

2001: A spatial oddity—urbanization and biodiversity on a new trajectory

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ABSTRACT

Questions: Are patterns of human use of rural versus urban habitats changing through the Anthropocene? Can patterns in human abundance and the human enterprise predict national threats to biodiversity? Can we use the results to better preserve Earth's biodiversity?

Data: Publicly available national estimates of human populations in urban and rural environments throughout the Anthropocene, threats of extinction to mammals and birds, CO₂ emissions, GDP, and the Living Planet Index.

Concepts: Isodars, cooperative behavior.

Analyses: Binary logistic regressions, generalized linear models, model selection, checking residuals.

Answers: Increases in baseline human preference for urban habitat began to decelerate in 2001. Selection of urban and rural habitats in combination with energy use are general, but not specific, predictors of threats to mammals and birds. The human enterprise is strongly associated with reductions in species abundances. The preservation of global biodiversity hinges on the abilities of individuals, corporations, and governments to stop expansion of the human enterprise. That future depends on cooperative actions that favor common good over self-interest.

Keywords: Anthropocene, birds, conservation, density-dependence, extinction, mammals, Poliscene.

INTRODUCTION

The human predicament is driven by overpopulation, overconsumption of natural resources and the use of unnecessarily environmentally damaging technologies and socio-economic-political arrangements to service Homo sapiens' aggregate consumption.

—Paul and Anne Ehrlich (2013: 1)

It is a truism that Earth's biodiversity crisis is a consequence of human population size (e.g., Ehrlich and Holdren, 1971; Holdren and Ehrlich, 1974; Waggoner and Ausubel, 2002; Scott, 2008; McKee, 2009; Cincotta and Gorenflo, 2011; Ceballos et al., 2015; Pimm and Raven, 2017, and many others). There are myriad indirect causes: habitat degradation, loss, and fragmentation; invasive species; pollution; climate disruption; exploitation; and illegal trade to name but a few (Sodhi and Ehrlich, 2010; Ceballos et al., 2020; Almand and Petersen, 2020).

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Although the severity of those anthropogenic effects depends on the characteristics of species and their populations, the ultimate threats are nonetheless caused by humans (Cardillo et al., 2004). But there is also a somewhat perverse optimistic side. Knowing the connections, and with reasonable and realistic demographic models, we should be able to predict future risks to biodiversity. Predicting those risks is the first step in achieving workable alternatives that preserve biodiversity.

At least two studies have used human populations to predict future threats to global biodiversity. Morris and Kingston (2002) created habitat isodars (regressions of density between habitats; Morris, 1987, 1988) from 154 nations for which data were available in 1980. They used the isodars to test whether theories of habitat selection (Fretwell and Lucas, 1969; Rosenzweig, 1981) could explain human occupation of urban versus rural habitats. Highly significant isodars, which were improved by including a binary estimate of a nation's energy use (CO₂ emissions per capita), confirmed the theory. Morris and Kingston (2002) validated the model with new data from 2000, then created new binary variables to categorize whether each nation's threat to biodiversity was high or low. They analyzed those data with binary logistic regression to test whether threats could be predicted by the human isodar, and to calculate the probability that a nation belonged to the high-threat group. Morris and Kingston (2002) completed their analyses by coupling those relationships with future estimates of urban and rural human populations and energy use to rank 137 nations' future 2020 threats to mammals, birds, and plants. A parallel analysis evaluated 23 additional potential indicators of threats to biodiversity. Eight of those variables were also associated in some way with threats to biodiversity, but isodars outperformed other demographic variables in predicting threats to mammals, birds, and plants.

McKee et al. (2004) applied multiple regression to data gathered from 114 continental nations. A combination of human population density and species richness accounted for 88% of the common variation in the densities of threatened birds and mammals. Future projections based on that model predicted an average 7% increase in numbers of threatened species by 2020. A subsequent publication validated the main results (McKee et al., 2013).

Others have explored the relationships between human population density and biodiversity hotspots (e.g., Cincotta et al., 2000; Luck, 2007; Cunningham and Beazley, 2018). Those analyses and meta-analyses clearly document the need to integrate human population dynamics (Cincotta et al., 2000; McKee and Chambers, 2011) and human settlement patterns (Luck et al., 2004) into conservation strategies.

