 24.05%, and total land area ranged from 5202 km² to 9,458,906 km². New Zealand is an extreme outlier.

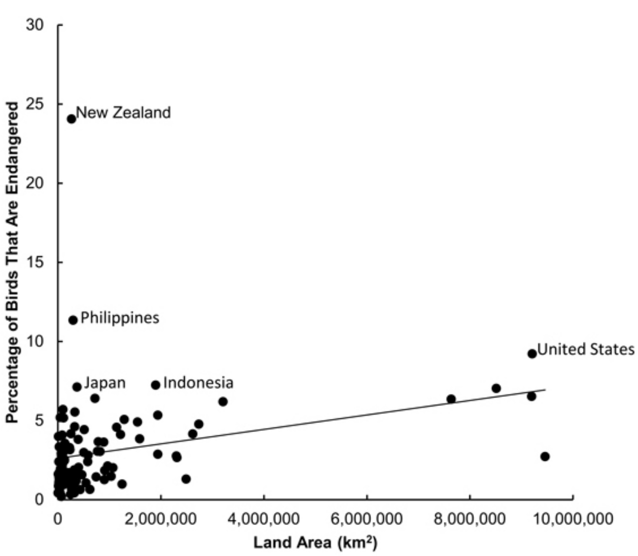

Fig. 3. The model best explaining the proportion of invasive birds was the per capita GDP in a country. The proportion of invasive birds ranged from 0% to 11.73% and per capita GDP ranged from $630 to $38,165. New Zealand is an extreme outlier.

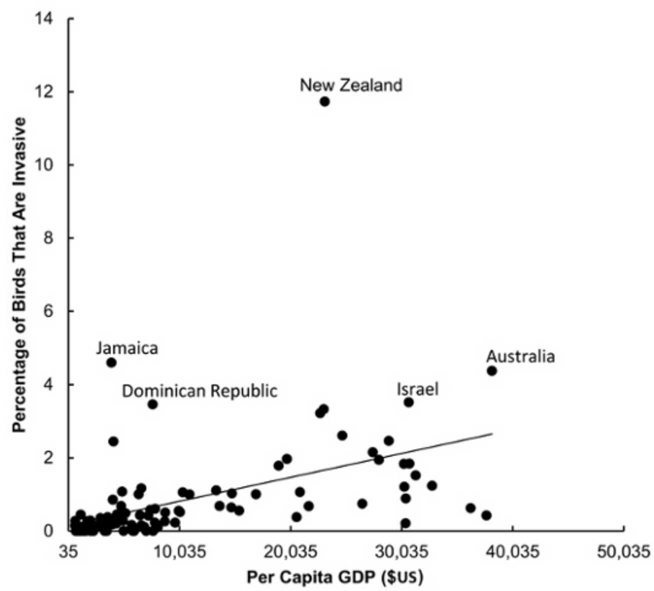

Fig. 4. The model best explaining the proportion of invasive mammals was the per capita GDP in a country. The proportion of invasive mammals ranged from 0% to 70.46%, and per capita GDP ranged from $630 to $38,165. New Zealand and the United Kingdom were extreme outliers.

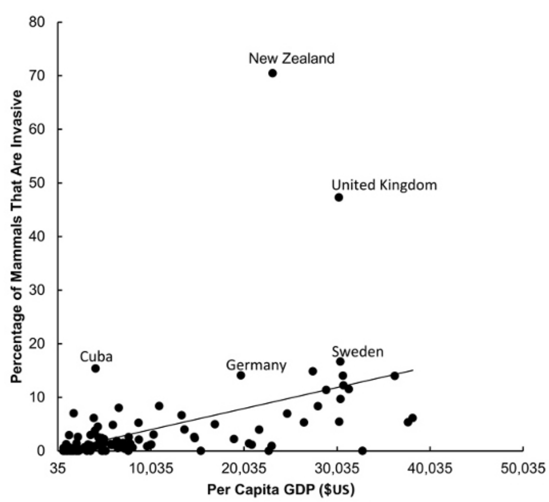

Table 7. A comparison of support for the top 10 models of social-ecological factors and the proportion of invasive mammals in 100 different countries. Models were ranked by Akaike's information criteria (AIC), and parameter abbreviations are as follows: ΔAIC_c is the difference between AIC_c values from each model, and w_i is the Akaike weight. Bold values indicate variables in the best model.

Model	AIC_c	ΔAIC_c	w_i	Evidence ratio
Per capita GDP	418.705	0.000	0.837	1.00
Political stability	422.967	4.262	0.099	8.42
Latitude	425.283	6.578	0.031	26.82
Life expectancy + adult literacy + pesticide regulation + political stability + female participation in government	426.261	7.556	0.019	43.74
Per capita GDP + export-import ratio + tourism + undernourishment + energy efficiency	427.430	8.725	0.011	78.47
Life expectancy	431.141	12.436	0.002	501.70
Adult literacy	433.987	15.282	0.000	2081.83
Undernourishment	434.133	15.428	0.000	2239.48
Pesticide regulation	434.323	15.618	0.000	2462.67
Female participation in government	435.917	17.212	0.000	5464.35

Table 8. Parameter estimates for variables selected in the best model of social-ecological factors and the proportion of invasive mammals in 100 different countries.

