ECONOMIC INEQUALITY AND BIODIVERSITY LOSS: AN EXAMINATION AT TWO SCALES

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ABSTRACT

Human activity is causing rapid loss of biodiversity. Although the direct drivers of this are well understood, the indirect socio-economic drivers are not.

This thesis examines the role of economic inequality in predicting rates of biodiversity loss at two different scales. First, I perform a cross-national analysis of the proportion of plant and vertebrate species that are threatened, as defined by the IUCN (World Conservation Union) red lists. Second, I examine the role of land cover and socio-economic variables in determining trends in bird species richness in the USA.

At the international scale, inequality is consistently an important predictor: the proportion of species threatened is higher in countries that have higher inequality, all else being equal. At the smaller scale of the US, socio-economic variables can explain up to 20% of the variation in species richness. However, inequality does not significantly improve this prediction.

SOMMAIRE

Présentement, l'activité humaine cause une perte rapide de la biodiversité. Alors que les causes directes de cela sont bien comprises, les causes socio-économiques indirectes ne le sont pas.

Le rôle des inégalités économiques dans la prédiction des taux de perte de biodiversité sera examiné à deux échelles différentes dans la présente étude. D'abord, il sera question d'une analyse transnationale de la proportion d'espèces végétales et d'espèces vertébrées qui sont menacées, tel que définit par la liste rouge de l'UICN (Union mondiale pour la nature). Ensuite, le rôle de la couverture terrestre ainsi que celui des variables socio-économiques seront examinés afin de déterminer les tendances de l'abondance des espèces aviennes aux États-Unis.

À l'échelle internationale et de façon constante, les inégalités sont un prédicteur. À toute autre qualité égale, la proportion d'espèces menacées est plus élevée dans les pays qui ont de plus grandes inégalités. À la plus petite échelle de l'étude, les variables socio-économiques peuvent expliquer près de 20% de la variation. Cependant, l'inégalité économique n'améliore pas considérablement la prédiction.

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CONTRIBUTIONS OF CO-AUTHORS

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GREGORY MIKKELSON

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TABLE OF CONTENTS

ABSTRACT I

SOMMAIRE I

ACKNOWLEDGEMENTS II

CONTRIBUTIONS OF CO-AUTHORS III

TABLE OF CONTENTS IV

INTRODUCTION AND LITERATURE REVIEW 1

ECONOMIC DETERMINANTS OF ENVIRONMENTAL OUTCOMES 2

INEQUALITY 3
Measurement and Trends 5

TRENDS IN BREEDING BIRD DIVERSITY IN USA 6
Land Cover as a Direct Driver 7
Indirect Drivers 8

RESEARCH GOAL AND THESIS OUTLINE 9
Chapter 1: International Analysis 9
Chapter 2: USA Analysis 9
Conclusion 10

CHAPTER 1: ECONOMIC INEQUALITY AND BIODIVERSITY LOSS: A CROSS-NATIONAL SURVEY 11

INTRODUCTION 11
Drivers of Environmental Impact 11
Economic Distribution 12
Comparing Hypotheses 14
Contextualizing countries 15
Approach 15

METHODS 16
Model Comparison Approach 16
Data Sources 18
Biodiversity 18
Socio-economic data 19
Time lag between human activity and effect on biodiversity 22

RESULTS 22
Comparison Among Models 22
Comparison Among Different Time Periods 24
Economic footprint + Inequality 26
Environemental Governance 27

DISCUSSION 28

PREFACE TO CHAPTER 2 32

CHAPTER 2: RELATIONSHIPS BETWEEN SOCIO-ECONOMIC VARIABLES, LAND COVER, AND BIRD SPECIES RICHNESS - A CASE STUDY IN THE UNITED STATES 33

INTRODUCTION 33

METHODS 35
- Biodiversity 36
- Land Cover 38
- Socio-Economic Indicators 42
- Analysis 44

RESULTS 44
- Socio-Economic Variables as Predictors of Species Richness 44
  - *Change in richness (1992-2005*) 44
  - *Richness in 20*05 45
- Socio-Economic Variables as Predictors of Forest Cover 47
- Forest Cover as Predictor of Species Richness 49
  - *Change in richness (1992-2005*) 49
  - *Richness in 1992 and 2005* 50

DISCUSSION 52
- Forest Cover and Bird Richness 53
- Inequality 54
- Importance of Scale 55

CONCLUSION 57

APPENDIX A: MODEL COMPARISON USING PROPORTION OF PLANTS AND VERTEBRATES THAT ARE ENDEMIC. 60

APPENDIX B: COUNTRIES ANALYZED 61

APPENDIX C: DATA USED FOR INTERNATIONAL STUDY 62

REFERENCES 65

INTRODUCTION AND LITERATURE REVIEW

The drivers of environmental change have long been a topic of debate (e.g. Ehrlich & Holdren 1971; World Bank 1992; York *et al*. 2003). Although we have good knowledge of the processes that directly cause environmental change, our understanding of the indirect socio-economic drivers of that relationship is much weaker. An understanding of the connections between socio-economic factors and environmental outcomes is crucial if we want to develop effective strategies for managing the environment.

In this thesis, I will examine one specific aspect of this nexus: the relationship between economic inequality and biodiversity loss. Inequality has been neglected by much of the literature on connections between the economy and the environment; often, only the absolute size of the economy is looked at while the distribution of the economy is ignored (Ehrlich & Holdren 1971; York *et al*. 2003). This is despite theory suggesting inequality will have an impact on the environment (Olson 1965; Ostrom 1990; Boyce 1994; Ostrom 2001), as well as empirical evidence demonstrating that inequality has an effect on other social outcomes (Ronzio *et al.* 2004; Ross *et al.* 2005). Of the possible environmental indicators to examine, biodiversity loss is particularly critical, both because of its importance to human well-being and because of alarming current trends. If we consider biodiversity loss on a global scale, it is also irreversible.

I will focus on biodiversity loss at two different scales. Globally, I examine the proportion of species in each country that are listed as threatened based on the World Conservation Union (IUCN)'s Red List (IUCN 2006). At a national scale within the United States, I look at trends in the richness of permanent resident breeding bird species at a relatively localized scale. Data on birds is taken from the North American Breeding Bird Survey (Sauer *et al.* 2005).

ECONOMIC DETERMINANTS OF ENVIRONMENTAL OUTCOMES

Primarily as a result of human activity, species are being lost globally at rates 100 to 1000 times greater than would be expected in nature (MA 2005). The most significant direct drivers of this loss are habitat reduction, introduction of invasive species, over-harvesting, pollution, and climate change (MA 2005). Driving other species to extinction is clearly undesirable from an ethical standpoint. However, even ignoring ethics and focusing only on human utility, causing such declines in biodiversity is against our better interests. In addition to losing potential species for medicinal or economic uses, reducing biodiversity may impact overall ecosystem functioning, with detrimental effects to human well-being (Costanza *et al.* 1997; Chapin *et al.* 2000; Tilman 2000).

At a global scale, there has been only a small amount of work on the indirect socio-economic drivers of biodiversity loss. A study by Naidoo and Adamowicz (2001), however, did show that gross domestic product (GDP) is a significant predictor of numbers of species threatened for five out of seven taxonomic groupings. In the case of plants, amphibians, reptiles, and invertebrates, the number of species threatened increased with increasing GDP, while for birds the number decreased.

This study by Naidoo and Adamowicz (2001) is part of a general body of literature that focuses on the socio-economic determinants of environmental impacts and outcomes. One of the earliest statements on this question was by Ehrlich and Holdren (1971) in their development of the IPAT framework. This was based on the IPAT equation (standing for Impact = Population × Affluence × Technology), which implied that a society's impact on the environment was a function of the number of people, their wealth, and the technology they used. The latter determined the degree to which each unit of wealth or economic activity affected the environment. The IPAT framework was widely applied, but had the major difficulty that the technology term was very difficult to quantify. As a result, it was often simply dropped, with only the population and affluence terms being taken into account (Naidoo & Adamowicz 2001; York *et al.* 2003).

In the early 1990s, theory was developed suggesting that environmental outcomes would follow a U-shaped trajectory as the economy grew, worsening as countries progressed through the initial stages of economic development, but improving again beyond a certain threshold of wealth (World Bank 1992). This was referred to as the Environmental Kuznets Curve hypothesis (EKC). The EKC was based on the idea that initially as countries increased their economic activity, their pressure on the environment increased; however at a certain level of wealth, there would be sufficient investment in conservation and efficient technologies so that the environmental decline would be reversed (World Bank 1992; Stern *et al.* 1996; Stern 2004). The EKC seems to be true for certain environmental indicators; however, it is not generally applicable (Stern *et al.* 1996; York *et al.* 2003; Stern 2004). Naidoo and Adamowicz (2001) showed that for biodiversity in particular, the EKC does not provide a strong predictive model.

INEQUALITY

Much of the literature on the determinants of environmental impact focuses on the size of the human economy, generally represented by the gross domestic product (GDP) or a similar indicator (e.g. Ehrlich & Holdren 1971; Naidoo & Adamowicz 2001; York *et al.* 2003). However, there is reason to believe that it is not only the size of the economy that matters to the environment, but also the way in which the economy is distributed (Olson 1965; Ostrom 1990; Boyce 1994; Ostrom 2001; Mikkelson *et al.* 2007). Economic inequality may have an effect on environmental degradation that is independent of the size of the economy by affecting either the effectiveness of institutions, or the decision-making of individuals. Examining the role that inequality plays as a predictor of environmental outcomes is the central theme of this thesis.

One of the earliest perspectives on equality and the environment was stated by Mancur Olson in 1965. Olson theorized that greater inequality would improve conservation of natural resources. His idea followed from the fact that at higher levels of inequality, control of resources would be concentrated among a smaller number of people. This group would reap most of the benefits of the resource, and would therefore have a strong incentive to conserve. Because the incentive to conserve would thus be concentrated in a relatively small and powerful group, conservation in general would be more effective, as each powerful individual would have more influence to effect conservation than would an average individual. The smallness of the group that controlled the resource would also partly prevent a 'Tragedy of the Commons' (Hardin 1968) in that each individual would stand to lose enough by irresponsible use of the resource that they would act responsibly. These kinds of positive outcomes from concentration of wealth were termed "Olson effects."

The opposing perspective, that inequality in fact interferes with effective conservation, is described in detail by Elinor Ostrom (1990, 2001). Ostrom suggests that in the management of common pool resources, collective action for conservation may be made more difficult when inequality is high and members of the society have highly heterogeneous priorities and needs. Although she recognizes that Olson effects (Olson 1965) may exist and may cause wealthier individuals to pay a disproportionately large share of conservation costs, her overall contention is that by reducing the effectiveness of collective action, inequality will have a negative net effect on the success of resource conservation.

Boyce (1994) similarly argues that inequality would have a negative impact on the environment; however, he gives different reasons. While Ostrom focuses primarily on the effect of inequality on institutions, Boyce focuses more on the behaviour of individuals, as Olson (1965) did. He describes 'winners' and 'losers' in any use of resources, where the winners are those who profit from the exploitation and the losers are those who bear the external costs of exploitation. As inequality increases, the power differential between the two groups increases, and the winners become more able to impose costs on the losers (by over-exploiting the resource). Partly as a response to Boyce, Heerink and colleagues (2001) developed a model of environmental degradation based on household economic status. This model implied the reverse of what Boyce predicted: that greater inequality would result in lower environmental degradation. However, Heerink and colleagues rested their model entirely upon the assumed validity the Environmental Kuznets Curve holds true, which, as was discussed above, is a questionable assumption.

In a combination of theory with modeling experiments of individual behaviour, Baland and Plateau (1999) suggest that the relationship between inequality and conservation would be U-shaped. They suggest that conservation would be least effective at moderate ranges of inequality. At high levels of inequality, Olson effects would cause an improvement in conservation, while at low levels, reduced disparity between individuals would result in better collective action and a similar improvement in conservation.

Recently, work by Mikkelson and colleagues has shown an empirical relationship between inequality and indicators of biodiversity loss at two different scales: nations, and states within the USA (2007). In both cases, inequality was shown to be positively correlated with indicators of worsening biodiversity.

MEASUREMENT AND TRENDS

There are many possible ways to measure income inequality. The ratio between the mean income and the median income, the percentage of income received by a top quintile, or the ratio between top and bottom quintiles are all straightforward measures. However, these are all largely dependent on changes at the extremes of the income distribution, and thus do not represent distribution well in the middle of the income spectrum. The Gini index, named for Italian mathematician Corrado Gini, describes an entire distribution, and is thus a better measure of overall inequality. This index ranges from 0 to 100, where 0 is perfect equality, and 100 is perfect inequality.

Even more important than how inequality is measured is the scale at which it is measured. The term 'global inequality' can mean many things: it can refer to inequality between countries or regions, it can refer to average inequality within countries or regions, and it can refer to the aggregate inequality of global individuals while national borders are ignored (Milanovic 2005, 2006). These three different approaches can yield strikingly different results. For example, from 1980 to 1990, inequality between continents decreased while inequality within continents increased (Chotikapanich *et al.* 1997). During a similar time frame, global inequality taken as the aggregate of individuals decreased, while three quarters of countries with available data saw their within-country inequality increase (Milanovic 2005; Pitt Inequality Project 2005). There is no single correct choice regarding which approach to take; rather, the desired measure will depend on the question being asked. If national-level institutions are the primary interest, as they are in Chapter 1 of this thesis, looking at within-country inequality is most appropriate (Milanovic 2006).

As with the majority of countries, inequality in the United States has increased in recent decades (Lee 1999; Gottschalk & Danziger 2005). This increase was most rapid in the 1980s, and reached a plateau in the early 2000s (Gottschalk & Danziger 2005). These general trends were consistent across the population as a whole, as well as within gender, racial, and educational groups. Patterns among groups were varied, however. Inequality between genders declined, inequality between races stayed constant, and inequality between different levels of educational attainment increased (Gottschalk & Danziger 2005).

TRENDS IN BREEDING BIRD DIVERSITY IN USA

Although inequality in the United States may be worse than in much of the world, biodiversity of birds in the USA is faring far better than biodiversity is globally. From 1966 to 1979, significantly more species of woodland birds saw their populations increasing than saw their populations decreasing (Peterjohn & Sauer 1994). This worsened slightly through the 1980s as the proportion of species that saw increases in their population declined (Peterjohn & Sauer 1994). Reports on data from the 1990s show roughly similar proportions of species increasing as decreasing (Peterjohn *et al.* 1995; Pardieck & Sauer 2000). These proportions are not homogenous, however, and vary significantly between groups of birds and between regions (Pardieck & Sauer 2000).

Land cover as a direct driver

Land cover has been shown to be an important factor in explaining spatial and temporal variation in population abundance and species richness of birds in the USA. This can be (and has been) looked at in many different ways. Often, only forest cover is examined (e.g. Villard *et al.* 1999; Fauth *et al.* 2000; Howell *et al.* 2000; Boulinier *et al.* 2001; Donovan & Flather 2002), while in some cases other cover types such as urban areas or agriculture are also included (e.g. Cam *et al.* 2000; Rodewald & Yahner 2001; Mayer & Cameron 2003). Patterns between land cover and birds can be scale dependent, both in terms of extent, and in terms of grain. The studies just mentioned range in their spatial extent anywhere from a fraction of a state, to several states. With regards to grain, the relationship between land cover metrics and bird richness can vary depending on the size of the sampling landscapes (Mayer and Cameron 2003).

In addition to variation in the focal land cover, previous studies vary in how they measure that land cover. The simplest measure is the percentage of a landscape that is occupied by the given land cover type. This is an indicator of the total amount of habitat available to species. The way in which this habitat is arranged, however, can also have an effect on birds and other species that is independent of the effect of the total habitat amount (Fahrig 2003; Turner 2005). This arrangement can be quantified using many different types of landscape metrics. There are more of these metrics than could ever be used in a single analysis. However, there is much collinearity between the metrics, and most variation in landscapes can be described using a smaller number of key descriptors (Riitters *et al.* 1995; Li & Wu 2004).

The most common fragmentation metrics used in the literature on bird populations are the amount of edge per unit of habitat area, the average size of habitat patches, and the average distance between habitat patches. Several studies have found that greater amounts of edge have negative effects on bird richness or abundance, either because of increased predation or other mechanisms (Robinson *et al.* 1995; Jones *et al.* 2000; Karanth *et al.* 2006). In some cases, either larger distances between habitat patches or smaller sizes of habitat patches have been shown to be associated with decreased bird richness (Villard *et al.* 1999; Howell *et al.* 2000; Boulinier *et al.* 2001).

Studies vary in the degree to which they are careful to separate the effects of total habitat area from fragmentation effects (Fahrig 2003). In some cases, the strong collinearity between these two aspects is essentially ignored, which may lead to biased conclusions. For example, a study by Boulinier and colleagues (2001) demonstrated a connection between lower average forest patch size and higher rates of species turnover and extinction. Because patch size is so strongly correlated with total amount of forest (in this study, correlation = 0.94), it is likely that their result is more an effect of habitat amount than it is one of patch size (Fahrig 2003). There is no perfect way to separate the effect of the amount of habitat from the effect of fragmentation of habitat without experimental manipulation. Various statistical methods have been tried, such as using principal components analysis or looking at the residuals of fragmentation on habitat amount, but none of these are entirely without bias (Fahrig 2003; Koper *et al.* 2007).

Indirect drivers

Despite this well-developed body of literature on land cover, a direct driver of trends in US breeding birds, there has been little work looking at the indirect, socio-economic drivers of trends in North American breeding birds. There is, however, reason to believe that a relationship between socio-economic trends and bird populations exists in the USA. First, a very strong relationship has been shown between how well the US economy fares faring and two indicators of environmental investment: how much money is spent on conservation initiatives, and how much new land is being put into parks (Pergams *et al.* 2004). Birds in particular tend to attract more conservation funding than other species (Simon *et al.* 1995; Loomis & White 1996; Metrick & Weitzman 1996), and so the effect of changes in the economy on them may be particularly strong.