It is thus prudent to explore the accuracy of such projections, and especially so those of Morris and Kingston (2002) because they integrate human population size with spatial distribution. It is now possible to do so because the isodar analyses ranked nations by their anticipated threats to biodiversity in 2020. Nineteen of the 25 nations with the projected highest increase in threats were in Africa. Cardillo et al. (2004) made a somewhat similar prediction for carnivores in 2030. Ten of the most threatened mammalian carnivores exist in Africa (including Madagascar).

Roadmap

I begin with a short overview of the relevant isodar theory as it can be applied to humans. I describe how I extracted and compiled data on human population sizes, the human enterprise, and risks to biodiversity from publicly available and reliable web-based sources such as the World Bank, University of Oxford's Our World in Data, World Resources Institute, and the International Union for the Conservation of Nature (IUCN) (see Appendix 1, evolutionary-ecology.com/data/MorrisAppendix.pdf). Potential biases include differences among countries in classifying urban versus rural populations, the quality of the data used for the classifications, and

the quality of the biodiversity and threat estimates. I assume that any biases or differences in data quality are not systemic across nations.

I use the data to calculate global isodars through time and evaluate their ability, in combination with energy consumption, to infer current risks to biodiversity. I compare those forecasts, and actual changes in threats through time, with Morris and Kingston's (2002) predictions. I then evaluate whether temporal trends in the Living Planet Index (LPI; e.g., Loh et al., 2005) might yield better predictions of threats to biodiversity.

My final analyses explore potential sources and causes of an unexpected change in the transition toward urbanization in 2001. I discuss how relationships of extinction threats with human densities and enterprise can better inform conservation of Earth's rapidly disappearing biodiversity. I conclude with an essay on the future of biodiversity.

A synopsis of the human isodar

Morris and Kingston (2002) used the following logic to demonstrate how the generalized logistic equation (Gilpin and Ayala, 1973) yields human isodars of habitat selection. At equilibrium, adaptive human habitat choice should achieve an evolutionarily stable state (Cressman and Krivan, 2010) such that per capita fitness in urban environments is equal to that in rural areas:

$$r_U - \left(\frac{r_U N_U}{K_U} \right)^{\theta_U} = r_R - \left(\frac{r_R N_R}{K_R} \right)^{\theta_R}, \quad (1)$$

where r_i is the intrinsic rate of population growth in urban (U) and rural (R) habitats, N is density (represented by number of humans), K is carrying capacity, and θ is a coefficient of curvature reflecting interference among competing individuals. Recognizing that urban environments converge on rural habitats as density approaches zero, maximum population growth rates in each habitat must necessarily be equal. Taking logs and rearranging equation (1) yields the human isodar,

$$\log N_U = \left(\log K_U - \frac{\theta_R}{\theta_U} \log K_R \right) + \frac{\theta_R}{\theta_U} \log N_R. \quad (2)$$

METHODS

Predicted threats to biodiversity based on human isodars

I start with a series of analyses using annual data (Appendix 1) from more than 200 nations to identify possible trends in the global isodar through the Anthropocene (= "Anthropocene isodars," 1950–2020). I retained China and India, unlike Morris and Kingston's (2002) analysis, which excluded them as outliers (as well as Singapore, which lacks rural habitat), because they represent a substantial proportion of Earth's human population. I nevertheless eliminated nations with incomplete records that could bias overall temporal patterns, as well as any with zero rural (Anguilla, Bermuda, Cayman Islands, Gibraltar, Holy See, Hong Kong, Kuwait, Macao, Monaco, Nauru, Sint Maarten, Singapore) or urban populations (Tokelau, Wallis and Futuna Islands). I also excluded Montserrat where the urban population data revealed a peculiar drop from 1,027 in 1997 to just 4 in 1998. Although some of the excluded nations reported non-zero densities in some years, their undefined log-transforms of zero populations in other years altered sample sizes and caused an unequal weighting of data points that could bias long-term patterns in the isodar.

I complemented these analyses by calculating the percentage of people living in urban areas during the Anthropocene in two different ways: (1) the means of the annual percentage urban population for the pooled global total (means of the percentage of Earth's humans living in urban environments each year), and (2) the means of the annual percentage living in each "independent" nation (because each nation contributes equally to the isodar regression regardless of population size).