Variable	Estimate	Standard error
Intercept	0.06318	1.13218
Per capita GDP	0.39242	0.07576

The percentage of invasive and endangered birds and mammals within a country was best predicted by a model that included only life expectancy (w_i = 0.53; see Table 9). As human life expectancy increases, the percentage of invasive and endangered birds and mammals within a country increases (Table 10, Fig. 5). The island nation of new Zealand was an extreme outlier. Of the 26 countries in the Africa region, 23 were included in the top 25 countries with the lowest percentages of invasive and endangered birds and mammals.

DISCUSSION

Although our approach is exploratory and we did not seek mechanisms, the patterns we observed in this study provide insight into the dynamics of a complex global social-ecological system. The model best predicting the percentage of endangered birds in a country included total biodiversity and total land area. These results were similar to other analyses

Fig. 5. The model best explaining the proportion of endangered and invasive birds and mammals combined was the human life expectancy in a country. A higher proportion of endangered and invasive birds and mammals equates to a lower resilience. The proportion of endangered and invasive birds and mammals combined ranged from 1.21% to 41.82%, and life expectancy ranged from 38.6 years to 82.1 years. New Zealand is an extreme outlier.

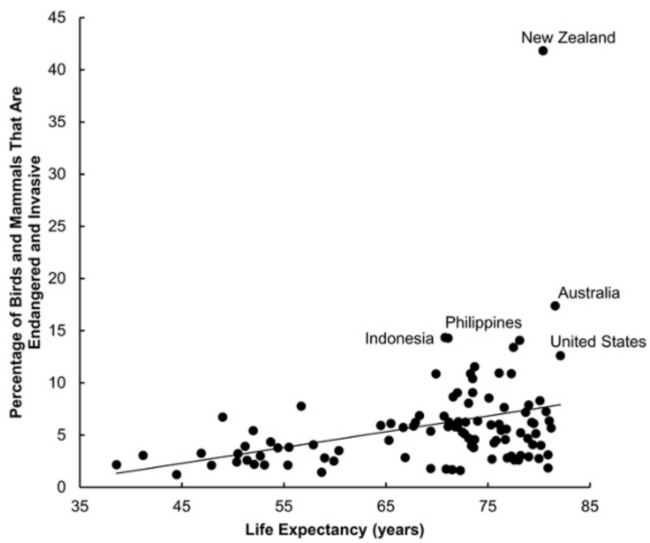

Table 9. A comparison of support for the top 10 models of social-ecological factors and the proportion of endangered and invasive birds and mammals in 100 different countries. Models were ranked by Akaike's information criteria (AIC), and parameter abbreviations are as follows: ΔAIC_c is the difference between AIC_c values from each model, and w_i is the Akaike weight. Bold values indicate variables in the best model.

Model	AIC_c	ΔAIC_c	w_i	Evidence ratio
Life expectancy	312.859	0.000	0.526	1
Total biodiversity	316.466	3.607	0.087	6.07
Pesticide regulation	316.796	3.937	0.073	7.16
Total land area	316.819	3.960	0.073	7.24
Adult literacy	317.581	4.722	0.05	10.6
Undernourishment	317.822	4.963	0.044	11.96
Per capita GDP	319.103	6.244	0.023	22.69
Total population	319.224	6.365	0.022	24.11
Life expectancy + adult literacy + pesticide regulation + political stability + female participation in government	319.745	6.886	0.017	31.28
Tourism	320.370	7.511	0.012	42.76

Table 10. Parameter estimates for variables selected in the best model of social-ecological factors and the proportion of endangered and invasive birds and mammals in 100 different countries.

Variable	Estimate	Standard error
Intercept	-4.1801	3.09793
Life expectancy	0.14422	0.04415

of the relationship between the percentage of endangered birds and total biodiversity (McKee et al. 2003, Orme et al. 2005). Although there was no evidence in the literature describing a relationship between the percentage of endangered birds and total land area, we could presume that an increase in sampling area would result in an increase in species richness (reviewed in Huston 1994) and therefore a possibility of there being more endangered species present.

The number of endangered birds and mammals is nested within total biodiversity. However, these metrics are very different and should be analyzed separately. Globally, there are varying levels of resolution for IUCN data on endangered species (Helfman 2011). Sampling efforts and protocols of each country are varied, there are missing assessments, and the quality of data varies by taxa. A country may have good data on birds, but poor data on mammals. Total biodiversity accounts for those inconsistencies, thus it is treated as a separate metric.