RESEARCH GOAL AND THESIS OUTLINE

The theoretical expectation that inequality should have an effect on biodiversity; preliminary empirical evidence that it does; and trends towards increasing inequality in much of the world all suggest that examining the effect of inequality on biodiversity is an important area for further research. The goal of this thesis will be to determine how well economic inequality predicts patterns of biodiversity loss. I will analyze this question at two different scales: internationally, and with a case study of the USA. This approach allows me to test if relationships between inequality and biodiversity loss are robust to changes in scale. There is a trade-off in these studies between breadth of coverage and consistency of data used. Using two scales allows me the best of both worlds: the international survey provides breadth while the USA survey provides data which is more complete and reliable.

CHAPTER 1: INTERNATIONAL ANALYSIS

This first part of this thesis looks at the relationship between inequality and the proportion of species threatened, as defined by the World Conservation Union Red Lists (IUCN 2006). This work draws heavily on previous work by York and colleagues (2003) and by Naidoo and Adamowicz (2001). Both of these established the importance of socio-economic indicators biodiversity loss or other environmental indicators using a similar analytical framework to the one I will use. In this chapter, I will compare between different established theories that describe the relationship between the economy and the environment. In particular, I will examine an Economic Footprint model (Ehrlich & Holdren 1971; York *et al.* 2003) and the Environmental Kuznets Curve (for review, see Stern 2004). I will then evaluate how including inequality in these frameworks may or may not improve their predictions.

CHAPTER 2: USA ANALYSIS

In the second chapter I draw upon the same conceptual literature regarding both the relationship between socio-economic indirect drivers and environmental outcomes and the relationship between inequality and the environment. However, in the case of this paper I have much richer data. Socio-economic data is from the US DecENN_MNial

Census (USCB 1990, 2000), while biodiversity data is from the North American Breeding Bird Survey (Sauer *et al.* 2005). In addition, I will use high-resolution land cover data from the National Land Cover Database (MRLC 1992, 2001). My analysis will have three parts. First, I will look at the effect of socio-economic indicators on species richness. The second and third part of the analysis will involve breaking the first relationship into its hypothesized components: an effect of socio-economic indicators on land cover, and an effect of land cover on species richness. With respect to the first two of the three relationships just mentioned, a strong connection has been shown between economic indicators and conservation decisions in the USA (Pergams 2005). However, there are few papers that empirically test environmental outcomes in relation to economic indicators. The third relationship, between land cover and species, draws on a large body of literature regarding the landscape ecology of bird species (e.g. Cam *et al.* 2000; Boulinier *et al*. 2001, Donovan and Flather 2004; Mayer and Cameron 2003).

CONCLUSION

The conclusion of this thesis will synthesize results of these two manuscripts in order to provide any general conclusions regarding the relationship between inequality and biodiversity loss. I will also suggest avenues that would be useful for future study.

CHAPTER 1: ECONOMIC INEQUALITY AND BIODIVERSITY LOSS: A CROSS-NATIONAL SURVEY

INTRODUCTION

As a result of human activity, species extinctions are currently happening at a rate 100 to 1000 times greater than we would expect based on natural processes (Pimm *et al.* 1995; MillENN_MNium Ecosystem Assessment (MA) 2005). The loss of this biodiversity is certainly undesirable from an ethical or aesthetic point of view; however, even from an anthropocentric utilitarian perspective, these trends are very troubling (Costanza *et al.* 1997; Chapin *et al.* 2000). The most important direct driver of this loss is habitat change, but climate change, introduction of exotic species, over-harvesting, and pollution also cause significant declines in biodiversity (Sala *et al.* 2000, MA 2005). Although the direct drivers of biodiversity loss are thus fairly clear, the indirect drivers – those factors that cause habitat loss, over-harvesting, etc. – are more difficult to discern. The primary goal of this chapter is to identify the socio-economic indirect drivers that best predict rates of biodiversity loss.

DRIVERS OF ENVIRONMENTAL IMPACT

This question is part of a broader debate surrounding the socio-economic causes of environmental degradation. Some of the earliest discussion on this topic can be traced to Thomas Malthus and his concern that human population growth would eventually outpace the growth in food production (Malthus 1798). More recently, this idea has been refined by the realization that a society's impact on its resources or on the broader environment cannot be explained solely by population numbers because of the large variation that exists between societies in their level of impact per person. Ehrlich and Holdren (1971) attempted to capture this idea with their IPAT formula, where IPAT stands for Impact = Population x Affluence x Technology. That is to say, the total environmental impact of a society is a product of the number of people (P), the average level of consumption of each person (A), and the amount by which a given unit of consumption impacts the environment (T). This idea has often been further simplified by subsuming the technology term into the affluence one. York and colleagues (2003) take this approach: in their analysis of ecological footprint, they simplify the IPAT framework to a product of population density and GDP per capita (affluence). This simplified version can be thought of as the 'economic footprint' of a country, in that it describes the total amount of economic activity per unit of land area.

The environmental Kuznets curve (EKC) hypothesis is a modified version of the IPAT theory that is more nuanced in its treatment of technology. It posits that increasing economic activity and wealth will increase environmental degradation as a country moves from low-income to middle-income, but will decrease degradation as a country moves from middle-income to high-income. This decrease in the high-income stages would be due to choices made for greener technology and greater resources available for conservation. This would give the degradation-income relationship an inverse 'U' shape. Empirically, the EKC does seem to be true for some environmental variables, particularly those that can be managed locally and through technological advances (Magnani 2000). However, the validity of the EKC in relation to environmental degradation in general has often been called into question (Stern *et al.* 1996; Magnani 2000; Stern 2004). For many environmental indicators, the turning point above which the EKC hypothesizes they would improve is simply never reached. With respect to biodiversity loss in particular, country cross-sectional data behaves according to the predictions of the EKC only in the case of birds. For all other taxa, the pattern is either the reverse of the EKC or is simply a steady increase with GDP in the number of species threatened (Naidoo & Adamowicz 2001).

ECONOMIC DISTRIBUTION

The drivers discussed so far have focused only the size of the economy, generally represented by GDP per capita. However, countries with the same GDP per capita can have economies that are structured very differently from each other. The GDP per capita is an average value, but it can be distributed very evenly or it can be skewed such that most of it is controlled by a comparatively small portion of the population. Several theories have been advanced suggesting that this variation in distribution may have an effect on environmental outcomes. The majority of these suggest that greater inequality is related to greater environmental degradation (Ostrom 1990; Boyce 1994; Magnani

2000; Ostrom 2001; Margreiter *et al.* 2005), but there are some exceptions (Olson 1965; Heerink 2001).

Two of the more influential researchers on this issue, Mancur Olson and Elinor Ostrom are on opposite ends of the debate. Mancur Olson, in his *Logic of Collective Action* (1965) hypothesized that greater inequality has the effect of concentrating the financial gains from conserving a resource within a group that is small enough and powerful enough to effectively act towards the conservation of the resource. This concentration was later termed the Olson Effect. By contrast, many researchers coming from a political science perspective look at the issue in terms of co-operation and institution building. They take the perspective that greater inequality makes it more difficult for effective co-operation to occur in a society, which then makes all institutions – including those devoted to conservation – less effective (Ostrom 1990, 2001).

Magnani (2000) and Boyce (1994) both argue, similar to Ostrom (1990, 2001), that greater inequality will be worse for conservation. Magnani (2000) suggests that individuals' income relative to each other is more important than their absolute income in determining their perceptions of how well off they are. Greater inequality thus decreases the average perception of economic well being of those in the lower part of the economic spectrum, which in turn decreases their desire to spend money on environmental conservation. Boyce (1994) draws a similar conclusion, but by different reasoning; he describes a process by which increasing inequality changes power relationships in a society such that those who are most likely to benefit from environmental degradation (the rich) become less accountable to those who are most likely to suffer from the consequences of it (the poor). In a critique of Boyce (1994), Heerink et al. (2001) provide a mathematical model describing why environmental degradation should decrease as inequality increases. However, their argument is based on the assumption that the Environmental Kuznets Curve holds true for most environmental indicators, which, as was discussed above, is a very questionable assumption.

Using a game theory modelling approach, Baland and Platteau (1999) hypothesized a U-shaped relationship between inequality and environmental conservation. Their model indicated that conservation was most successful when a community was either very equal or very unequal. Conceptually, this can be seen as a combination of the theory of both of the theories discussed in the preceding paragraph. Initially, increasing inequality hinders the development of effective institutions, and therefore causes a decrease in conservation success. However, after a certain point, higher inequality allows certain individuals to control enough of the resource that they conserve to serve their own interest. An important point to note here is that on the falling part of this U-curve – i.e. the part where conservation success decreases as inequality increases – the relationship is being driven by changes in the effectiveness of institutions. By contrast, on the rising part of the curve, the process is being driven by changes in the actions of individuals.

On this question, theory has advanced further than have empirical tests. The general idea that inequality can have a negative effect on public goods has been demonstrated in the health field (Ronzio *et al.* 2004; Ross *et al.* 2005). This work has hypothesized that the effect is due to a change in institutional spending priorities caused by inequality. On the environmental question in particular, Heerink and colleagues (2001) tested the effect of inequality on a collection of environmental variables with mixed results. Mikkelson and colleagues (2007) found that greater inequality was associated with indicators of biodiversity loss when human population and GDP were controlled for. The present paper will be an extension of that work, but will test a broader range of competing models across a greater number of countries.

COMPARING HYPOTHESES

In this paper, I use a model comparison approach similar to that used by York et al. (2003). I take several competing models, each based on theoretical expectations of the indirect drivers of environmental change, and evaluate which best predicts differing rates of biodiversity loss among countries. This analysis differs from that of York et al. (2003) in that while their models were used to predict ecological footprint (the amount of land area per person that a country requires to support its current level of consumption), mine looks at effects on biodiversity. Thus York et al. (2003) look at an indicator of human impact on the environment as their dependent variable, whereas I look at one of the end results of that impact. The common ground is that both studies use the socio-economic drivers of environmental change as their independent variables.

CONTEXTUALIZING COUNTRIES

Any analysis that compares national-level statistics among countries is complicated by the great variation that exists among countries. This is particularly true when the study, like ours, is global in extent. Wealth in 2004, as represented by GDP per capita, varies globally among countries by factor of several hundred (World Resources Institute 2007). However, differences in GDP do not capture all of the variation in national contexts. Differences between countries at varying levels of development may not simply be a matter of degree, but may also be one of nature. Historical and political contexts can greatly influence how institutions have been built, and as a result, how economic circumstances affect a country and its policy (Acemoglu *et al.* 2002).

To begin to address this issue, I will break down the analysis by development categories as defined by the United Nations Development Program's (UNDP) Human Development Reports (HDR) and its Human Development Index (HDI) (United Nations Development Programme 2006). The HDI is partly based on GDP, but it also controls for two other aspects of development: education and health. Looking at predictive models for biodiversity loss within each development category as well as with all countries taken together will allow me to see if relationships between socio-economic variables and biodiversity loss take different forms at different levels of development. If patterns are robust across development categories, then I will be more confident generalizing conclusions regarding those relationships.

APPROACH

My goal for this analysis is to evaluate the different theoretical frameworks in order to determine which function best as predictors of biodiversity loss. I will compare the partially competing Economic Footprint (York 2003) and Environmental Kuznets hypotheses to determine which provides a more accurate picture of levels of threatened species. Next, I will test if the inclusion of inequality into those frameworks improves their predictive strength. Finally, I will examine a model of environmental governance. As was discussed above, much of the effect that inequality is hypothesized to have on the environment would be through its impact on institutions and their effectiveness. By looking at environmental governance, I can test that relationship directly.

METHODS

MODEL COMPARISON APPROACH

To determine which socio-economic factors are most likely to be indirect drivers of biodiversity loss, I used a model comparison approach. Five models were evaluated in addition to the fully saturated one. The models were as follows:

i) *Saturated*: all variables included.

ii) *Economic Footprint*: I follow York et al. (2003) in employing a simplified version of the IPAT (Impact = Population x Affluence x Technology) framework. Gross domestic product (GDP) per capita was used as an indicator both of affluence and of technology in a country. Population density was included to describe the spatial concentration of the per capita impact.

iii) *Economic Footprint + Inequality*: The basic Economic Footprint model plus inequality.

iv) *Environmental Kuznets*: The Environmental Kuznets Curve (EKC) is the theory that increasing wealth initially has a negative effect on many environmental outcomes (as industry intensifies and consumption increases), but above a certain level has a positive effect (as societies are wealthy enough to afford greener technology) (Stern 2004). By including GDP/capita in both its linear and quadratic forms in this model, I allow for the U-shaped relationship between affluence and biodiversity that the EKC would predict.

v) *Kuznets + Inequality*: This model adds the Gini to the basic Kuznets model. This allows for a U-shaped relationship between Gini and biodiversity as well as between GDP and biodiversity. The former is included to test the validity of the theorized U-shaped relationship between inequality and conservation that was mentioned in the Introduction.

vi) *Environmental Governance*: This final model tests how well differences in governance can predict biodiversity loss. An index of environmental governance (discussed further below) was included in addition to a dummy variable representing whether or not a country was communist during the time period in question.

In addition to the variables mentioned above, all models were controlled for the level of endemism of the species in each country. This will be discussed in more detail below. Initially, inequality models were run with both the linear inequality term and the quadratic inequality term. This was to test for the U-shaped relationship between inequality and conservation that was theorized by Baland and Platteau (1999). In both cases, the quadratic Gini was non-significant, and so was left out of the models presented here.

Models were compared using both the Adjusted R^2 and the Aikike Information Criterion (AIC) from an OLS multiple linear regression. A correction for small sample sizes will be used with the AIC (Burnham & Anderson 2004). Because the theory this analysis is grounded in focuses largely on institutions, particularly in terms of how inequality is hypothesize to effect conservation, I made the decision to not weight the analysis (either by country area or human population) on the idea that each country has an independent set of institutions that should be treated equally. For the sake of consistency at the model comparison stage, I only included countries that had data for all the variables in the saturated model. Three models of the above six were then selected for further analysis. These three were tested for consistency between three development categories (high, medium, and low) as defined by the UNDP in their human development reports (United Nations Development Programme 2006). Because these models involved fewer total variables than the full model comparison, I was able to include more countries in the sample at this stage of analysis.

DATA SOURCES

Biodiversity

To measure the status of biodiversity in each country, I looked at the proportion of plant and vertebrate species that were threatened in 2006, as defined by the World Conservation Union (IUCN). This data was obtained from the World Resources Institute's (WRI) Earthtrends Database (World Resources Institute 2007). By using the proportion, I implicitly control for the total number of species known, which varies between countries by more than two orders of magnitude and which is certainly 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. That challenges one of the assumptions of this analysis, namely, that the socio-economic variables we are measuring at the country-level are having an impact on the threat status of species at the same scale. That assumption may not be entirely true. However, there is no reason to expect that this issue will bias the results in any one direction; rather it will simply make any pattern more difficult to detect.

All else being equal, the risk of global threat or extinction for a species is greater for highly endemic species than it is for very widespread ones. It is therefore important to control for levels of endemism when comparing numbers of threatened species among countries. Endemism data for plants is unavailable for many countries; however, endemism data for vertebrates alone is relatively complete. As such, controlling for endemism using data from all plants and vertebrates combined greatly restricts the sample size of countries I am able to use relative to the case where I use endemism data from vertebrates only (46 countries as opposed to 64). In addition to improving the sample size, an index of endemism based on vertebrates has far more explanatory power with respect to the proportion of species that are threatened (Adj.R^2 = 0.33, $p<10^{-16}$; Figure1) than does an index of endemism based on both plants and vertebrates (Adj.R^2 = 0.15, $p<10^{-6}$). I therefore made the decision to use an index of endemism based on vertebrates for the rest of the analysis. For reference, results of the model comparison had it used an index of endemism based on all species is included as Appendix A.