Next, I used World Bank data (Appendix 1) to calculate isodars for the subset of nations that reported numbers or percentages of threatened species as well as national values for CO₂ emissions. I used these data to confirm that the 1980 isodar calculated with these data was comparable with Morris and Kingston's (2002). I repeated the analysis using the countries listed in Morris and Kingston's (2002) appendices. I then used the full data set to evaluate the joint ability of the isodar and CO₂ emissions to predict threats to biodiversity. The data for these analyses are not identical to those used for the Anthropocene isodars for two reasons. First, I could not use the World Bank data for the Anthropocene isodars because the time series lacked data for the decade beginning in 1950. Second, I chose not to use the Anthropocene isodars for the "threats to biodiversity analyses" because I wanted to eliminate possible discrepancies between the United Nations and World Bank databases.

I followed Morris and Kingston's (2002) protocol by forcing the 1980 human isodar into binary logistic regressions predicting threats to birds and mammals in 2000, then used forward selection (likelihood ratio) to assess whether binary CO₂ per capita (cut at the median) was an additional significant contributor to the threat. I then calculated isodars from more recent data (2000, 2016) that included many more countries. I repeated the logistic regression analyses in an attempt to predict binary threats to mammals and birds with recently available data for 2020. I completed the comparisons with Morris and Kingston's (2002) predictions by ranking the differences in proportions of threatened mammals and birds by country in 2020 relative to those reported during the interval of 1992–2002 (data sources in Appendix 1). Although the ranks aren't exactly the same as Morris and Kingston's (2002) logistic regression predictions, they represent a reasonable estimate of temporal changes in the conservation status of the two taxa.

Predicted threats to biodiversity based on the Living Planet Index

My isodar predictions are based on IUCN evaluations of species under threat of extinction. I reasoned that a better assessment of risks to biodiversity might be made by exploring temporal patterns in the Living Planet Index. I downloaded summaries of the WWF and Zoological Society of London's Living Planet Index (LPI) data (1970–2016; with help from Thekraiati Al-Okaili) from the University of Oxford's Our World in Data website.

Full descriptions of the LPI are given in Loh et al. (2005). The LPI uses a 1970 benchmark value of 1. Subsequent values less than 1 indicate a decline in "biodiversity." One might thus reasonably expect that the LPI varies with metrics of the human condition. So I included models that separately assessed contributions from rural and urban populations, as well as potential dependencies on GDP and CO₂ emissions. The global LPI has declined more-or-less linearly through time (see online Appendix 2) while its potential predictors from the human enterprise have increased consistently.

None of the data, or their transformations, fit a normal distribution. So I split each variable at the median and analyzed high versus low values of LPI with a series of generalized linear

models (binomial distribution with logit link function; IBM SPSS v. 26). Converting variables to binary indicators removes problems of non-normality but does not eliminate the likelihood of quasi-dependent separation (e.g., low values of LPI are predicted almost uniquely by high values of the binary predictor). Indeed, at the global scale the temporal trends in all indicators, except binary CO₂ emissions, were perfectly opposite to binary LPI.

I merged data from the three “biogeographic regions” (North America, Latin America and the Caribbean, Europe and Central Asia) common in both the LPI data and the World Bank’s World Development Indicators, in order to overcome global quasi-dependence. I reasoned that these three regions should yield mostly independent LPIs (Appendix 2), and similarly for estimates of the human enterprise. Including data calculated separately for the three separate biogeographic regions ought to enable more clarity and insights into factors potentially responsible for variation in LPI.

I converted all variables into binary estimates relative to each region’s separately calculated median value. Doing so retained the potential for a “region effect” without including it as a factor in the analysis (including “region” would recreate the quasi-dependent separation that I aimed to negate). Variation among the remaining binary variables was sufficient to eliminate quasi-dependent separation. I used information criteria to select among models and judged the model with the smallest ΔAIC_c as the best fit with the data (e.g., Burnham and Anderson, 2002). I deemed competing models with $\Delta AIC_c \leq 2$ as equally likely explanations for the steady decline in the LPI.