The model best predicting the percentage of endangered mammals in a country included the ecological class of variables. The results were similar to other analyses of the relationship between endangered mammals and agricultural intensity (Dobson et al. 1997), and between total annual rainfall and total biodiversity (McKee et al. 2003). Water stress has been reported as a threat to endangered species populations throughout the United States (Flather et al. 1998). There is evidence that the preservation of more habitat will allow for the survival of more species (Bruner et al. 2001), therefore we might assume fewer endangered species to be present in areas with more protected habitat. The inverse relationship observed in this study between wilderness protection and the percentage of endangered mammals suggests that this may be true.

The relationship between GDP per capita and invasive species has been observed in other studies. GDP per capita and invasive species have been found to correlate with the richness of alien spiders (Kobelt and Nentwig 2008), plants (Liu et al. 2005), fishes (Leprieur et al. 2008), birds and mammals in Europe (Hulme 2007), and with all taxonomic groups combined (Lin et al. 2007). The United Kingdom had a far greater percentage of invasive mammals than predicted by the model. This may be due to the unique history of this island nation. Around 1775 A.D., London was at the crossroads of the globalization of European trade routes, establishing trade with the Dutch, Spanish, Portuguese, and French (Di Castri 1989). This vast trade economy at an early period in this island nation’s history presumably has also meant a long history of biological invasions (Di Castri et al. 1990).

The countries with the lowest percentage of invasive and endangered birds and mammals were those located in Africa; this may be due to the lack of invasive and endangered species of all taxa in most of these countries. There were only 29 invasive bird species and 39 invasive mammal species reported in the 26 African countries included in this study. The lack of invasive species in these African countries may best be explained by international trade. Increased international trade has been positively correlated with an increase in invasive species (Wittenberg and Cock 2001, Perrings et al. 2002). We obtained international trade data of the past 60+ years from the World Trade Organization (2008) and found that African countries comprised approximately 50% or more of a list of the 25 countries with the lowest average amount in U.S. dollars of exports, imports, and of both figures combined. These countries have had very little international trade relative to a majority of the countries in this analysis because of their closed trade policy (Sachs and Warner 1997).

In every analysis, New Zealand was an extreme outlier. New Zealand has the highest percentage of endangered birds, invasive birds, and invasive mammals, and also has the highest percentage of all endangered and invasive species combined. New Zealand’s complete lack of native terrestrial mammals (Diamond 1990) is a key factor in its outlier position relative to the rest of the countries analyzed. New Zealand has had a massive invasion by nonindigenous species since its human colonization in the past 700 to 800 years, and this has resulted in catastrophic biodiversity loss (Clout 2001). New Zealand’s invasive species crisis may be due in large part to its isolation, high endemism, and recent human colonization (Norton 2009). Island ecosystems are often the most invaded and consequently the most threatened worldwide (Towns et al. 2006).

We found a positive relationship between life expectancy and the percentage of endangered and invasive species in a country. Previous studies found no relationship between life expectancy and environmental impact (Dietz et al. 2007). The overall trend in high-income countries with improvements to the Human Development Index, which includes human life expectancy as one of its variables, is toward a disproportionately larger negative impact on a country’s ecological footprint. However, some lower-income countries have a high level of development without a high impact on ecosystem services (Moran et al. 2008). Increased life expectancy means that people live longer and affect the planet longer; each year is another year of carbon footprint, ecological footprint, use of natural resources, etc. The magnitude of this impact is increased as more people live longer.

The Environmental Sustainability Index, Environmental Performance Index, and Environmental Vulnerability Index incorporated a diverse range and number of indicators, and a unique categorical organization of indicators; they were created to measure a country's environmental performance and sustainability. A more relevant measure of a country's sustainability or performance lies in its ecological resilience (Carpenter et al. 2001). Ecological resilience is defined as the magnitude of disturbance that can be absorbed by a system before it changes its structure and control (Holling and Gunderson 2002). We suggest that a reasonable surrogate measure for ecological resilience is the percentage of invasive and endangered species within a country. Those countries with a higher percentage of invasive and endangered species presumably have lower ecosystem resilience.

Humans are an integral part of the ecosystems that they inhabit, accounting for the consumption of nearly 40% of potential terrestrial net primary productivity (Vitousek et al. 1986). Total population was not included in the best models, but understanding the effects of overpopulation may be one of many crucial steps that must be taken to conserve global biodiversity (McKee et al. 2003). Conservation will only be successful if local communities are given the incentives, tools, and capacity to manage ecosystems sustainably (Leader-Williams 2002) and if they understand that they are living on environmental capital rather than on interest (Jones 2003). Fischer et al. (2012) propose a "transformation strategy" that assumes that direct links between people and nature are better than indirect links. This paradigm shift would recouple the social-ecological system.

Responses to this article can be read online at:
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