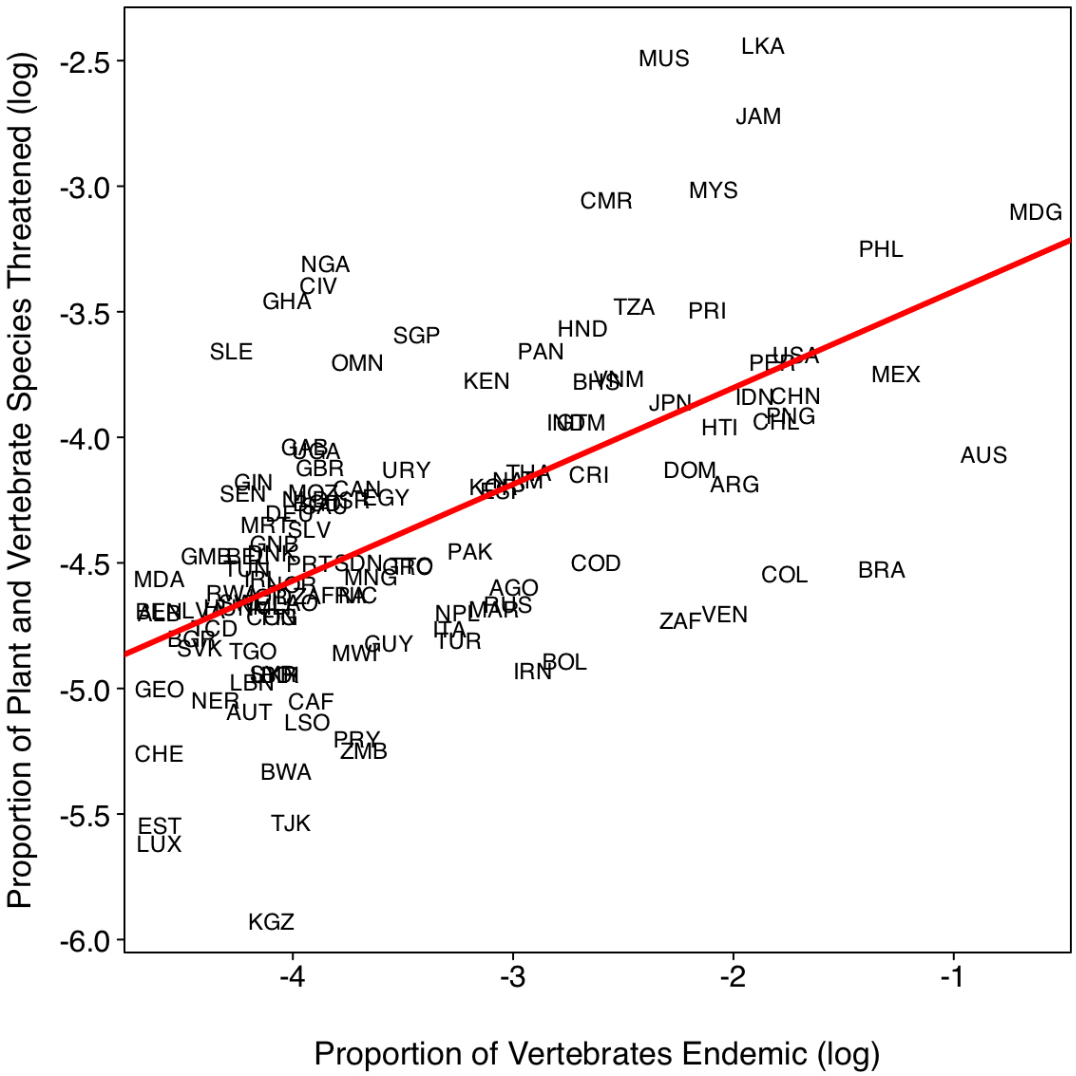

Figure 1.1: Relationship between the proportion of vertebrate species that are endemic and the proportion of plant and vertebrate species that are threatened. Adjusted $R^2 = 0.33$, p-value $< 10^{-16}$. See Appendix B for full country names.

Socio-Economic 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 data, I used data that was normalized for purchasing power, which corrects for differences in cost of living and exchange rates between countries. The value thus better represents economic activity in the country in question. This data was obtained from the WRI's Earthtrends Database for all years between 1975 and 1999 (World Resources Institute 2007). In order to achieve better sample sizes, I averaged GDP over five-year periods, because in any given year many countries are missing data.

Environmental governance was measured using an index (CAP.GOV) calculated by the Yale Center for Environmental Law and Policy (YCELP Pitt Inequality Project; 2006). This index is a composite of several variables including general governance indicators (such as corruption and level of democracy) as well as factors more specific to the environment (such as knowledge creation in environmental science and number of IUCN member organizations). One challenge with the environmental governance data is that it is not available over the same time scale as is the GDP data: only recent (2005) values are available.

Inequality was measured using the Gini Index, which ranges (theoretically) from 0 to 100 where 0 is perfect equality and 100 is perfect inequality. In practice, national Gini indices presently range from a global high of 59 (Brazil) to a global low of 23 (Slovakia). I used the Standardized Income Distribution Database as my source for the Gini (Pitt Inequality Project 2005). This is a relatively new database which corrects for data inconsistencies that were a problem for previous studies of inequality (Babones & Alvarez-Rivadulla 2007). In a similar fashion to the way in which the GDP data was treated, Gini was averaged over five year periods to improve the sample size. See Appendix C for a full listing of all data used in this analysis.

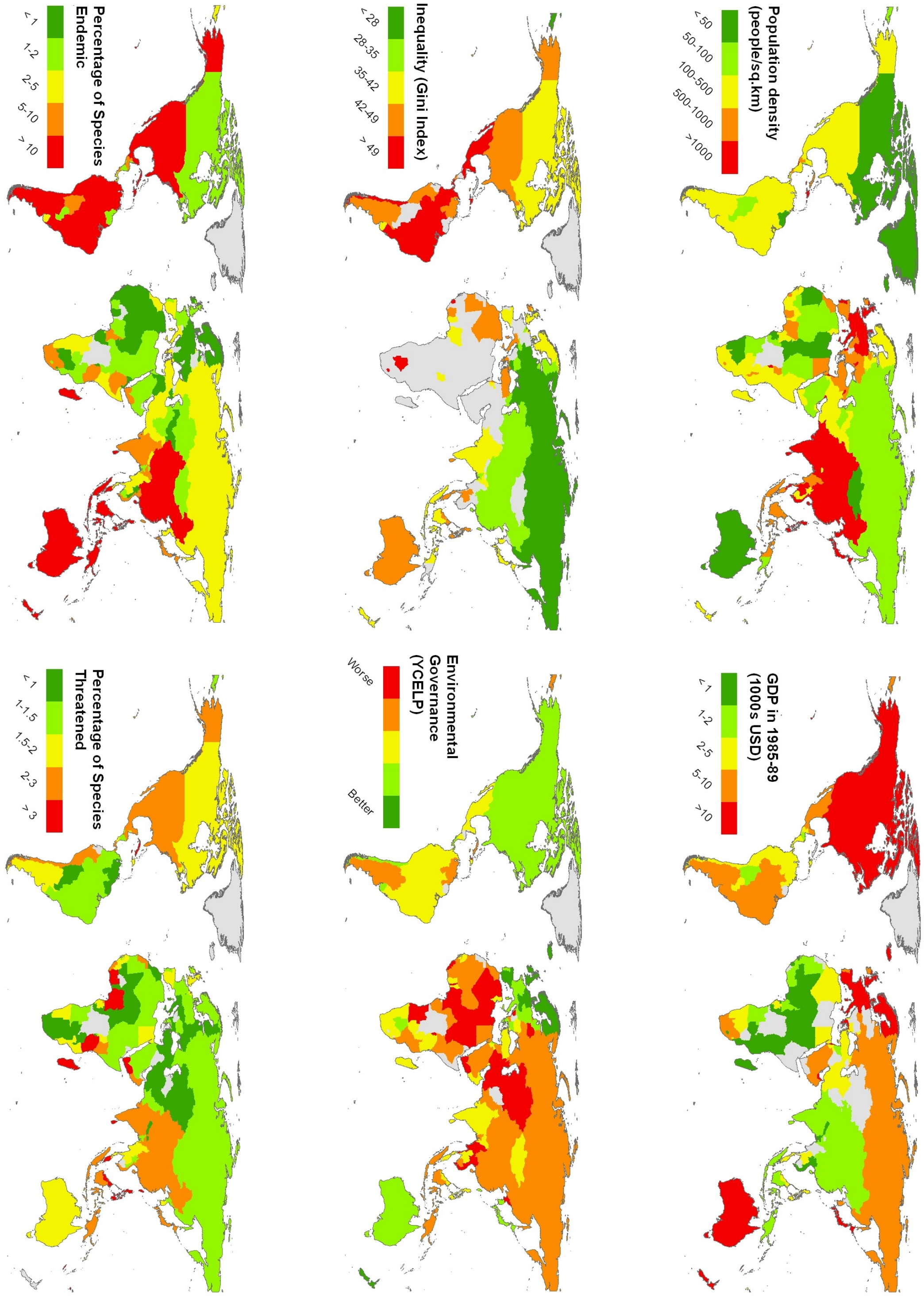

Figure 1.2: Data used in this analysis (see Appendix C also). Population density, gross domestic product, and inequality are all from the time period 1985-1989. Environmental governance data is 2005, while species indicators are from 2006. Countries shaded in grey had no available data for the indicator in question.

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 certain amount of time. The length of this time lag will be dependent on both the species and the impact in question. Mikkelson and colleagues (2007) found that the strongest relationship between socio-economic data and 2004 species indicators was found when socio-economic data from 1989 was used. In this paper, I addressed multiple potential time lags by analyzing data from all five-year periods between 1975 and 1999. For the sake of simplicity of discussion, the results section will focus on results from the time period identified by Mikkelson et al. (i.e. 1985-1989) both for the model comparison and for the examination of results by development category. In the subsection 'comparison of different time periods,' some relevant differences between time periods will be discussed.

RESULTS

COMPARISON AMONG MODELS

Among the 64 countries with sufficient data (Appendix B), the fully saturated model explained 51.1% of the total variance (adjusted R^2) in the proportion of plant and vertebrate species threatened (Table 1.1). These countries represented 67.7% of the world's land area and 78.7% of its human population. Of the variables included, two stand out as significant: human population density and the proportion of vertebrate species that are endemic to the country. Both have positive coefficients meaning that higher population density and higher levels of endemism are both related to a greater proportion of threatened species.

Using the AIC in a stepwise simplification of the saturated model results in a model which retains all of the original terms except for the communism dummy variable. Of the terms that remain, all are statistically significant at the 0.05 level except for environmental governance. The regression coefficients for all remaining variables are of the same sign and similar magnitude to the saturated model just discussed. This simplified model has slightly better adjusted R^2 and AIC values than the fully saturated model (Table 1.1).

Model two, although retaining only three of the seven variables in the saturated model, explains 39.8% of the variance in proportion of species threatened. The three variables included, GDP per capita, population density, and level of endemism are all significant. The latter two have the same direction of effect as in the first model. GDP has a negative coefficient, meaning that higher GDP is associated with fewer threatened species.

The third model, Economic Footprint + Inequality, has the best (lowest) corrected AIC value of all of the models excepting the saturated one. Adding the Gini index as a variable relative to model 2 increases the adjusted R^2 to 0.45. All four terms in this model are significant, with no coefficients changing sign relative to model 2. The Gini index has a positive coefficient, meaning greater inequality is associated with a greater proportion of species threatened. As was mentioned in the methods section, the quadratic of the Gini coefficient was non-significant when included in this model, and in any other inequality models. As such, only the linear inequality term was included in this presentation.

Model four, the environmental Kuznets model, explains 41.2% of the variance with three variables, all of which are significant. GDP and endemism have the same direction of effect as previous, while the quadratic of GDP has a positive coefficient. This combination (negative GDP and positive GDP squared) is the opposite of what the environmental Kuznets curve theory would predict.

Introducing the Gini index causes a slight increase in the strength of model 5 relative to model 4 causes an improvement in both the adjusted R^2 and the corrected AIC. The three variables from the previous model remain significant with the same sign of coefficient. The Gini term in this model is non-significant.

The final model introduces two new variables relative to the others. The dummy variable for communism is significant and has a negative coefficient, meaning that communist countries tended to have lower proportions of threatened species when endemism and environmental governance was held constant. Environmental governance as defined by the Yale Centre for Environmental Law and Policy (YCELP 2006) was not a significant predictor of threatened species. Although two of the four terms were non-significant, this model was behind only the saturated model and model 3 as measured by its corrected AIC value.

COMPARISON OF DIFFERENT TIME PERIODS

GDP, population density, and inequality are the three variables for which we have data for different ranges of years. Of the three, population density is the most consistent between years: in any range of years chosen, it has positive coefficients across all of the models that were described above. It stays significant in the later time periods, but is non-significant in the two earliest periods (1975-79 and 1980-84). GDP is slightly less consistent in that it sometimes has a positive coefficient in the earliest time period (1975-79). However, after 1980, it consistently has a negative coefficient across all models. The significance of its relationship with the proportion of species threatened is greatest in the 1985-89 time period. Inequality is similarly most significant when data from the 1985-89 time period is used. In the Economic Footprint + Inequality model, it has a positive coefficient for the first three time periods, but a non-significant negative one for the final two (1990-94 and 1995-99). These two most recent periods are both after pronounced increases in the inequality of many European nations that occurred with the break-up of the Soviet Union (Pitt Inequality Project 2005).

Table 1.1: Comparison of models predicting the proportion of plant and vertebrate species threatened (log). Sample size is 64 countries, representing 67.7% and 78.7% of the world's land area and human population respectively.

	Model 1a Saturated	Model 1b Stepwise-reduced	Model 2 Economic Footprint	Model 3 Econ. Footprint + Inequality	Model 4 Environmental Kuznets	Model 5 Kuznets + Inequality	Model 6 Environmental Governance
Independent Variables	ß	ß	ß	ß	ß	ß	ß
GDP per capita (log)	-2.14	-2.54 *	-0.155 *	-0.128 *	-2.75 *	-3.18 **	—
Quadratic of GDP per capita (log)	0.115	0.138 *	—	—	0.156 *	0.183 **	—
Population density (log)	0.114 *	0.117 *	0.120 *	0.147 **	—	—	—
Gini index	0.010	0.016 *	—	0.018 *	—	0.014	—
Environmental Governance	0.186	0.232	—	—	—	—	-0.133
Communist (1=yes; 0=no)	-0.222	—	—	—	—	—	-0.612 **
Proportion of vertebrates endemic (log)	0.293 ***	0.305 ***	0.236 ***	0.178 ***	0.245 ***	0.299 ***	0.239 ***
Constant	6.16	7.59	-1.76	-3.07	10.63	9.74	-3.33
Corrected AIC	90.7	89.1	98.85	94.2	97.4	95.8	94.7
Adjusted R^2	0.511	0.512	0.398	0.451	0.412	0.437	0.380

$* p < 0.05$ $** p < 0.01$ $*** p < 0.001$

ECONOMIC FOOTPRINT + INEQUALITY

When the best-performing model, Economic Footprint + Inequality, was applied to countries grouped by development category, the results were largely similar to what was seen in the initial model comparison (Table 1.2). Only high and medium development categories were compared as there was not sufficient data on low development countries to be able to run the model. The sample size for this model increased slightly over the model comparison stage to 70 countries, representing 67.8% and 79.0% of the world's land area and population respectively (Appendix B).

The model was slightly stronger among just high HDI countries (Adj.R^2 = 0.61) or just medium HDI countries (Adj.R^2 = 0.55) than it was when all the data was looked at together (Adj.R^2 = 0.46). The signs of coefficients remained the same from what they were in the model comparison stage. Level of endemism continued to be significant in both categories. The Gini index was significant in the high HDI category, while population density was significant among medium HDI countries (Figure 2). GDP per capita was not significant in either development category.

Table 1.2: Comparison between development categories of Economic Footprint + Inequality model

	All countries	Countries with high human development	Countries with medium human development
Independent Variables	ß	ß	ß
GDP per capita (log)	-0.109	-0.054	-0.039
Population Density (log)	0.162 ***	0.070	0.366 ***
Gini index	0.015 *	0.023 *	0.021
Proportion of vertebrates endemic (log)	0.316 ***	0.238 **	0.306 *
Constant	-2.85	-3.92	-3.69
Adjusted R^2	0.458	0.610	0.551
N	70	32	32

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

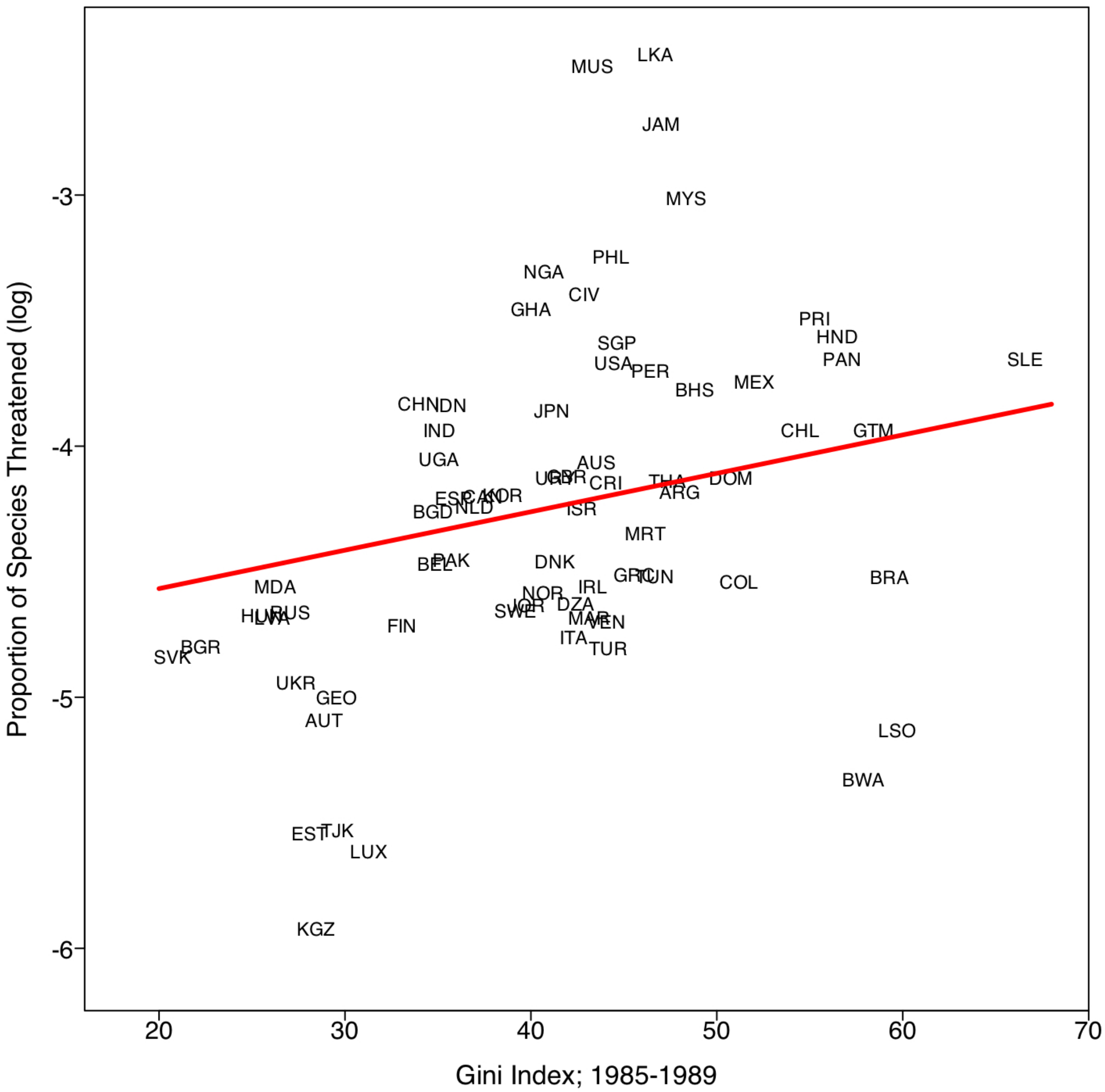

Figure 1.3: Relationship between the Gini index and the proportion of species threatened. The solid line is that predicted by the Economic Footprint + Inequality model for the relationship between Gini and the proportion of species threatened; it assumes mean values for all other variables in the model. For full country names, see Appendix B.