I concluded my analyses by re-examining patterns in isodars and LPI through time. The patterns reveal a dip in isodar intercepts near the turn of the current century that settle toward new trajectories in 2001. I sought an explanation by plotting the actual numbers of humans in each habitat through time, and checking for patterns in residual variation.

RESULTS

The global human isodar through the Anthropocene

I calculated annual isodars during the Anthropocene for 219 countries. The isodar intercept, which was initially negative (more humans in rural habitat in low-population nations [equation 2]), increased more-or-less linearly until 1992 (Fig. 1). Intercepts declined slightly in the early 1990s before rebounding to a lower linear rate beginning in 2001. The isodar slope, which was near unity in 1950, declined at a mostly constant rate ever since. Despite the linear trends, the 95% confidence intervals for intercepts were less than zero only during the early 1950s (1950–1954, 1956), while slopes were not significantly and consistently less than unity until 1986. Taken together, these patterns reveal progressively more people living in cities, but with similar interference to that in the country (slope = 1, logarithmic scale) during the first four decades of the Anthropocene. During the most recent decades, however, the relative degree of interference in habitat choice has increased in cities (slope < 1, Fig. 1A) while the incremental increase in urban populations continues to exceed that of rural areas (Fig. 1B).

These patterns can also be seen, but with less information, in graphs of percent urbanization (Fig. 2). The early linear rate of increase in the global percentage of humans in urban environments transits to a shallower slope in the early 1980s. A similar slowing down of the expected percentage in the “average nation” occurs about a decade later, in 1992. Urbanization is complete when all humans live in cities, so the percentages necessarily approach asymptotes as ever more people aggregate in urban settings.

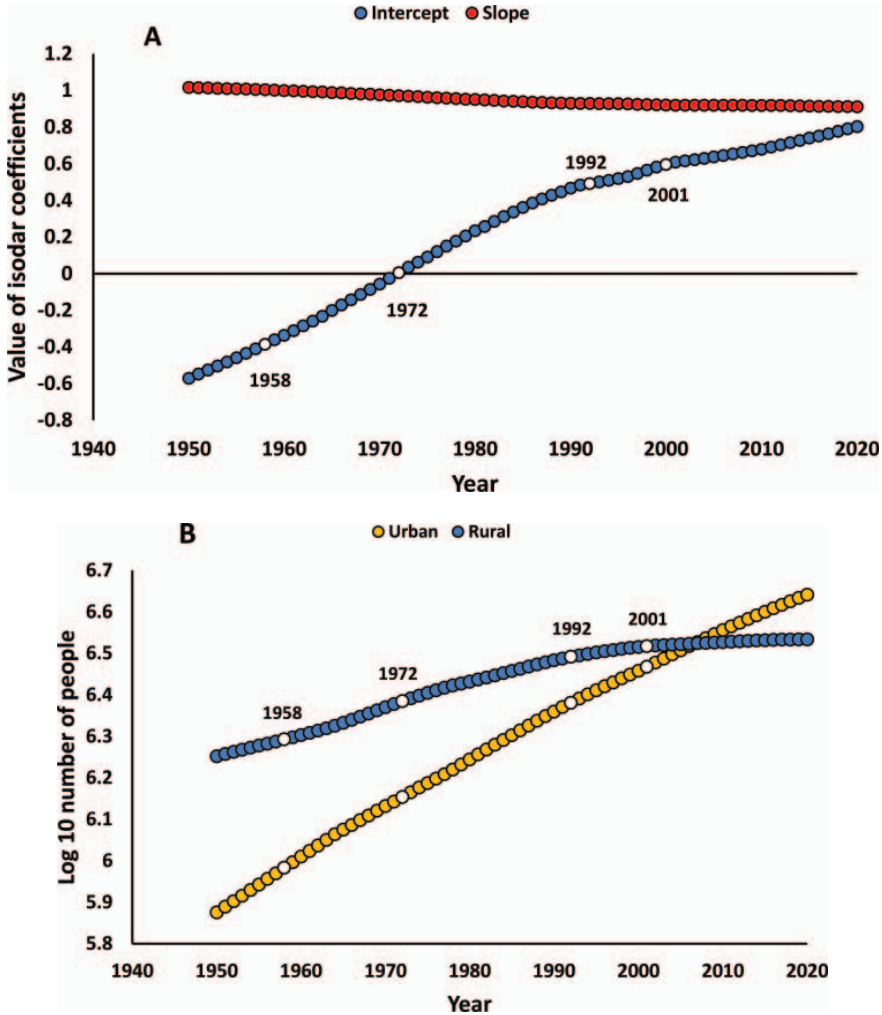


Fig. 1. (Top) Human isodar intercepts and slopes for 219 nations through the Anthropocene (1950–2020; data from United Nations Department of Economic and Social Affairs; see online Appendix 1). Positive intercepts indicate a preference for urban habitat, even at low population sizes. Unit slopes signify similar degrees of “interference” in both urban and rural habitats. A brief period of instability begins with a reduced intercept value in 1992 and ends a decade later (2001) with an altered trajectory. The isodar’s intercept first surpassed a value of 0 in 1972 (but 95% confidence intervals > 0 did not emerge until 1987). (Bottom) The global totals of urban and rural humans through the Anthropocene.

Comparison with Morris and Kingston’s isodars

My attempt to replicate Morris and Kingston’s (2002) isodar for 1980 was only partially successful. One reason for the discrepancy is that my analyses were restricted to the subset of nations listed in their 2002 appendices, rather than the larger unlisted sample of 154 nations (excluded Singapore, China, and India from the initial sample of 157) that they used to calculate the isodar.

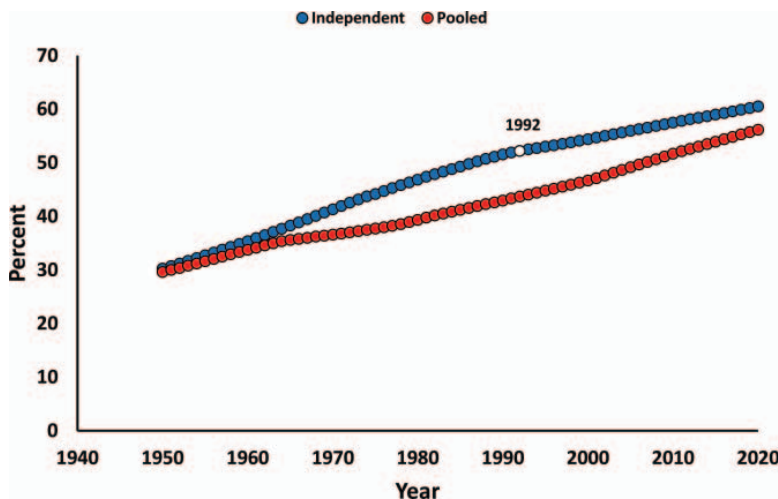


Fig. 2. The percentage of humans living in urban environments through time. Pooled data are calculated from the annual global totals of humans in urban and rural habitats ($N = 1$). Independent data are calculated across countries as the annual mean percentage of humans in urban environments ($N = 219$). Data are the same as those used to create the isodar statistics in Fig. 1.

The intercept for the 144 nations in the analysis was not significantly different from zero (it was less than zero in Morris and Kingston’s analysis). The slope was not greater than 1; the same as the result reported by Morris and Kingston (2002) (Table 1). The intercept for the same subset of nations’ data in 2000, and in the most recent data—2019 (Table 1, 143 nations, Kuwait excluded because it reported zero rural inhabitants)—was also not significantly greater than zero, nor was the slope greater than 1.

The same general pattern was maintained in the highly significant isodars calculated for more than 200 nations in each 20-year time period. The patterns also mirrored those from the Anthropocene analysis. Intercepts that were not significantly different from zero in 1980

Table 1. Human habitat isodars for three different time periods

Year ($N =$ sample size)	Intercept (95% CI)*	Slope (95% CI)*	F^{**}	P^{**}
1980 ($N = 206$)	0.207 (−0.278 to 0.692)	0.955 (0.038 to 1.032)	638.71	< 0.001
1980 ($N = 144$)***	−0.853 (−1.913 to 0.206)	1.115 (0.956 to 1.275)	156.47	< 0.001
2000 ($N = 206$)	0.542 (0.025 to 1.059)	0.927 (0.847 to 1.007)	707.97	< 0.001
2000 ($N = 144$)***	0.463 (−0.921 to 1.847)	0.942 (0.737 to 1.146)	166.32	< 0.001
2019**** ($N = 204$)	0.646 (0.092 to 1.200)	0.931 (0.850 to 1.013)	711.30	< 0.001
2019**** ($N = 143$)***	0.737 (−0.147 to 1.621)	0.921 (0.789 to 1.053)	179.91	< 0.001