ENVIRONMENTAL GOVERNANCE

The governance model allowed a large increase in sample size relative to the model comparison. 113 countries had sufficient data to be included here, representing 89.5% and 92.0% of land area and population respectively (Appendix B). Similar to the Economic Footprint + Inequality model, the governance model has better explanatory power at the higher end of the development spectrum. The Adjusted R^2 falls from 0.58 to 0.32 to 0.20 going from high to medium to low development categories (Table 1.3). Of the four variables included, only endemism is significant. Similar to the model comparison, the sign of the GDP coefficient is negative in all categories except low HDI, and the sign of the environmental governance coefficient is positive in all categories except low HDI. Communism has a negative coefficient except in low HDI because there were no communist countries in that category.

Table 1.3: Comparison between development categories of Environmental Governance model

	All countries	Countries with high human development	Countries with medium human development	Countries with low human development
Independent Variables	ß	ß	ß	
Environmental Governance	-0.023	0.042	0.167	-0.128
Communist (1=yes; 0=no)	-0.305 *	-0.276	-0.192	—
Proportion of vertebrates endemic (log)	0.324 ***	0.275 ***	0.357 ***	0.363 **
Constant	-3.21	-3.37	-3.13	-3.32
Adjusted R^2	0.334	0.569	0.302	0.198
N	113	34	54	25

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

DISCUSSION

Patterns of biodiversity loss are complex, and no single statistical model is able to predict them perfectly. That said, much of the variation we see between countries can in fact be explained by collections of relatively simple socio-economic variables. The total economic footprint of a country, as expressed by a simplified version of the IPAT framework, is a strong predictor of threat to species. This basic framework can be improved upon: here I have shown that taking into account the distribution of the economy helps us predict threatened species better than we can by simply looking at the size of the economy.

Similar to York et al. (2003), my analysis found that the total size of the economy was a significant predictor. However, in their study, they found that ecological footprint increased monotonically with increasing GDP, whereas I found that the proportion of species threatened decreases through much of the range of global GDP. This suggests a disjuncture between environmental impact (ecological footprint) and environmental outcome (biodiversity) that may be partly explained by differences in governance in the high-income, high-impact countries. The predictive power of my models is about half that of the models used by York et al. (2003) when equivalent sets of terms were compared. This is likely because, as mentioned above, York et al. use a measure of human impact as their dependent variable, whereas I use one of the outcomes of that impact. By proceeding one step further down the causal chain, we introduce more variation. However, we also gain a better understanding of the actual outcomes of human impact, which is ultimately where our interest lies.

The most useful model for explaining the proportion of species threatened was the Economic Footprint + Inequality model, which included population density, GDP per capita, inequality, and was controlled for endemism (Table 1.1). Its explanatory power with all countries included (Adjusted $R^2 = 0.46$) was slightly lower than the full models developed by Naidoo and Adamowicz (2001), but was more parsimonious in that it contained four terms as opposed to eight.

The inequality term consistently had a positive coefficient in the Economic Footprint + Inequality model, and was usually significant. The coefficient of the Gini term (0.023) for the high HDI countries in that model (Table 1.2) means that the 8 point difference in Gini between the United Kingdom (Gini = 42) and Spain (Gini = 34) could represent a 20% increase in the proportion of species threatened in the UK over Spain. Alternatively, taking a time-scale approach, the five point change in Gini in the USA from 1990 to 1997 (from 44 to 49) could eventually be responsible for a 12% increase in the proportion of species threatened, all else being equal. Being more conservative and using the regression coefficient of all countries treated together (instead of the coefficient for high HDI countries) changes these values to 13% and 8% respectively.

The Environmental Governance model performed almost as well as the Economic Footprint + Inequality model at the model comparison stage, but was not as strong when it was broken down by development categories. It did, however, allow more countries to be included than the Footprint + Inequality model. Surprisingly, the environmental governance term itself was not significant in any of the model runs. It is possible that governance is having little effect on biodiversity trends; however, drawing that conclusion would be premature. It is quite likely that an aggreagate measure such as the one produced by the YCELP is simply not sufficient to adequately describe the complexities of governance.

The Kuznets Curve theory proved to be a poor predictor of environmental degradation. In fact, the relationship between GDP per capita and the proportion of species threatened showed the reverse relationship than would be expected from the EKC: proportion of species threatened initially declined with increasing GDP, but then began to increase again. The basic Kuznets Model predicts that a minimum value for threatened species would be seen at a GDP per capita value of about $6700. Naidoo and Adamowicz (2001) showed roughly similar results for several taxa, although the turning points predicted by their models tended to be lower. The fact that biodiversity loss is not easily reversed by improvements in technology or policy is one reason why we may not expect it to demonstrate the EKC. Biodiversity loss is a cumulative process: if species populations are severely depleted, even the most foresighted policy change cannot reverse trends instantly. In cases of extinction, there is no policy change that can undo the loss.

The theory that environmental degradation should be worst in medium equality societies while highly equal and highly unequal societies cause lower degradation was not supported by this study. When the Gini term was included in both linear and quadratic form, the coefficients did consistently describe the inverted-U that theory predicts (Baland & Platteau 1999); however, the quadratic Gini term was never significant. As was mentioned in the Introduction, the inverted-U theory relies on institutional effects at the rising end (where inequality increases environmental degradation), but is dominated by the actions of individuals at the falling end (where inequality decreases environmental degradation). At country-level, it may be that the scale is too large for individuals' conservation decisions to directly benefit the individuals themselves; therefore, Olson

Effects may not be important at this scale. As a result, institutional effects may dominate the pattern, meaning that only a monotonic increase in degradation will be seen as inequality increases.

A sub-national analysis would be a useful approach to further examine this question. Spatial variation in inequality can often be as great or greater at the sub-national scale than it is at the national one (Ross *et al.* 2005). A smaller scale would also have greater potential to capture individual and community-level effects that may be lost at a national scale of analysis. We might therefore expect therefore expect the relationship between inequality and biodiversity loss to become even more pronounced at smaller scales.

An awareness of economic distribution improves our understanding of the socio-economic drivers of biodiversity loss. The importance of inequality as a determinant of environmental degradation is asserted theoretically by many different disciplines; this study and the one by Mikkelson and colleagues (2007) have now provided empirical confirmation. While the total size of the economy is an important explanatory factor, inclusion of the Gini index consistently improves or ability to predict threatened species. The distribution of the economy is a factor that we clearly cannot ignore as we try to better understand those processes that drive humanity's impact on biodiversity.

PREFACE TO CHAPTER 2

As was alluded to in the conclusion of Chapter 1, the effect of inequality can be expected to vary with scale. At larger scales, such as nations, institutional effects will likely dominate the pattern with inequality, while effects of inequality on the behaviour of individuals may be less important. As a result, at broad scales, we may see only the negative effects of inequality on the environment that were described by Ostrom (1990, 2001), and we may not see any of the potential positive effects that Olson (1965) hypothesized.

In Chapter 2, I turn the analysis to a smaller scale to determine whether the effect of inequality on biodiversity changes from what was seen at the country level. I will examine data in the United States, using county-level socio-economic data and biodiversity data at an even finer scale. In addition to allowing me to look at a smaller scale, the analysis in the USA is able to go further than the international analysis in other ways. The first benefit of an analysis within the USA is that the data available is of very high quality, and is consistent across all sampling points. Second, in the United States, it is possible to take a mechanistic approach to the inequality – biodiversity relationship. This is because of land cover data which exists for the entire continental USA.

As was discussed in the introduction of this thesis, habitat loss is the most important direct driver of biodiversity loss. Having land cover data will let me look directly at the connections between the indirect socio-economic drivers of biodiversity loss and this direct driver. In turn, I will be able to look at the relationship between land cover and biodiversity outcomes. By tracing the mechanism itself, I will gain a better understanding of the overall relationship between inequality and biodiversity.

If the relationship is robust at two different scales, global and national, and can be followed through a mechanistic pathway at the national scale, that will be very strong evidence for the general importance of inequality in the prediction of biodiversity loss.

CHAPTER 2: RELATIONSHIPS BETWEEN SOCIO-ECONOMIC VARIABLES, LAND COVER, AND BIRD SPECIES RICHNESS - A CASE STUDY IN THE UNITED STATES

INTRODUCTION

Biodiversity loss is occurring worldwide at an alarming rate, and is primarily the result of human activity (MA 2005). If we hope to mitigate this loss, it is important that we improve our understanding of its indirect drivers, that is those aspects of human societies that make them more or less damaging to biodiversity. The wealth of societies and the extent of their economic activity have often been shown to be strong predictors of environmental impact (e.g. Ehrlich & Holdren 1971; York *et al.* 2003; Stern 2004). More recent work has indicated that the distribution of the economy may improve our ability to predict threat to biodiversity relative to models which only take into account the absolute size of the economy (Mikkelson *et al.* 2007; preceding chapter). So far, this work has been done at broad scales: either nations or states within the United States. The goal of this present study is to examine the same question, but at a much finer scale. This approach has two primary advantages. First, it allows me to use data which is of very consistent quality across the sample. Second, by zooming in, I am able to take a more mechanistic approach and quantify a direct driver of biodiversity trends – land cover – in addition to the indirect socio-economic drivers. I focus on land cover because of the primary role habitat modification plays globally in human-caused biodiversity loss (MA 2005). As such, I hypothesize that any effect socio-economic variables have on bird diversity in the US will be largely mediated by land cover.

The USA is an ideal case in which to test this relationship. It has high-quality data for all three components of this analysis. Socio-economic variables are measured regularly and reliably by the US Census Bureau (USCB 2000). Land cover data is available for the entire country at fine (30m x 30m) resolution for two different years (MRLC 1992, 2001). Finally, biodiversity data is available from a reliable, long-term, and broad-scale source: the North American Breeding Bird Survey (BBS; Sauer *et al.* 2005). Because

BBS data is collected every year, using it as the dependent variable allows me to test for changes through time in a way that is not possible for an international analysis.

It has been shown in the United States that conservation initiatives are tightly related to economic factors (Pergams *et al.* 2004). This may be particularly true for birds in that they are charismatic species that tend to attract more funding for their conservation than different taxa facing similar levels of risk (Metrick & Weitzman 1996). It has been shown that willingness to pay to conserve bird species is higher than for many other taxa both for institutions (Simon *et al.* 1995) and for individuals (Loomis & White 1996). These factors combined suggest that birds may be particularly responsive to variation in economic factors. However, to date no study that I am aware of has directly looked at the effect between economics and trends in bird species richness.

Relationships between breeding birds and land cover indices have been described by many different researchers. The majority of these studies have looked at the relationship using a cross-sectional approach, that is they use a single time period 'snapshot' of species richness (Cam *et al.* 2000; Fauth *et al.* 2000; Jones *et al.* 2000; Mayer & Cameron 2003). However, a few studies have used a panel approach in that they use change through time in species richness (Boulinier *et al.* 2001; Donovan & Flather 2002). The latter approach is preferable because if change through time in the dependent variable can be linked to change through time in the independent variable, it gives greater confidence that the relationship is actually a causal one and not simply the result of correlation with external, unmeasured factors. In this study, I will look at both measures: changes in richness through time from 1992 to 2005 as well as snapshot richness in both years. The majority of the previous studies mentioned above have been relatively localized, focusing either on regions or single states. I will extend the analysis to all routes in the continental United States.

This analysis consists of three main components: biodiversity, socio-economic indicators, and land cover. Data for the three are available at different scales. Biodiversity data is available at the level of the sampling routes, which, as I will discuss further below, are

40km long and spread somewhat evenly across the USA. The finest resolution at which inequality data is available is at the county level, which is a considerably larger scale than the sampling routes. Other socio-economic indicators are also available at county level. Finally, land cover data exists at a 30m by 30m resolution, and can therefore be scaled up to any size. For the analysis, these data sources must be brought to a consistent scale. This raises what has been referred to as the Modifiable Unit Areal Problem (MAUP), the idea that the relationship between variables will change depending on what scale one measures them at (Jelinski & Wu 1996). There is no way to 'fix' the MAUP; addressing it simply requires that scales of analysis be chosen carefully and that, if possible, results from different scales be compared (Dungan *et al.* 2002). Instead of aggregating data to larger scales, it is generally preferable to perform analyses as close to the scale of the source data as possible (Jelinski & Wu 1996; Koper & Schmiegelow 2006). With this in mind, I decided to base my analysis at the scale of the bird survey routes, and take the socio-economic data from the county in which the route was situated (instead of trying to generalize bird data at the county level). For the land cover data, I constructed landscapes based on a one-kilometre buffer around each route.

The analysis proceeds by looking at three potential causal relationships in order to evaluate their relative strengths. The first relationship is between socio-economic variables and species richness. Species richness I measure both in terms of its change through time (1992 – 2005) and in terms of its final value (2005). The second and third relationships looked at are both intended to break down the first relationship into its mechanistic components. One will look at the relationship between socio-economic variables and land cover, and the other will look at the relationship between land cover and bird richness.

METHODS

In order to answer my question, I use three very different sets of data. Species richness of breeding birds is the biodiversity outcome in which I am primarily interested. Indicators of human activity are the indirect drivers whose ultimate effect I am trying to test. Finally, forest cover is the connector by which I hypothesize human actions will affect biodiversity.

BIODIVERSITY

To measure a component of biodiversity in the USA, I looked at data from the North American Breeding Bird Survey (Sauer *et al.* 2005). This is one of the most extensive databases on animal populations in existence. It consists of more than three thousand 40-kilometer-long survey routes, many of which have been surveyed for abundance of breeding birds annually since 1966. This data is available freely on-line (Sauer *et al.* 2005). I used richness data at the level of survey route, excluding runs which were flagged in the dataset as questionable either because of weather during the sampling, because of observer quality, or for other reasons. I only looked at richness of permanent resident birds because trends in migratory species will be influenced to an unknown degree by processes in areas distant to the bird routes on which they are sampled.

I used program ComDyn (Hines *et al.* 1999), which was designed particularly for use with BBS data, to quantify species richness. ComDyn corrects for the fact that species detection probability can vary greatly among species and among survey routes, and produces estimates for species richness and for trends in richness that are more reliable than simple count data (Boulinier *et al.* 1998). The primary indicators I used were simple number of species in the final focal year (2005), and the proportional change in species richness over the focal period (1992-2005; Figure 2.1). The focal years were chosen such that their starting point would coincide with the first available land cover data (1992). The final year was set as recently as was possible given data availability to allow as much time as possible for trends to appear. If data was not available for the year in question, data from the preceding or following year was used. If no data was available from any of the three years, the route was not used.