* 30 bootstrapped estimates of the 95% confidence interval (values from constrained non-linear regression). ** Significance determined by linear least squares regression. *** Nations common to the analyses included in Morris and Kingston (2002; their appendices 1 and 2). **** The most recent year for which data were available, Kuwait excluded because it had no rural population in 2019. *Source:* Data from The World Bank (Appendix 1).

(approximately equal numbers of urban and rural residents in low-population nations) increased through time while the slopes declined. Even so, no 95% confidence interval for the slopes exceeded 1. The degree of “interference” was similar in urban and rural habitats (equation 2).

Do isodars predict risks to biodiversity?

The 1980 isodars, when merged with binary estimates of CO₂ emissions, were highly significant predictors of the proportions of threatened birds and mammals in 2000 (Table 2). Neither the 1980 or 2000 isodar was capable of predicting current threats to mammals. The 2016 isodar was incapable of predicting avian threats in 2020, and was only a marginally significant predictor of mammalian threats (Table 2). The separation of high versus low CO₂-emitting nations has deteriorated since 1980 (Fig. 3) and would thus appear at least partially responsible for the isodars’ reduced predictive capability.

Table 2. Results from logistic regressions assessing high versus low threats to avian and mammalian species as predicted by the human isodar and a binary variable representing high versus low CO₂ emissions

Response variable	No. of countries	Classification success (%)	Model*	Wald	df	P
Avianthreat2000	125	68.8	Constant	10.27	1	0.001
			1980 isodar	11.49	1	0.001
			1980 CO ₂	3.93	1	0.048
Mammalthreat2000	124	68.5	Constant	7.32	1	0.007
			1980 isodar	9.05	1	0.003
			1980 CO ₂	12.22	1	<0.001
Avianthreat2020	161	67.1	Constant	5.66	1	0.017
			1980 isodar	8.59	1	0.003
			1980 CO ₂	14.53	1	<0.001
Mammalthreat2020	127	NS	Constant	0.20	1	0.651
			1980 isodar	0.36	1	0.548
Avianthreat2020	190	66.3	Constant	8.95	1	0.003
			2000 isodar	11.29	1	0.001
			2000 CO ₂	7.64	1	0.006
Mammalthreat2020	152	NS	Constant	2.02	1	0.16
			2000 isodar	2.00	1	0.16
Avianthreat2020	190	NS	Constant	5.96	1	0.15
			2016 isodar	6.00	1	0.14
Mammalthreat2020	148	60.8	Constant	3.69	1	0.055
			2016 isodar	3.73	1	0.053

Note: Threats in 2000 assessed with a 20-year time-lagged model as in Morris and Kingston (2002). Threats in 2020 assessed with both time-lagged and a “current” (2016) model.

* Isodars were forced into the logistic regression before assessing an additional significant contribution from CO₂ emissions. 1980 isodars excluded China and India. Values for CO₂ emissions are included only for statistically significant models.

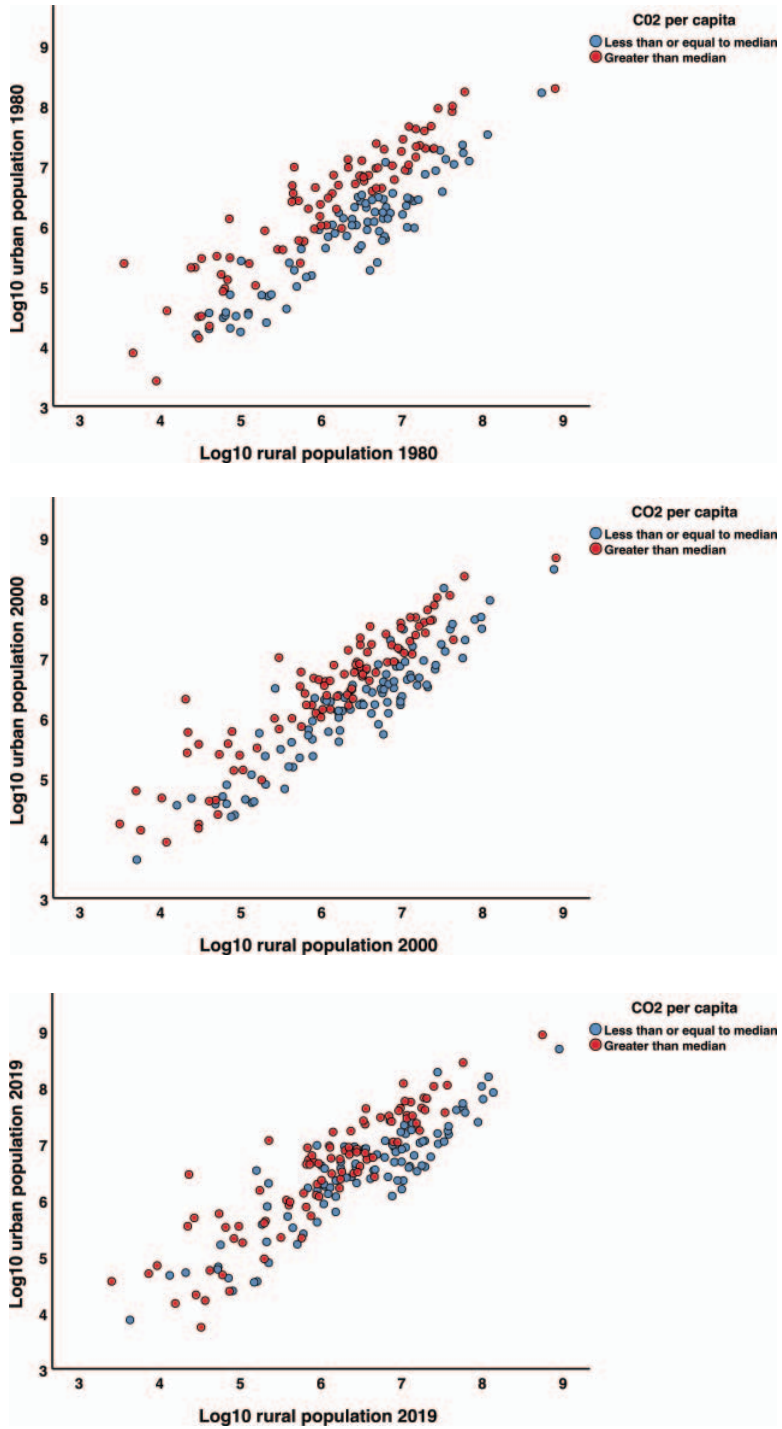


Fig. 3. Globally calculated isodars and the distribution of high versus low CO₂-emitting nations through time.

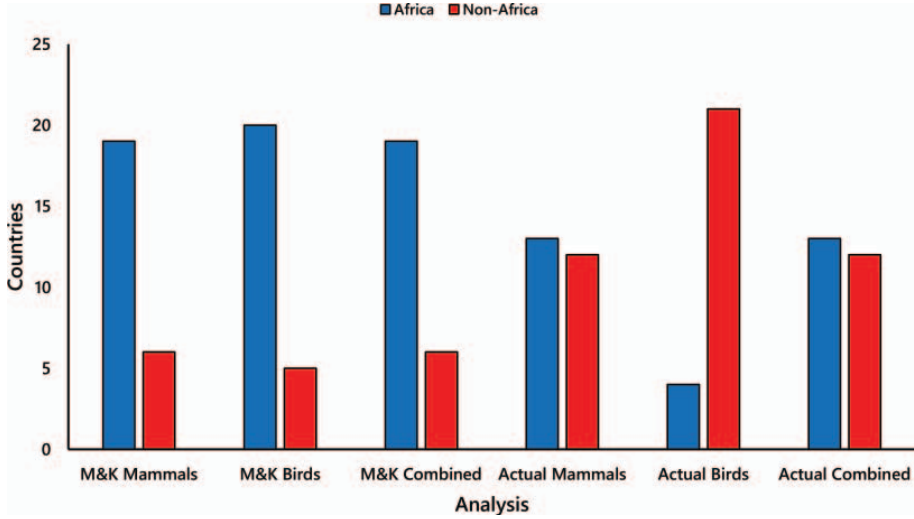


Fig. 4. The 25 nations with the highest predicted increases in risks to their biodiversity from Morris and Kingston (M&K; 2002), and the actual change in numbers of threatened species between 2000 and 2020. Combined threat is the proportion of mammals plus birds at risk of extinction. All comparisons based on the same set of nations as included in Morris and Kingston's (2002) list.