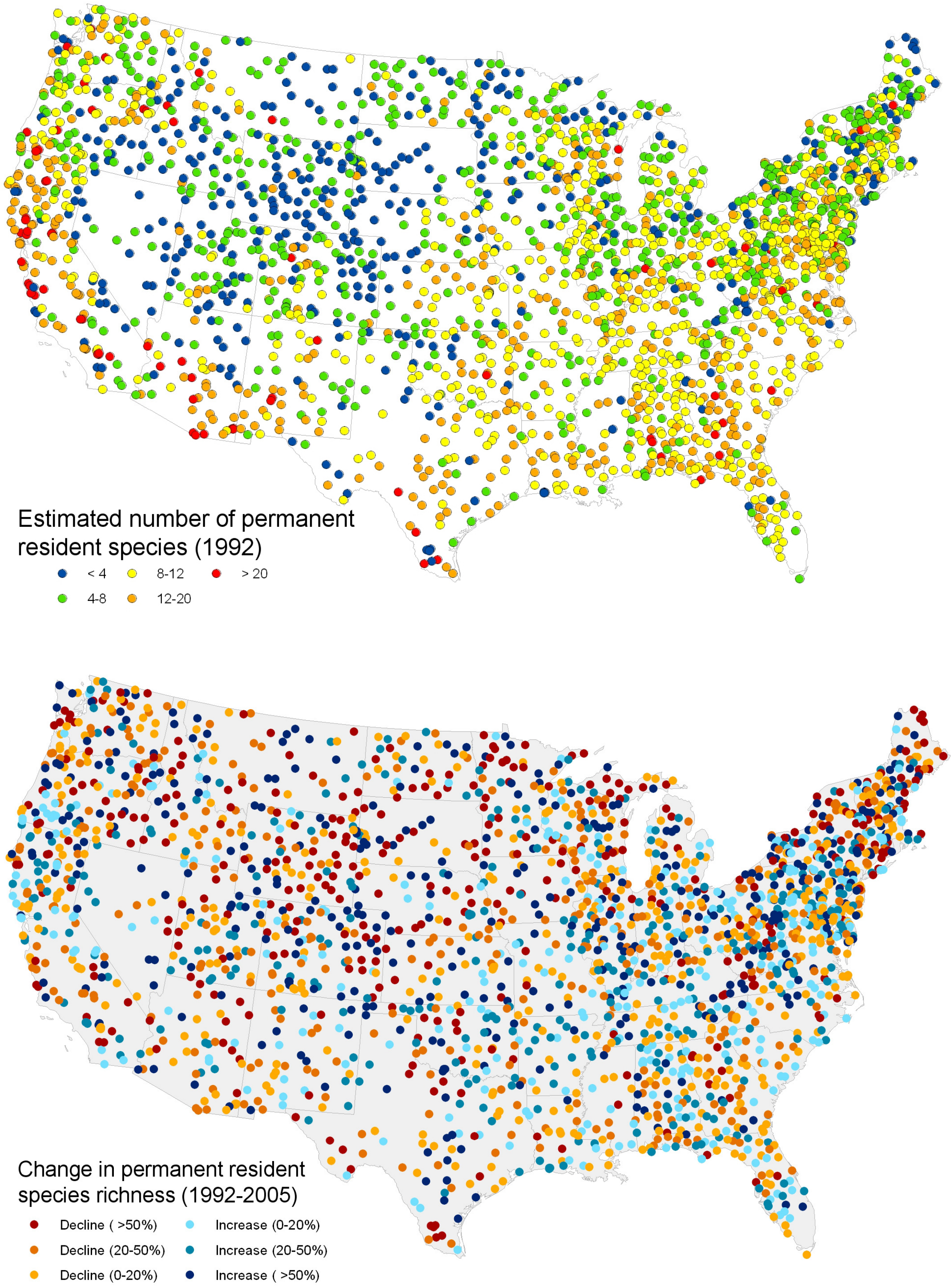

Figure 2.1: (top panel) Richness of permanent resident species in 1992. (bottom panel) Change in permanent resident species richness (1992-2005) as a percentage of richness in 1992. Routes were evenly split between ones that saw richness increase or stay the same (1221) and those that saw richness decrease (1073).

Because the proportion change in permanent resident species richness is expressed as a ratio, it could in theory be independent of the initial number of species. However, the proportion change and the initial number are in fact correlated because large multiplicative changes are uncommon at high species numbers (Figure 2.2). As a result, I included initial species richness in any analysis that involved the change in species.

LAND COVER

Land cover data for the contiguous continental United States is available at 30m by 30m resolution from the National Land Cover Dataset 1992 (MRLC 1992) and the National Land Cover Database 2001 (MRLC 2001). For my analysis, I grouped the original 17 land cover types into seven broader categories (water, developed, forest, shrub land, grassland, agriculture, and wetland) according to an Anderson level 1 reclassification scheme (Anderson *et al.* 1976). I classified each pixel according to the majority land cover type within a 3x3 window centred on the pixel in question. This majority sampling approach was used in order to reduce the effect of misclassification of the dataset.

Using Fragstats (McGarigal & Marks 1994), I generated five descriptive metrics for the forest category. These metrics were the percentage of the landscape covered (PLAND); the percentage of the landscape covered by core forest (CPLAND; core defined as > 100m from the edge); the mean patch size (AREA_MN); the mean distance to the nearest neighbouring patch of forest (ENN_MN_MN); and the length of forest edge relative to total forest area (ED). Examination of the data revealed that at this scale and using this buffer size, the correlation between PLAND and CPLAND was 99.3 percent. I therefore decided to not use CPLAND in the analysis, as PLAND is a simpler metric and will explain the same variation as CPLAND. Values for the landscape metrics tend to be non-normally distributed. In particular, PLAND and AREA_MN tend to have a high number of routes with low values, and a few rare routes with very high values. For the analysis, I log transformed all of the forest metric variables.

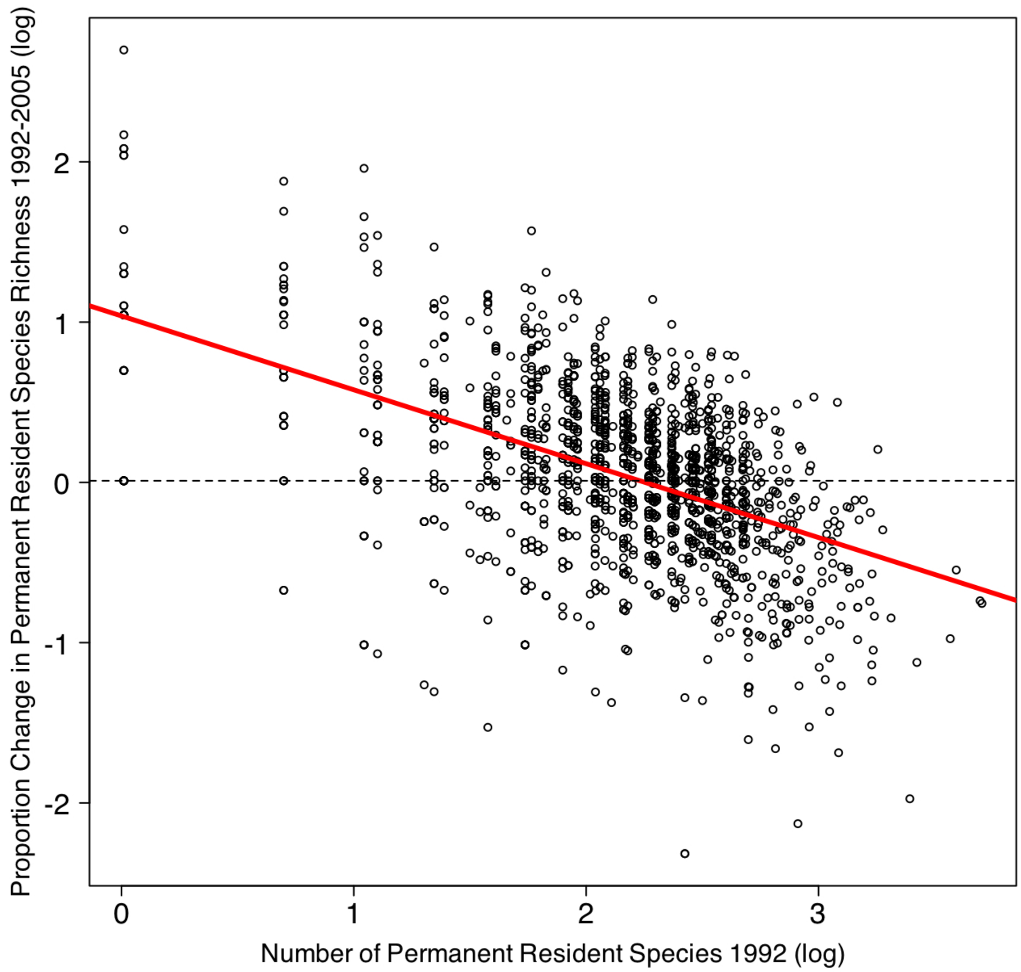

Figure 2.2: The proportional change in species richness (1992-2005) in relation to the initial number of species (1992). At lower numbers of species it is more likely that the proportional change will be greater, because a smaller change in numbers will cause a larger change in the ratio between 1992 and 2005 values. The dotted line on the graph indicates no change in richness (i.e. a log ratio of zero).

There is a large amount of colinearity between landscape metrics. In particular, AREA_MN and ED both vary with percentage forest cover, but in a non-linear fashion (Figure 2.3). Because indices of habitat fragmentation (such as AREA_MN and ED) are usually strongly correlated with the total amount of habitat (PLAND), it is difficult to separate these varying effects (Fahrig 2003; Turner 2005). One approach that can be used is to take the residuals of the fragmentation indices relative to the total habitat amount (Villard *et al*. 1999). This approach does tend to favour finding effects of habitat amount over effects of habitat fragmentation; however, there are few other options for separating the effects of these two aspects of habitat quality (Fahrig 2003; Koper *et al.* 2007).

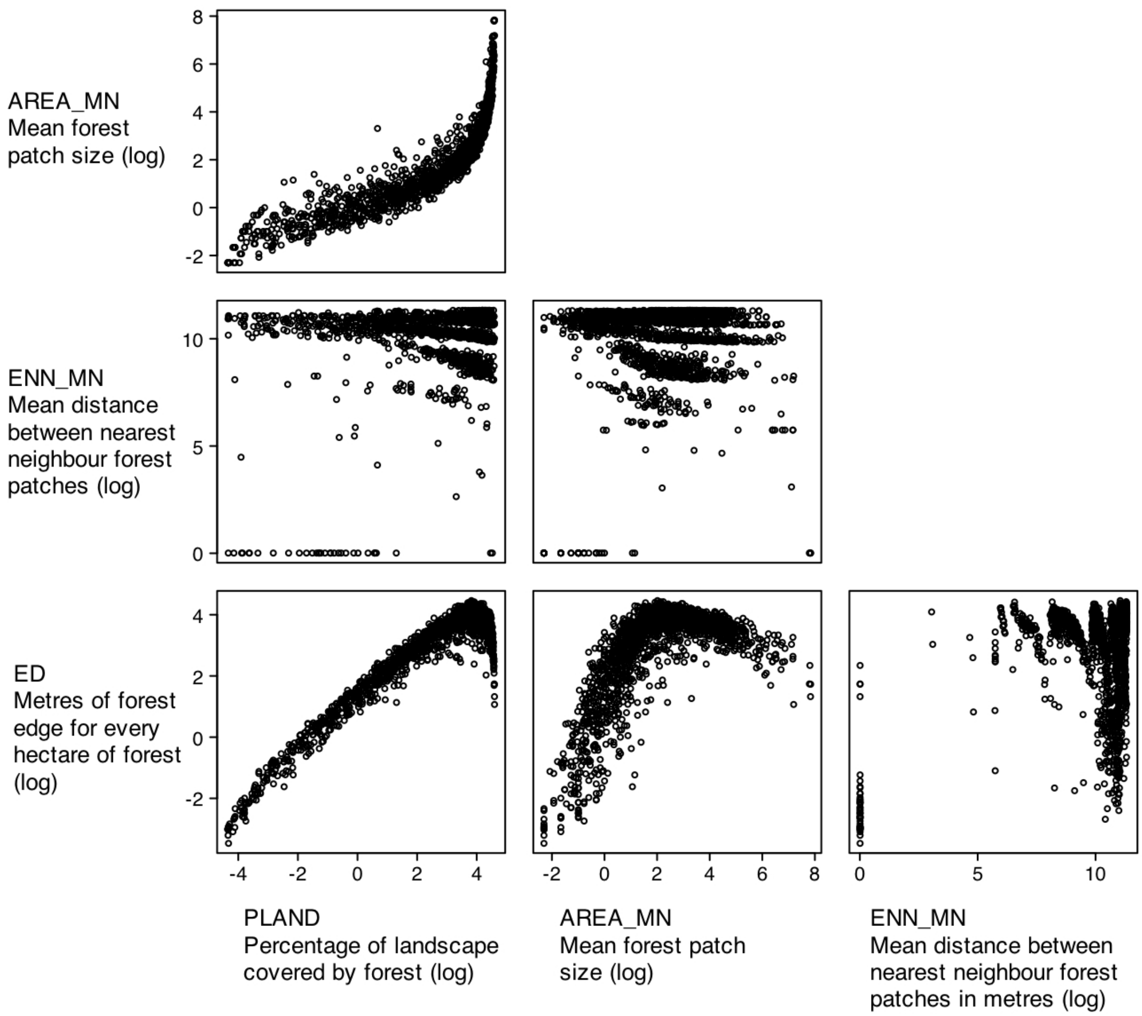

Figure 2.3: Relationships among four measures of forest cover.

Both AREA_MN and ED showed curvilinear relationships with PLAND. I tested two potential models to fit this relationship: quadratic and exponential. In the case of both variables, the exponential model fit the data better (Table 2.1). For the rest of this analysis, I will use the residuals from the exponential model every time I use these two variables. Nearest neighbour distance was not explained very well by PLAND (Table 2.1, Figure 2.3). I therefore will use the raw values for ENN_MN in the analysis.

Table 2.1: Adjusted R^2 values for models of PLAND predicting fragmentation metrics. Both AREA_MN and ED were strongly predicted by PLAND, and in both cases were better predicted by the exponential model (right column)

Fragmentation metric	PLAND + $PLAND^2$	PLAND + e^{PLAND}
AREA_MN	0.835	0.913
ED	0.239	0.107
ENN_MN	0.936	0.958

Although land cover data is available for two different years, the methodology changed significantly between them, and so reliable quantification of changes in land cover is not possible (Homer *et al.* 2004). Land cover change data is currently being created, but was not available at the time of writing. It should be available by the end of 2007 (Wickham 2007).

Mayer and Cameron (2003) demonstrated that the relationship between breeding bird richness and landscape characteristics varies depending on the scale of landscape looked at. How well a landscape represents the land cover in the county as a whole, and by extension how good a measure it is for examining the socio-economic determinants of land cover, is also a function of the landscape size: the larger a landscape is, the more likely it is to be representative of the broader area around it. To balance these two issues, I chose to use landscapes created with a one-kilometre buffer around survey routes. Landscape characteristics at that scale have been shown previously to have an effect on bird species richness at the survey route level (Mayer & Cameron 2003). At the same time, the roughly 80 square kilometres the landscapes cover should be large enough to provide a reasonable representation of land cover at a broader scale.

SOCIO-ECONOMIC INDICATORS

Population density, median income, and inequality data were all originally from the 1990 and 2000 US censii (USCB 1990, 2000). Density and income for each county in the US I obtained directly from the census. Inequality data in an accessible form is not available directly from the census. However, researchers at the University of North Carolina have converted income distributions into county-level Gini indices and have made that data freely available (Nielsen 2000; Moller & Nielsen 2005) (Figure 2.4).

For each bird survey route, I took the census data from the county in which the route was situated. Sometimes routes crossed county borders, in which case I used the census data from the county where the centre of the route was situated. For analyses, I used data from 1990 as well as the change between 1990 and 2000. By using change values instead of raw values for 2000, I reduce the strong colinearity between data from the two years, and am therefore able to focus on spatial patterns that are unique to 2000 (Figure 2.4).

Because of the U-shaped relationships that some have predicted between environmental impact and both GDP (Environmental Kuznets Curve; Stern 2004) and inequality (Baland & Platteau 1999), I will include the quadratic form of both of those variables in this analysis.

Using population density, I classified routes into three categories: rural, urban, and peri-urban. Using the criteria set by the US Census, urban routes were any that were in counties with population density over 500 people per square mile (195 people per square kilometre; 92 routes) (USCB 2000). We defined rural routes as those in counties with population less than 100 people per square mile (39 per square kilometre; 1688 routes). Remaining routes we defined as peri-urban (376 routes).

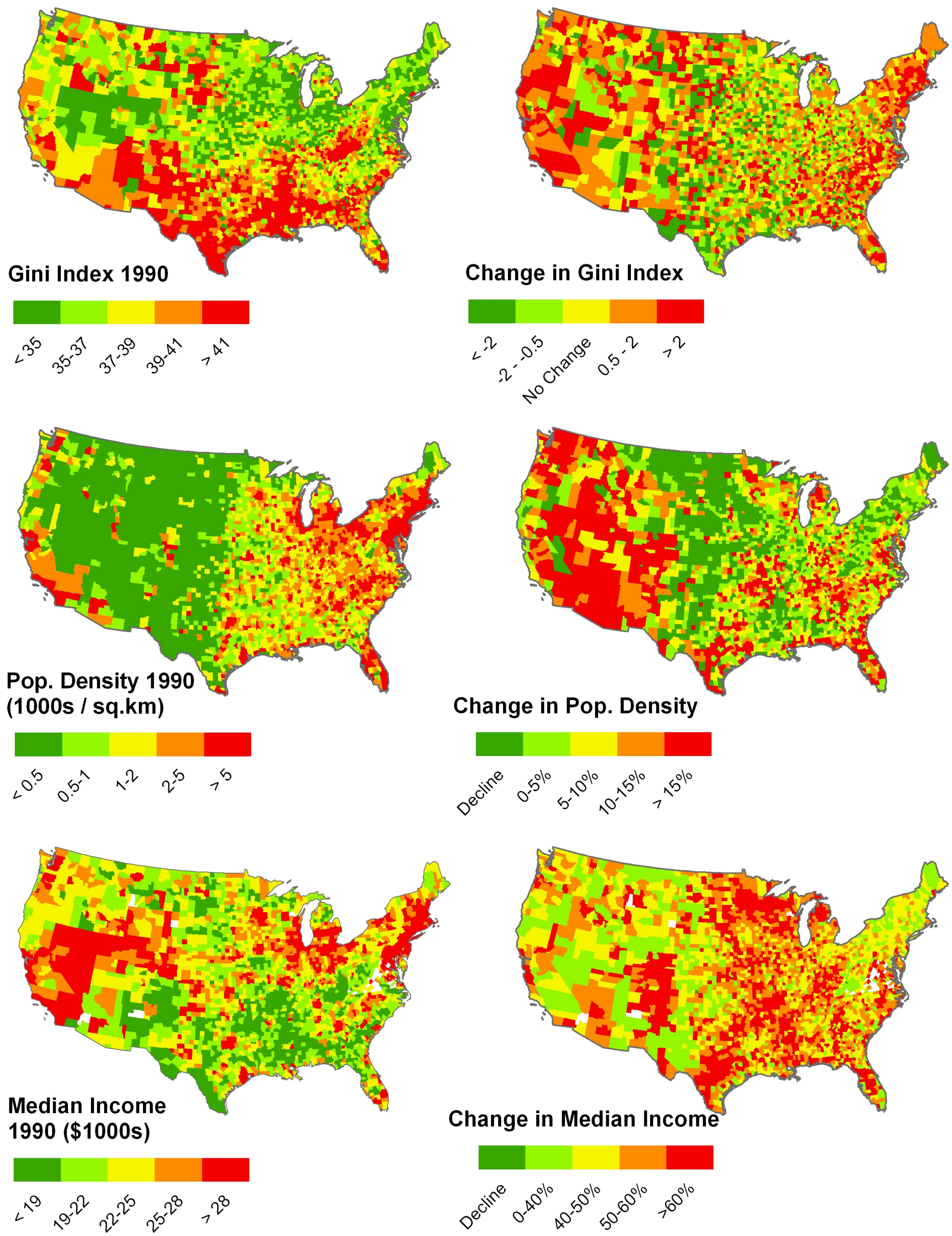

Figure 2.4: Spatial patterns in inequality, population density, and median income in the United States. Data are by county. Maps on the left are values in 1990, while maps on the right show the change between 1990 and 2000.

ANALYSIS

As discussed in the Introduction, there will be three sets of relationships examined: between socio-economic variables and bird richness; between socio-economic variables and forest cover; and between forest cover and bird richness. These relationships will be evaluated in a multiple regression framework by using the Adjusted R^2 and the Aikike Information Criterion. The latter was corrected for small sample sizes, as this correction prevents overfitting at smaller values of n (my sample size for the urban routes would fit the criteria for small here), and converges to the raw AIC at large values of n (Burnham & Anderson 2004).

RESULTS

The three parts of the relationship between human activity and breeding bird richness will be discussed section by section. First, I will address the overall relationship between socio-economic variables and species richness. Following that I will present two potential subsets of that relationship: the effect of socio-economic variables and forest cover, and the effect of forest cover on species richness.

SOCIO-ECONOMIC VARIABLES AS PREDICTORS OF SPECIES RICHNESS

Change in richness (1992-2005)

When all bird survey routes are examined together, socio-economic variables at the county level are poor predictors of local trends in permanent resident breeding bird species richness. Median income in 1990, population density in 1990, inequality in 1990, the change in the preceding three variables between 1990 and 2000, and the quadratic forms of median income and inequality together explained hardly any of the proportional change in the number of species at particular BBS sampling routes. Whether one looks at absolute change in species richness, proportional change in species richness, species extinction probability, or species turnover, the fully saturated socio-economic model never results in an adjusted R^2 greater than 0.02.

Looking at the proportional change in species richness, when routes were split according to human population density, the socio-economic models performed better. Although among rural routes (n=1507) the model was still very weak (Adjusted $R^2 = 0.014$), among urban (n=81) and peri-urban (n=338) routes the socio-economic variables were able to more effectively predict the change in species richness (Adjusted R^2 = 0.165 and 0.291 respectively). The linear and quadratic forms of median income were the two variables that had a significant effect on richness change among both urban and peri-urban routes. However, the coefficients of the median income term are of opposite sign between urban and peri-urban. In both cases, the quadratic term dominates the linear over the range of median income values: among peri-urban routes, the model predicts a more positive change in species richness as income increases, while among urban routes the model predicts a more negative change with increasing income. Looking at the other three indices of species change – turnover, extinction, and absolute change in richness – the predictive power of the models were still very weak (all adjusted $R^2 < 0.05$) even when routes were split by population density.

Richness in 2005

Socio-economic variables predict the absolute number of permanent resident species more universally than they predict change through time in the number of species. The same set of eight variables that were discussed above predict 22.6, 5.3, and 14.2 percent of the variance (adjusted R^2) in species richness among urban routes, peri-urban routes, and rural routes respectively. In all cases, human population density in 1990 is the most significant term. Surprisingly, although it is associated with lower species richness in urban and peri-urban routes, higher population density is actually associated with higher species richness in rural routes.

Taking all routes together causes a reduction in the predictive strength of the models. In this case, the full socio-economic model explains 4.7% of the variance in 2005 species richness (Table 2.2). In contrast to above, human population density is actually not a significant predictor of species richness in any of the models. This is likely due to the fact that, as was seen above, it has opposite effects at different levels of population density; therefore, when all routes are taken together, the pattern can no longer be resolved.

Table 2.2: Comparison of socio-economic models predicting 2005 species richness of permanent resident breeding birds (n=1806)

	Model 1 Population Density	Model 2 Median Income	Model 3 Inequality	Model 4 Economic Footprint	Model 5 Footprint and Distribution	Model 6 Saturated
Independent Variable	ß	ß	ß	ß	ß	ß
Population density (log; 1990)	4.8×10^{-6}	—	—	1.2×10^{-4}	4.2×10^{-5}	2.4×10^{-5}
Change in population density (log; 1990-2000)	2.9×10^{-3} ***	—	—	4.6×10^{-3} ***	3.8×10^{-3} ***	3.7×10^{-3} ***
Median income (1990)	—	-7.0×10^{-5} ***	—	-2.6×10^{-5} ***	-1.3×10^{-5} **	-2.7×10^{-5}
Change in median income (1990-2000)	—	1.8×10^{-5} **	—	1.4×10^{-5} *	1.7×10^{-5} **	1.7×10^{-5} **
Quadratic of median income (1990)	—	9.8×10^{-10} ***	—	—	—	2.8×10^{-10}
Inequality (1990)	—	—	0.167 *	—	3.4×10^{-2} ***	0.233 **
Change in inequality (1990-2000)	—	—	0.011	—	1.4×10^{-2}	0.011
Quadratic of inequality (1990)	—	—	-1.7×10^{-3} *	—	—	-2.6×10^{-3} **
Corrected AIC	4145	4091	4107	4067	4045	4041
Adjusted R^2	0.008	0.018	0.024	0.032	0.044	0.047

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

SOCIO-ECONOMIC VARIABLES AS PREDICTORS OF FOREST COVER

When all routes are taken together, socio-economic variables explain relatively little of the variance in forest metrics. Adjusted R^2 values are 0.029, 0.021, 0.015, and 0.020 for total forest area (PLAND), residual mean patch size (AREA_MN), mean distance to nearest neighbour (ENN_MN_MN), and residual edge density (ED) respectively (Table 2.3). Many of the variables in the model are significant, but have relatively small effects. Population density has a – perhaps surprising – positive relationship with total forest area, while increases in population density have a negative relationship are associated with smaller forest areas. Median income has a negative effect, while change in median income between 1990 and 2000 has a positive association with forest cover. Routes in counties with higher inequality and routes in counties where the change in inequality is more positive both show a tendency for greater forest cover. The coefficient in this case is actually quite large, with each percent increase in the Gini index being associated with nearly a one percent increase in the percentage of the landscape that is forested. An increase in Gini from the 25th percentile to the 75th would therefore be associated with a ten percent increase in PLAND.

Table 2.3: Forest metrics (2001) as predicted by socio-economic variables.

	Dependent Variable			
	Percent of landscape forested (log)	Residual mean patch size (log)	Mean distance between nearest neighbour forest patches (m) (log)	Residual edge density (meters per hectare of forest) (log)
Independent Variable	ß	ß	ß	ß
Population density (log; 1990)	5.1 x 10^{-4} *	2.0 x 10^{-6}	-4.2 x 10^{-5}	-6.3 x 10^{-5}
Change in population density (log; 1990-2000)	-3.2 x 10^{-3}	-1.8 x 10^{-3} **	2.9 x 10^{-3}	1.8 x 10^{-3} **
Median income (1990)	-1.7 x 10^{-4} ***	2.9 x 10^{-5} **	-2.2 x 10^{-5}	3.6 x 10^{-5}
Change in median income (1990-2000)	6.1 x 10^{-5} ***	-5.8 x 10^{-6}	4.4 x 10^{-5} **	-6.0 x 10^{-6}
Quadratic of median income (1990)	2.62 x 10^{-9} **	-4.4 x 10^{-10} *	-2.2 x 10^{-10}	-6.3 x 10^{-10}
Inequality (1990)	0.835 ***	-0.075	-0.141	-0.198
Change in inequality (1990-2000)	0.088 ***	-2.3 x 10^{-3}	0.061 **	-0.021
Quadratic of inequality (1990)	-9.7 x 10^{-3} ***	8.6 x 10^{-4}	2.3 x 10^{-3}	2.6 x 10^{-3}
Adjusted R^2	0.029	0.021	0.015	0.020
N	1840	1781	1840	1781

When trends in total forest cover are looked at within categories based on population densities, the predictive power of the socio-economic variables improves greatly for both urban routes and rural (Adjusted R^2 for urban, peri-urban, and rural routes are 0.336, 0.066, and 0.127 respectively; Table 2.4). In the cases of both the urban and rural routes population density has a negative association with forest cover, which contrasts both the rural routes and the results discussed above for all routes combined. Change in population density has a negative coefficient across all categories, but is only significant among urban and rural routes. Median income has a negative association with forest cover, as it did above; however, when categories are separated it ceases to be significant. Change in median income has a significant positive association with forest cover in both urban and rural categories, and a non-significant positive one among peri-urban routes. Inequality has a significant negative association with forest cover among urban routes, and a significant positive association with forest cover among rural routes. The coefficients suggest that a change in inequality from the 25^{th} to the 75^{th} percentile would be associated with a 14 percent decrease in forest cover among urban routes, and an 11 percent increase in forest cover among rural routes. Change in inequality is only significant among rural routes, and there it has a negative effect.

Table 2.4: Predicting percent total forest cover at different levels of population density.

	Dependent Variable = Percent total forest cover		
	Urban Routes	Peri-urban Routes	Rural Routes
Independent Variable	ß	ß	ß
Population density (log; 1990)	-3.3×10^{-4} *	-4.3×10^{-4}	0.028 ***
Change in population density (log; 1990-2000)	-8.7×10^{-3} ***	-8.8×10^{-3} *	-0.025
Median income (1990)	-5.0×10^{-5}	-1.5×10^{-4}	-1.6×10^{-5}
Change in median income (1990-2000)	8.0×10^{-5} **	-3.8×10^{-5}	7.5×10^{-5} ***
Quadratic of median income (1990)	9.0×10^{-10}	3.12×10^{-9} *	-2.5×10^{-9}
Inequality (1990)	-1.15 **	0.243	0.866 ***
Change in inequality (1990-2000)	0.256	0.133	-0.074 **
Quadratic of inequality (1990)	0.016 **	-3.6×10^{-3}	-0.011 ***
Adjusted R^2	0.336	0.066	0.127
N	84	338	1418

FOREST COVER AS PREDICTOR OF SPECIES RICHNESS

Change in richness (1992-2005)

Forest cover metrics varied in their ability to predict change in species richness depending on what measure of change was used. The weakest model was for the proportional change in species richness, which had an adjusted R^2 of only 0.04. Predictive models for the absolute change in species number and the probability of extinction both had adjusted R^2 values of about 0.11. Species turnover was the most responsive to changes in forest metrics with an adjusted R^2 of 0.46 (Table 2.5). In the case of models of absolute and proportional change in richness, and extinction probability, the total amount of habitat and the initial number of species present at the route were the most significant predictors. Greater total area of forest was associated with more positive increases in species richness, and also with a lower proportion of 1992 species being absent in 2005. Higher initial richness was associated with more negative trends in species richness, but also with a lower proportion of 1992 species disappearing by 2005.

The patterns were quite different with the strongest model – the one predicting species turnover. Here, the total amount of forest was not significant, but two indices of fragmentation were: the residual mean patch size, and the residual edge density. Given a constant amount of forest area, larger mean patch sizes were associated with a higher proportion of 2005 species that were present in 1992. That is to say that species turnover is lower when mean patch size is larger. The result for edge density is perhaps more surprising. It implies that a greater amount of forest edge per unit area is associated with lower turnover as well (Table 2.5).

Table 2.5: Prediction of changes in permanent resident species richness (1992-2005) using forest cover data from 1992.

	Dependent Variable			
	Absolute change in species richness	Proportional change in species richness	Proportion of 1992 species still present in 2005 (converse of extinction probability)	Proportion of 2005 species that were present in 1992 (converse of turnover)
Forest metric	ß	ß	ß	ß
Percent cover (log)	0.229 ***	0.018 **	0.020 ***	-0.007
Residual mean patch size as % total forest area (log)	-0.187	-0.016	0.026	0.083 **
Residual edge density (log)	-0.219	-0.036	0.111	0.180 ***
Mean nearest neighbour distance (log)	0.038	0.007	-0.008	-0.003
Species richness 1992	-2.57 ***	-0.196 ***	0.201 ***	0.520 ***
Adjusted R^2	0.113	0.041	0.109	0.458
N	1640	1636	1640	1640

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Richness in 1992 and 2005

The relationship between forest cover and richness is measured for three time frames. The first uses forest cover in 1992 to predict bird richness in 1992; the second uses forest in 1992 to predict richness in 2005; and the third uses forest in 2001 to predict richness in 2005 (Table 2.6). As with the socio-economic variables, forest cover is better at predicting the absolute value of richness than it is at predicting change. Adjusted R^2 values for forest cover metrics predicting species richness range from 0.095 to 0.152 depending on the years in which forest cover and richness are measured. Percent forest cover is positively associated with species richness in both 1992 and 2005. The relationship is strongest when 1992 forest cover is used to predict 1992 richness. In that case, a one percent increase in forest area is associated with a 0.12 percent increase in species richness. This value falls to 0.09 percent when 1992 forest area predicts 2005 species richness, and to 0.10 percent when 2001 forest area is used to predict 2005 species richness. Higher residual mean patch size in 1992 is significantly associated with lower richness in both 1992 and 2005. Greater amounts of forest edge in 1992, given the same total amount of forest, are associated with lower species richness in both 1992 and 2005 (Table 2.6)

Table 2.6: Prediction of permanent resident species richness using forest cover data. The first two columns use forest data from 1992, the third column uses data from 2001.

	Dependent Variable		
	Species richness 1992 (log)	Species richness 2005 (log)	Species richness 2005 (log)
Forest metric	ß	ß	ß
Percent cover (log)	0.119 ***	0.092 ***	0.095 ***
Residual mean patch size as % total forest area (log)	-0.206 ***	-0.138 ***	-0.075
Residual edge density (log)	-0.183 *	-0.152 *	-0.060
Mean nearest neighbour distance (log)	0.033 ***	0.010	5.4×10^{-3}
Adjusted R^2	0.135	0.152	0.095
N	1743	1636	1555

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

DISCUSSION

This study demonstrated that socio-economic variables can explain a significant portion of the variation in both forest cover and breeding bird species richness. In addition, at least one measure of land cover, percent forest cover, is a consistent predictor of bird species richness across all survey routes in the US.

The greatest difficulty with this study is differentiating between true causation and simple correlation. This is particularly a challenge in the case of the relationship between socio-economic indicators and land cover. Often, associations between socio-economic variables and land cover are simply the result of history, rather than being one of cause and effect. For example, rural areas in the United States have always tended to be poorer than urban ones. They also tend to have a greater proportion of forest cover. As a result, we see a negative correlation between median income and percent forest cover, although this is not a process where it could be said that the greater wealth is causing lower forest cover. One way to begin to understand which processes are truly causal is to look at changes through time. Unfortunately, although time series data is available on socioeconomic indicators, it is not yet available for land cover (Homer *et al*. 2004).

As another example of the issue of correlation versus causation, consider the fact that median income has a negative association percent coverage of forest, while change in median income between 1990 and 2000 has a positive association. What this may actually demonstrate is the process of people with wealth being attracted to areas that have a greater proportion of green space. So while these areas have traditionally been poorer than the denser urban centres, they are seeing their median income increase as people move in. This is therefore less an effect of income on forest cover, but rather a process of forest cover attracting income. Even if this pattern does not demonstrate a direct cause-and-effect, it may be indicative of a general social desire for green space that may cause forest cover to generally increase with income. In an integrated economy, however, one person's desire to live surrounded by green space may not change choices they make that affect the environment in other areas.

FOREST COVER AND BIRD RICHNESS

Forest cover explains much of the variation in the values and trends of bird species richness. The total amount of forest is generally the strongest predictor; however, it was also possible to detect an effect of forest fragmentation that was independent of the total amount of forest. Some have criticized the residual approach, as I have used, as a means of separating out the independent effects of habitat amount and habitat fragmentation (Koper *et al.* 2007). Much of this criticism is based on the fact that taking the residuals of fragmentation on amount, as opposed to the other way around, biases the analysis in favour of finding habitat amount to be more important than fragmentation. The fact that I have used this technique and have still detected an effect of fragmentation suggests that this effect is robust.

The association I found between larger mean patch size and lower rates of species turnover confirms results by Boulinier and colleagues (2001). The result that greater edge density was associated with lower turnover, however, was more surprising, because several studies have shown negative effects of edge density on birds (e.g. Villard *et al*. 1999; Howell *et al*. 2000; Mayer & Cameron 2003). It is possible that communities in areas with large amounts of edge tend to be composed of more generalist species, and as a result have a composition that less likely to change in response to environmental variation. However, this is simply a hypothesis that would need to be tested.

One difference between my study and others that have looked at the relationship between birds and land cover is the scale of analysis. Most studies have tended to focus on smaller areas (either one or a few states), whereas my study encompassed the entire continental USA. Many of the above studies therefore tended to be in a single ecoregion for the most part. The fact that the coarser metrics were more effective in my study may be because my routes cover such a wide variety of ecoregions. Variation in more descriptive metrics such as edge density may therefore be masked by more significant regional differences.

INEQUALITY

Inequality had a somewhat inconsistent effect throughout this analysis. When all bird routes were considered together, inequality was shown to be significantly associated with greater species richness in 2005 (Table 2.1) and with a higher percentage cover of forest. However, in one case, inequality seemed to have the opposite effect. Among the highest density routes, inequality was associated with a lower percentage of forest cover. Because forest cover was consistently associated with higher richness, in this case inequality would have a negative overall effect on richness.

The lack of a consistent relationship between inequality and environmental outcomes in this study may have to do with the scale of the analysis. BBS survey routes are very small relative to most levels of government in the USA. The socio-economic data, taken at county level, may similarly be measuring patterns at a resolution below where we would expect patterns with inequality. Environmental policy in the USA that relates specifically to species preservation is often set at the federal level (Simon *et al.* 1995; Hoekstra *et al*. 2002). Although states have some jurisdiction over the environment as well, it is not likely that there will be pronounced differences in environmental policy between counties. It has been suggested that inequality would have an impact on the environment through its effect on institutions (Ostrom 2001). It may be that in this case, there is simply not enough variance between institutions at the scale of analysis used. The empirical confirmation for the relationship between inequality and biodiversity has so far come at the scale of nations (Mikkelson *et al*. 2007; preceding chapter) or states in the USA (Mikkelson *et al*. 2007). It may be that these larger scales show sufficient variation in institutions, whereas counties do not. In addition, if local-scale management institutions are ineffective, as Ostrom (2001) suggests will be more likely with higher inequality, in the United States there will often be a higher level of government that will be able to step in and provide a framework for management. Intervention of higher levels of government may thus mask differences in institutions at smaller scales.

Others have hypothesized that inequality will affect the environment because of its influence on individual behavior (Olson 1965; Boyce 1994; Baland & Platteau 1999).

However, these studies tended to focus on community management of common property resources, or situations where differences in power between individuals could greatly affect the resource extraction opportunities open to those individuals. In the case of this study, the regulatory structure in the United States may be such that individuals are not always totally free to act in their selfish best interests with respect to the environment.

IMPORTANCE OF SCALE

Scale is a central issue in this study. As was just discussed, patterns between inequality and land cover or bird richness may not have been seen because the resolution of the study is smaller than that at which inequality may have an effect in the USA. On the other hand, some patterns between land cover metrics and bird richness may have been missed because the extent of the study was too large and encompassed ecoregions that varied more between each other than bird routes varied within the region.

Future studies will be greatly benefited by inclusion of land cover change data, as will be available by the end of this year. In addition, they should consider their scale of analysis carefully. If the primary goal is to study the relationship between landscapes and biodiversity, the ideal scale is probably of similar resolution to ours, but with a smaller extent, so that results are less confounded by regional differences. If, on the other hand, the goal is to examine the effects of inequality, it may be helpful to scale up the resolution of the analysis to a scale that is consistent with the institutions that drive environmental management.

CONCLUSION

This thesis has shown that to achieve an understanding of the indirect drivers of biodiversity loss, or of environmental degradation in general, we should not limit our focus simply to the size of the economy. The distribution of the economy is also important, and can have signifcant effects on societies' relationships with their environment that are not explained by looking at gross domestic product (GDP) or median income alone.

The relationship I observed between inequality and the environment is broadly consistent with the theory that inequality has a negative effect on institutions (Ostrom 2001; Margreiter *et al*. 2005). In the contexts that I examined, I was not able to detect evidence of the smaller-scale effect of inequality on individual actions that some has been proposed as an alternate mechanism by which inequality may affect the environment (Olson 1965; Boyce 1994; Baland & Platteau 1999).

In the first chapter of this thesis, I showed that the proportion of species in a country that are threatened can be predicted using relatively simple models of population density and GDP. This provides support to results by Naidoo and Adamowicz (2001). These models were made significantly stronger, however, when inequality was included, with inequality being associated with a greater proportion of threatened species in all cases. This result was generally consistent when the relationship was examined at different levels of development, indicating that it is not simply a spurious correlation between two variables following a parallel gradient between wealthy countries and poor ones. In general, patterns with inequality were stronger at higher levels of development than they were at lower levels. This is certainly indicative that data quality is higher in richer countries. However, it also suggests that the relationship between environmental policy and its outcomes may be tighter in rich countries than in poor ones.

If the paper focused more on the institutional effects of inequality, the second paper, by nature of its scale of analysis, gave more importance to the effects of inequality as mediated through the actions of individuals. At this scale, inequality was not a consistent predictor of environmental outcomes, either in terms of species richness or of forest cover. Socio-economic variables in general were able to predict environmental outcomes relatively well, but both median income and population density were better predictors than was inequality. This study also faced the difficulty of disentangling causation from correlation in terms of the relationship between socio-economic variables and land cover.

Although this result may not have been conclusive with respect to the effect of inequality on land cover or on richness, it did bring attention to issues of scale and context which are important considerations when thinking about inequality. In a developed country context, individual actions with respect to resource extraction and landscape modification may be strongly regulated. As a result, in these contexts the hypothesized 'Olson Effects' whereby a small number of very wealthy and powerful individuals determine most decisions regarding resource use, may be of limited importance.

In general, situations where actions by individuals with respect to the environment are not heavily regulated by government authority are likely to show more of an impact of inequality at the local scale than situations that are more regulated. For example, we might expect to see an effect of inequality in a locally managed fishery in the developing world or in patterns of frontier forest clearing in Amazonia more than we would in decisions regarding land cover in the United States.

Inequality may be more generally important if the scale of analysis is consistent with the scale of the institutions that are most important for determining environmental policy. This is likely why a pattern with inequality can be detected at the international scale: national inequality can have an effect on larger scale institutions that can in turn have a beneficial or negative effect on the environment. The lack of association between inequality and biodiversity outcomes in the United States may be as a result of this issue. The socio-economic data in that analysis was all scaled at county level; however, county-level governments are not responsible for environmental policy or the creation of regulatory institutions to the same extent as state-level and federal governments. Policies protecting threatened species in particular tend to be enacted at the federal level in the USA (Simon *et al*. 1995; Hoekstra *et al*. 2002). As a result, even if inequality does interfere with institutions at county-level, there may not be much detectable effect on biodiversity at that scale

Inequality has varying effects at different scales, and in different social and political contexts. In some cases, it is a significant predictor of biodiversity and other environmental outcomes, and should therefore be considered in any discussion of the socio-economic indirect drivers of environmental change.

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APPENDIX A: MODEL COMPARISON USING PROPORTION OF PLANTS AND VERTEBRATES THAT ARE ENDEMIC.

The sample size here is 46 countries, representing 45.9% and 67.6% of the world's land area and human population respectively.

	Model 1 Saturated	Model 2 Economic Footprint	Model 3 Econ. Footprint + Inequality	Model 4 Environmental Kuznets	Model 5 Kuznets + Inequality	Model 6 Environmental Governance
Independent Variables	ß	ß	ß	ß	ß	ß
GDP per capita (log)	-2.74	-0.234 *	-0.174	-2.86	-2.73	-0.42
Quadratic of GDP per capita (log)	0.144	—	—	0.158	0.151	—
Population density (log)	0.093	0.073	0.129	—	—	—
Gini index	0.139	—	0.022 *	—	0.103 *	—
Quadratic of Gini index	-1.3×10^{-3}	—	—	—	-1.3×10^{-3}	—
Environmental Governance	0.282	—	—	—	—	0.317
Communist (1=yes; 0=no)	0.228	—	—	—	—	-0.539 *
Proportion of plant and vertebrates endemic (log)	0.112	0.094	0.075	0.133 *	0.097	0.122 *
Constant	5.58	-1.84	-3.32	8.98	5.88	-0.30
Corrected AIC	79.7	81.6	78.0	79.6	77.0	77.7
Adjusted R^2	0.369	0.226	0.306	0.259	0.339	0.310

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

APPENDIX B: COUNTRIES ANALYZED

Countries are sorted by their 3-letter ISO code (which is what appears on graphs). Inclusion in different models is indicated by the Inc. column. 1 indicates that a country was included at the model comparison stage, 2 that it was included in the extended analysis of the Modified IPAT model, and 3 that it was included in extended analysis of the Environmental Governance model.

CODE	COUNTRY	INC.						
AGO	Angola	3	GMB	Gambia	3	NOR	Norway	1,2,3
ALB	Albania	3	GNB	Guinea-Bissau	3	NPL	Nepal	3
ARG	Argentina	1,2,3	GRC	Greece	1,2,3	OMN	Oman	3
AUS	Australia	1,2,3	GTM	Guatemala	1,2,3	PAK	Pakistan	1,2,3
AUT	Austria	1,2,3	GUY	Guyana	3	PAN	Panama	1,2,3
BDI	Burundi	3	HND	Honduras	1,2,3	PER	Peru	1,2,3
BEL	Belgium	1,2,3	HTI	Haiti	3	PHL	Philippines	1,2,3
BEN	Benin	3	HUN	Hungary	1,2,3	PNG	Papua New Guinea	3
BGR	Bangladesh	1,2,3	IDN	Indonesia	1,2,3			
BGR	Bulgaria	1,2	IND	India	1,2,3	PRI	Puerto Rico	2
BHS	Bahamas	2	IRL	Ireland	1,2,3	PRT	Portugal	3
BOL	Bolivia	3	IRN	Iran	3	PRY	Paraguay	3
BRA	Brazil	1,2,3	ISR	Israel	1,2,3	RUS	Russia	1,2,3
BWA	Botswana	1,2,3	ITA	Italy	1,2,3	RWA	Rwanda	3
CAF	Central African Republic	3	JAM	Jamaica	1,2,3	SAU	Saudi Arabia	3
			JOR	Jordan	1,2,3	SDN	Sudan	3
CAN	Canada	1,2,3	JPN	Japan	1,2,3	SEN	Senegal	3
CHE	Switzerland	3	KEN	Kenya	3	SGP	Singapore	2
CHL	Chile	1,2,3	KGZ	Kyrgyzstan	1,2,3	SLE	Sierra Leone	1,2,3
CHN	China	1,2,3	KOR	South Korea	1,2,3	SLV	El Salvador	3
CIV	Côte d'Ivoire	1,2,3	LAO	Laos	3	SVK	Slovakia	1,2,3
CMR	Cameroon	3	LBN	Lebanon	3	SWE	Sweden	1,2,3
COD	D. R. Congo	3	LKA	Sri Lanka	1,2,3	SYR	Syria	3
COG	Congo	3	LSO	Lesotho	2	TCD	Chad	3
COL	Colombia	1,2,3	LUX	Luxembourg	2	TGO	Togo	3
CRI	Costa Rica	1,2,3	LVA	Latvia	1,2,3	THA	Thailand	1,2,3
DEU	Germany	3	MAR	Morocco	1,2,3	TJK	Tajikistan	1,2,3
DNK	Denmark	1,2,3	MDA	Moldova	1,2,3	TTO	Trinidad and Tobago	3
DOM	Dominican Republic	1,2,3	MDG	Madagascar	3			
			MEX	Mexico	1,2,3	TUN	Tunisia	1,2,3
DZA	Algeria	1,2,3	MLI	Mali	3	TUR	Turkey	1,2,3
EGY	Egypt	3	MNG	Mongolia	3	TZA	Tanzania	3
ESP	Spain	1,2,3	MOZ	Mozambique	3	UGA	Uganda	1,2,3
EST	Estonia	1,2,3	MRT	Mauritania	1,2,3	UKR	Ukraine	1,2,3
FIN	Finland	1,2,3	MUS	Mauritius	2	URY	Uruguay	1,2,3
FRA	France	3	MWI	Malawi	3	USA	United States	1,2,3
GAB	Gabon	3	MYS	Malaysia	1,2,3	VEN	Venezuela	1,2,3
GBR	United Kingdom	1,2,3	NAM	Namibia	3	VNM	Vietnam	3
			NER	Niger	3	ZAF	South Africa	3
GEO	Georgia	1,2,3	NGA	Nigeria	1,2,3	ZMB	Zambia	3
GHA	Ghana	1,2,3	NIC	Nicaragua	3			
GIN	Guinea	3	NLD	Netherlands	1,2,3			

APPENDIX C: DATA USED FOR INTERNATIONAL STUDY

Data shown for population density, gross domestic product, and the Gini index are all averages of available data from the 1985-89 period. Environmental governance is from 2005, and threatened species and species endemism are both from 2006.

Country	Population density (people per sq.km)	GDP per capita (US$, PPP)	Gini index	Environmental Governance Index (higher values represent better governance)	Percentage of vertebrate species endemic	Percentage of plant and vertebrate species threatened
ALBANIA	1.08	2474	-	-0.32	0.00%	0.92%
ALGERIA	0.10	4145	42.4	-0.69	0.88%	0.99%
ANGOLA	0.08	1498	-	-0.96	3.99%	1.02%
ARGENTINA	0.11	7548	48.0	-0.34	12.61%	1.55%
AUSTRALIA	0.02	14451	43.5	0.97	41.20%	1.74%
AUSTRIA	0.91	15680	28.9	1.54	0.50%	0.62%
BAHAMAS	0.17	12567	48.8	-	6.27%	2.32%
BANGLADESH	6.75	849	34.8	-0.52	1.05%	1.43%
BELGIUM	3.24	15555	34.9	1.23	0.50%	1.16%
BENIN	0.42	671	-	-0.11	0.00%	0.93%
BOLIVIA	0.06	1539	-	0.05	5.30%	0.76%
BOTSWANA	0.02	3494	57.9	0.84	0.78%	0.49%
BRAZIL	0.17	5079	59.3	0.02	25.57%	1.10%
BULGARIA	0.80	4838	22.3	0.34	0.16%	0.83%
BURUNDI	1.87	611	-	-0.86	0.73%	0.72%
CAMEROON	0.22	1805	-	-0.69	6.61%	4.77%
CANADA	0.03	16364	37.4	0.78	1.45%	1.51%
CENTRAL AFRICAN REPUBLIC	0.04	981	-	-0.4	0.99%	0.65%
CHAD	0.04	681	-	-0.76	0.29%	0.87%
CHILE	0.17	3909	54.5	0.48	15.46%	1.98%
CHINA	1.15	1027	34.0	-0.58	16.97%	2.19%
COLOMBIA	0.29	4064	51.2	0.02	16.12%	1.08%
CONGO	0.07	683	-	-0.55	0.67%	0.91%
CONGO, THE DRC	0.15	1336	-	-0.87	6.27%	1.13%
COSTA RICA	0.56	4611	44.0	0.92	6.02%	1.60%
COTE D'IVOIRE	0.35	1373	42.9	-0.46	1.06%	3.40%
DENMARK	1.19	17189	41.3	1.59	0.67%	1.17%
DOMINICAN REPUBLIC	1.38	3156	50.8	0.07	10.12%	1.63%
EGYPT	0.52	2029	-	-0.54	1.80%	1.46%
EL SALVADOR	2.32	2598	-	0.01	0.98%	1.29%
ESTONIA	0.35	7096	28.1	0.78	0.00%	0.40%
FINLAND	0.15	15244	33.1	1.4	0.73%	0.91%
FRANCE	1.01	15151	-	1	1.31%	0.99%
GABON	0.03	4329	-	-0.35	0.93%	1.79%
GAMBIA	0.74	1277	-	-0.43	0.24%	1.16%
GEORGIA	0.77	4099	29.5	-0.45	0.00%	0.68%

Country	Population density (people per sq.km)	GDP per capita (US$, PPP)	Gini index	Environmental Governance Index (higher values represent better governance)	Percentage of vertebrate species endemic	Percentage of plant and vertebrate species threatened
GEORGIA	0.77	4099	29.5	-0.45	0.00%	0.68%
GERMANY	2.19	14058	-	1.57	0.81%	1.37%
GHANA	0.60	1113	40.0	-0.1	0.78%	3.20%
GREECE	0.76	10552	45.6	0.6	2.09%	1.11%
GUATEMALA	0.76	2415	58.4	-0.02	5.78%	1.97%
GUINEA	0.23	1372	-	-0.64	0.54%	1.55%
GUINEA-BISSAU	0.26	605	-	-0.07	0.68%	1.21%
GUYANA	0.03	2471	-	-0.28	1.83%	0.82%
HAITI	2.32	1868	-	-1	11.70%	1.93%
HONDURAS	0.40	1814	56.5	0	5.84%	2.87%
HUNGARY	1.13	8548	25.6	0.81	0.37%	0.95%
INDIA	2.43	1103	35.1	-0.1	5.34%	1.98%
INDONESIA	0.90	1419	35.7	-0.52	13.93%	2.18%
IRAN	0.31	3341	-	-0.72	4.45%	0.73%
IRELAND	0.50	9588	43.3	1.06	0.59%	1.06%
ISRAEL	2.01	12806	42.8	0.56	1.39%	1.45%
ITALY	1.88	14797	42.3	0.74	2.73%	0.86%
JAMAICA	2.12	2429	47.0	0.26	14.19%	6.69%
JAPAN	3.23	15192	41.2	0.99	9.19%	2.14%
JORDAN	0.32	3408	39.8	0.27	0.62%	0.98%
KENYA	0.36	799	-	-0.37	3.42%	2.33%
KOREA, REPUBLIC OF	4.20	5858	38.5	0.76	3.56%	1.52%
KYRGYZSTAN	0.21	1721	28.4	-0.69	0.66%	0.27%
LAOS	0.16	712	-	-0.81	0.85%	0.96%
LATVIA	0.41	7006	26.1	0.48	0.22%	0.94%
LEBANON	2.65	1398	-	-0.17	0.53%	0.70%
LESOTHO	0.50	777	59.7	-	0.95%	0.60%
LUXEMBOURG	1.43	19943	31.3	-	0.00%	0.37%
MADAGASCAR	0.19	712	-	-0.13	52.38%	4.56%
MALAWI	0.69	407	-	-0.22	1.43%	0.79%
MALAYSIA	0.50	3568	48.4	0.19	11.38%	4.98%
MALI	0.07	481	-	-0.26	0.67%	0.95%
MAURITANIA	0.02	1076	46.1	-0.35	0.62%	1.31%
MAURITIUS	5.05	4151	43.3	-	8.90%	8.41%
MEXICO	0.41	5519	52.0	-0.17	27.36%	2.40%
MOLDOVA	1.27	3009	26.3	-0.2	0.00%	1.06%
MONGOLIA	0.01	1148	-	0.26	1.61%	1.06%
MOROCCO	0.52	2345	43.1	-0.24	3.58%	0.94%
MOZAMBIQUE	0.17	435	-	-0.45	1.01%	1.49%
NAMIBIA	0.01	4939	-	0.14	4.09%	1.56%
NEPAL	1.21	717	-	-0.12	2.87%	0.92%
NETHERLANDS	3.53	15429	37.0	1.62	0.94%	1.45%
NICARAGUA	0.28	2676	-	0.06	1.47%	0.99%
NIGER	0.06	637	-	-0.47	0.29%	0.65%

Country	Population density (people per sq.km)	GDP per capita (US$, PPP)	Gini index	Environmental Governance Index (higher values represent better governance)	Percentage of vertebrate species endemic	Percentage of plant and vertebrate species threatened
NIGERIA	0.90	560	40.7	-0.89	1.12%	3.71%
NORWAY	0.13	18135	40.7	1.26	0.83%	1.03%
OMAN	0.05	7784	-	-0.18	1.46%	2.50%
PAKISTAN	1.28	1054	35.7	-0.54	3.09%	1.18%
PANAMA	0.30	3527	56.7	0.38	4.66%	2.62%
PAPUA NEW GUINEA	0.08	1489	-	-0.41	16.55%	2.03%
PARAGUAY	0.09	3473	-	-0.34	1.45%	0.56%
PERU	0.16	3726	46.4	-0.11	15.18%	2.50%
PHILIPPINES	1.90	2729	44.3	-0.15	25.51%	3.94%
PORTUGAL	1.09	9049	-	0.86	0.97%	1.12%
PUERTO RICO	3.84	9982	55.3	-	11.00%	3.08%
RUSSIAN FEDERATION	0.09	8237	27.1	-0.4	3.87%	0.96%
RWANDA	2.52	899	-	-0.7	0.39%	1.00%
SAUDI ARABIA	0.07	8374	-	-0.28	1.12%	1.41%
SENEGAL	0.37	1060	-	0.01	0.46%	1.49%
SIERRA LEONE	0.53	706	66.6	-0.74	0.39%	2.62%
SINGAPORE	45.57	9085	44.6	-	2.22%	2.80%
SLOVAKIA	1.06	8076	20.7	0.76	0.20%	0.80%
SOUTH AFRICA	0.28	7393	-	0.31	9.64%	0.90%
SPAIN	0.77	11385	35.9	1.08	3.75%	1.50%
SRI LANKA	2.59	1608	46.7	0.26	14.48%	8.83%
SUDAN	0.10	786	-	-1.1	1.47%	1.13%
SWEDEN	0.19	15550	39.2	1.26	0.47%	0.96%
SWITZERLAND	1.61	20580	-	1.39	0.00%	0.53%
SYRIAN ARAB REPUBLIC	0.63	1906	-	-0.63	0.68%	0.72%
TAJIKISTAN	0.34	1816	29.6	-0.88	0.81%	0.40%
TANZANIA	0.25	395	-	-0.01	7.63%	3.13%
THAILAND	1.02	2589	47.4	0.04	4.35%	1.61%
TOGO	0.63	1203	-	-0.69	0.53%	0.79%
TRINIDAD AND TOBAGO	2.33	5328	-	-0.09	2.14%	1.11%
TUNISIA	0.47	3230	46.7	-0.11	0.49%	1.10%
TURKEY	0.70	3734	44.2	0.21	2.89%	0.83%
UGANDA	0.66	605	35.0	-0.22	1.04%	1.76%
UKRAINE	0.85	6817	27.4	-0.34	0.69%	0.72%
UNITED KINGDOM	2.32	14968	41.9	1.37	1.08%	1.64%
UNITED STATES	0.26	19607	44.5	0.8	16.99%	2.58%
URUGUAY	0.17	5123	41.3	0.4	2.07%	1.63%
VENEZUELA	0.20	4397	44.1	-0.27	12.03%	0.92%
VIETNAM	1.87	862	-	-0.75	7.04%	2.35%
ZAMBIA	0.10	792	-	0.13	1.53%	0.53%

REFERENCES

Acemoglu D., Johnson S. & Robinson J.A. (2002). Reversal of fortune: Geography and institutions in the making of the modern world income distribution. *Quarterly Journal of Economics*, 117, 1231-1294.

Anderson J.R., Hardy E.E., Roach J.T. & Witmer R.E. (1976). A land use and land cover classification system for use with remote sensor data (US Department of Interior). United States Government Printing Office.

Babones S.J. & Alvarez-Rivadulla M.J. (2007). Standardized income inequality data for use in cross-national research. *Sociological Inquiry*, 77, 3-22.

Baland J.M. & Platteau J.P. (1999). The ambiguous impact of inequality on local resource management. *World Development*, 27, 773-788.

Boulinier T., Nichols J.D., Hines J.E., Sauer J.R., Flather C.H. & Pollock K.H. (1998). Higher temporal variability of forest breeding bird communities in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 7497-7501.

Boulinier T., Nichols J.D., Hines J.E., Sauer J.R., Flather C.H. & Pollock K.H. (2001). Forest fragmentation and bird community dynamics: Inference at regional scales. *Ecology*, 82, 1159-1169.

Boyce J.K. (1994). Inequality as a Cause of Environmental Degradation. *Ecological Economics*, 11, 169-178.

Burnham K.P. & Anderson D.R. (2004). Multimodel inference - understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33, 261-304.

Cam E., Nichols J.D., Sauer J.R., Hines J.E. & Flather C.H. (2000). Relative species richness and community completeness: Birds and urbanization in the Mid-Atlantic states. *Ecological Applications*, 10, 1196-1210.

Chapin F.S., Zavaleta E.S., Eviner V.T., Naylor R.L., Vitousek P.M., Reynolds H.L., Hooper D.U., Lavorel S., Sala O.E., Hobbie S.E., Mack M.C. & Diaz S. (2000). Consequences of changing biodiversity. *Nature*, 405, 234-242.

Chotikapanich D., Valenzuela R. & Prasada Rao D.S. (1997). Global and regional inequality in the distribution of income: Estimation with limited and incomplete data. *Empirical Economics*, 22, 533-546.

Costanza R., d'Arge R., de Groot R., Farber S., Grasso M., Hannon B., Limburg K., Naeem S., O'neill R.V., Paruelo J., Raskin R.G., Sutton P. & van den Belt M. (1997). The value of the world's ecosystem services and natural capital. *Nature*, 387, 253-260.

Donovan T.M. & Flather C.H. (2002). Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications*, 12, 364-374.

Dungan J.L., Perry J.N., Dale M.R.T., Legendre P., Citron-Pousty S., Fortin M.J., Jakomulska A., Miriti M. & Rosenberg M.S. (2002). A balanced view of scale in spatial statistical analysis. *Ecography*, 25, 626-640.

Ehrlich P.R. & Holdren J.P. (1971). Impact of population growth. *Science*, 171, 1212-1217.

Fahrig L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, 34, 487-515.

Fauth P.T., Gustafson E.J. & Rabenold K.N. (2000). Using landscape metrics to model source habitat for Neotropical migrants in the midwestern US. *Landscape Ecology*, 15, 621-631.

Gottschalk P. & Danziger S. (2005). Inequality of wage rates, earnings and family income in the United States, 1975-2002. *Review of Income and Wealth*, 231-254.

Hardin G. (1968). The Tragedy of the Commons. *Science*, 162, 1243-1248.

Heerink N., Mulatu A. & Bulte E. (2001). Income inequality and the environment: aggregation bias in environmental Kuznets curves. *Ecological Economics*, 38, 359-367.

Hines J.E., Boulinier T., Nichols J.D., Sauer J.R. & Pollock K.H. (1999). COMDYN: software to study the dynamics of animal communities using a capture-recapture approach. *Bird Study*, 46, 209-217.

Hoekstra J.M., Clark J.A., Fagan W.F. & Boersma P.D. (2002). A comprehensive review of Endangered Species Act recovery plans. *Ecological Applications*, 12, 630-640.

Homer C., Huang C.Q., Yang L.M., Wylie B. & Coan M. (2004). Development of a 2001 National Land-Cover Database for the United States. *Photogrammetric Engineering and Remote Sensing*, 70, 829-840.

Howell C.A., Latta S.C., Donovan T.M., Porneluzi P.A., Parks G.R. & Faaborg J. (2000). Landscape effects mediate breeding bird abundance in mid-western forests. *Landscape Ecology*, 15, 547-562.

IUCN (2006). Red List of Threatened Species. The World Conservation Union Gland, Switzerland. Available online at *http://www.iucnredlist.org/*.

Jelinski D.E. & Wu J.G. (1996). The modifiable areal unit problem and implications for landscape ecology. *Landscape Ecology*, 11, 129-140.

Jones K.B., Neale A.C., Nash M.S., Riitters K.H., Wickham J.D., O'Neill R.V. & van Remortel R.D. (2000). Landscape correlates of breeding bird richness across the United States mid-Atlantic region. *Environmental Monitoring and Assessment*, 63, 159-174.

Karanth K.K., Nichols J.D., Sauer J.R. & Hines J.E. (2006). Comparative dynamics of avian communities across edges and interiors of North American ecoregions. *Journal of Biogeography*, 33, 674-682.

Koper N. & Schmiegelow F.K.A. (2006). A multi-scaled analysis of avian response to habitat amount and fragmentation in the Canadian dry mixed-grass prairie. *Landscape Ecology*, 21, 1045-1059.

Koper N., Schmiegelow F.K.A. & Merrill E.H. (2007). Residuals cannot distinguish between ecological effects of habitat amount and fragmentation: implications for the debate. *Landscape Ecology*, 22, 811-820.

Lee D.S. (1999). Wage inequality in the United States during the 1980s: Rising dispersion or falling minimum wage? *Quarterly Journal of Economics*, 114, 977-1023.

Li H.B. & Wu J.G. (2004). Use and misuse of landscape indices. *Landscape Ecology*, 19, 389-399.

Loomis J.B. & White D.S. (1996). Economic benefits of rare and endangered species: Summary and meta-analysis. *Ecological Economics*, 18, 197-206.

Magnani E. (2000). The Environmental Kuznets Curve, environmental protection policy and income distribution. *Ecological Economics*, 32, 431-443.
Malthus T. (1798). *An Essay on the Principle of Population*. J. Johnson, London.
Margreiter M., Sutter M. & Dittrich D. (2005). Individual and collective choice and voting in common pool resource problem with heterogeneous actors. *Environmental & Resource Economics*, 32, 241-271.
Mayer A.L. & Cameron G.N. (2003). Landscape characteristics, spatial extent, and breeding bird diversity in Ohio, USA. *Diversity and Distributions*, 9, 297-311.
McGarigal K. & Marks B.J. (1994). Fragstats: Spatial pattern analysis program for quantifying landscape structure. Forest Science Department, Oregon State University.
Metrick A. & Weitzman M.L. (1996). Patterns of behavior in endangered species preservation. *Land Economics*, 72, 1-16.
Mikkelson G., Gonzalez A. & Peterson G. (2007). Economic inequality predicts biodiversity loss. *Public Library of Science One*, 2, e444.
Milanovic B. (2005). *Worlds Apart: measuring international and global inequality*. Princeton University Press, Princeton, NJ.
Milanovic B. (2006). Global income inequality: what it is and why it matters. *Policy, research working papers #3865*. World Bank, pp. 1-35.
MillENN_MNium Ecosystem Assessment (MA) (2005). Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington.
Moller S. & Nielsen F. (2005). 2000 County Family Income Inequality Data. In. University of North Carolina at Charlotte. Available online at *http://www.socanth.uncc.edu/smoller/*.
Multi-Resolution Land Characteristics Consortium (MRLC) (1992). National Land Cover Dataset 1992. Available online at *http://landcover.usgs.gov/natllandcover.php*.
Multi-Resolution Land Characteristics Consortium (MRLC) (2001). National Land Cover Database 2001. Available online at *http://www.mrlc.gov/mrlc2k_nlcd.asp*.
Naidoo R. & Adamowicz W.L. (2001). Effects of economic prosperity on numbers of threatened species. *Conservation Biology*, 15, 1021-1029.
Nielsen F. (2000). Income Inequality in US Counties. University of North Carolina at Chapel Hill. Available online at *http://www.unc.edu/~nielsen/data/data.htm*.
Olson M. (1965). *The logic of collective action; public goods and the theory of groups*. Harvard University Press, Cambridge, Mass.
Ostrom E. (1990). *Governing the commons: the evolution of institutions for collective action*. 4th (1993) edn. Cambridge University Press, New York.
Ostrom E. (2001). Reformulating the commons. In: *Protecting the commons: a framework for resource management in the Americas* (eds. Burger J, Ostrom E, Norgaard RB, Policansky D & Goldstein BD). Island Press Washington D.C., pp. 17-41.
Pardieck K.L. & Sauer J.R. (2000). The 1995-1999 summary of the North American Breeding Bird Survey. *Bird Populations*, 5, 30-48.
Pergams O.R.W., Czech B., Haney J.C. & Nyberg D. (2004). Linkage of conservation activity to trends in the US economy. *Conservation Biology*, 18, 1617-1623.
Pimm S.L., Russell G.J., Gittleman J.L. & Brooks T.M. (1995). The Future of Biodiversity. *Science*, 269, 347-350.

Peterjohn B.G., Sauer J.R. & Link W.A. (1995). The 1994 and 1995 summary of the North American Breeding Bird Survey. *Bird Populations*, 3, 48-66.

Peterjohn P.G. & Sauer J.R. (1994). Population trends of woodland birds from the North-American Breeding Bird Survey. *Wildlife Society Bulletin*, 22, 155-164.

Pitt Inequality Project (2005). Standardized Income Distribution Database. University of Pittsburg at *http://www.pitt.edu/~inequal/*.

Riitters K.H., Oneill R.V., Hunsaker C.T., Wickham J.D., Yankee D.H., Timmins S.P., Jones K.B. & Jackson B.L. (1995). A factor-analysis of landscape pattern and structure metrics. *Landscape Ecology*, 10, 23-39.

Robinson S.K., ThoAREA_MNon F.R., Donovan T.M., Whitehead D.R. & Faaborg J. (1995). Regional Forest Fragmentation and the Nesting Success of Migratory Birds. *Science*, 267, 1987-1990.

Rodewald A.D. & Yahner R.H. (2001). Influence of landscape composition on avian community structure and associated mechanisms. *Ecology*, 82, 3493-3504.

Ronzio C.R., Pamuk E. & Squires G.D. (2004). The politics of preventable deaths: local spending, income inequality, and premature mortality in US cities. *Journal of Epidemiology and Community Health*, 58, 175-179.

Ross N.A., Dorling D., Dunn J.R., Henriksson G., Glover J., Lynch J. & Weitoft G.R. (2005). Metropolitan-income inequality and working-age mortality: A cross-sectional analysis using comparable data from five countries. *Journal of Urban Health-Bulletin of the New York Academy of Medicine*, 82, 101-110.

Sala O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., HuENN_MNeke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M., Poff N.L., Sykes M.T., Walker B.H., Walker M. & Wall D.H. (2000). Biodiversity - Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774.

Sauer J.R., Hines J.E. & Fallon J. (2007). The North American Breeding Bird Survey, results and analysis 1966-2006. Version 7.23.2007. USGS Patuxent Wildlife Research Center, Laurel, MD. Available online at *http://www.mbr-pwrc.usgs.gov/bbs/bbs.html*.

Simon B.M., Leff C.S. & Doerksen H. (1995). Allocating scarce resources for endangered species recovery. *Journal of Policy Analysis and Management*, 14, 415-432.

Stern D.I. (2004). The rise and fall of the environmental Kuznets curve. *World Development*, 32, 1419-1439.

Stern D.I., Common M.S. & Barbier E.B. (1996). Economic growth and environmental degradation: The environmental Kuznets curve and sustainable development. *World Development*, 24, 1151-1160.

Tilman D. (2000). Causes, consequences and ethics of biodiversity. *Nature*, 405, 208-211.

Turner M.G. (2005). Landscape ecology: What is the state of the science? *Annual Review of Ecology Evolution and Systematics*, 36, 319-344.

United Nations Development Programme (2006). Human Development Reports. United Nations Development Programme. Available online at *http://hdr.undp.org*.

United States Census Bureau (USCB) (1992). DecENN_MNial Census. Available online at *http://factfinder.census.gov/*.

United States Census Bureau (USCB) (2000). DecENN_MNial Census. Available online at *http://factfinder.census.gov/*.

Villard M.A., Trzcinski M.K. & Merriam G. (1999). Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology*, 13, 774-783.

Wickham J.D. (2007). Director, Multi-Resolution Land Characteristics Consortium.

World Resources Institute (2007). EarthTrends: The environmental information portal. In. Washington DC: World Resources Institute Available online at *http://earthtrends.wri.org*.

Yale Center for Environmental Law and Policy (YCELP) (2006). Environmental Performance Index. Available online at *http://www.yale.edu/esi/*.

York R., Rosa E.A. & Dietz T. (2003). Footprints on the earth: The environmental consequences of modernity. *American Sociological Review*, 68, 279-300.