Comparison of rankings through time

My assessments of recent increases in the threats to biodiversity concentrated, as did Morris and Kingston (2002), on the 25 nations with the greatest increase in threats. Correspondence between Morris and Kingston's (2002) list, and that based on differences in the proportions of species reported at risk in 2020 versus those in 2000, depended on taxon (Fig. 4). The number of African nations (includes Madagascar and northern Africa) in the "top 25" for mammals dropped from 19 as predicted by Morris and Kingston to 13 (see online Appendix 3). Although the majority of nations in both lists lie in Africa, only five African countries were common to both. There was virtually no correspondence for birds. Only four African countries made the avian list that was dominated by European nations (Appendix 3). Only one African nation (Togo) was the same as predicted by Morris and Kingston (2002).

Predicting the Living Planet Index

The rapid rise in urbanization revealed by isodars through time reappeared in my assessments of the effect of humans on the Living Planet Index. The number of humans living in urban environments, and total population size, were tied for the most parsimonious model accounting for the continental decline in the LPI (Table 3). Three competing models were also tied: GDP, GDP per capita, and human population density. Intriguingly, models including CO₂ emissions and the number of people living in rural environments were far less likely to explain the temporal pattern in LPI.

A decadal anomaly

The isodar and urbanization patterns (Fig. 2) imply that all countries, on average, are becoming ever more urbanized at about the same rate. That rate changed in the 1990s. Although urbanization

Table 3. Analysis (generalized linear model) of statistically significant indicator variables used to predict the Living Planet Index (LPI; binary scale) from 1970 to 2016

Model	LR χ^2 *	df	P	AIC _c	Δ AIC _c **
Urban	123.610	1	<0.001	10.864	0
GDP	118.281	1	<0.001	11.063	0.199
CO ₂	23.711	1	<0.001	13.162	2.298
Rural	13.318	1	<0.001	13.322	2.458
Urban + CO ₂	133.209	2	<0.001	16.350	5.486
Urban \times Rural	129.311	3	<0.001	16.903	6.039
Urban \times CO ₂	133.314	3	<0.001	18.363	7.499

Note: Data calculated separately for North America, Latin America and the Caribbean, and Europe and Central Asia as identified by Our World in Data (accessed December 11, 2020 by T. Al-Okaili) and the World Bank (World Development Indicators, accessed January 20, 2021). $N = 141$; all models include the intercept. A model using the binary indicator for CO₂ per capita was non-significant ($P = 0.8$).

* Represents an omnibus test comparing the fitted model versus the intercept-only model. ** Analysis using total population was identical to that for urban; analyses of human density and GDP per capita were identical to those for GDP.

must necessarily slow down as ever more nations approach the asymptote of city-states, something odd appears to have occurred during the final years of the twentieth century (Fig. 1). Two major world events ushered the decade: (1) the break-up of the Soviet Union and (2) civil strife, starvation, and genocide in Eastern Africa. Each should leave its signature on the isodars' residuals, and most especially so during 1993 when the dip was most prominent (Figs. 1 and 2).

I searched for those signatures by calculating standardized residuals from a linear regression (isodar) using nations' data from the most extreme year, 1993. I was particularly interested in negative values (< -1) that might reveal the nations responsible for the downward dip in the isodar intercept. No residual was greater than, or less than, three standard deviations from its predicted value. The nations with large negative residuals represented two main classes: (mostly small) islands and African countries, particularly nations in Africa involved in conflicts and famines (see online Appendix 4) during that disruptive decade. The two most extreme negative values belonged to Burundi (-2.29) and Rwanda (-2.21). Nearby states, many experiencing similar conflicts (e.g., Malawi, Uganda, South Sudan, Ethiopia, Eritrea), also had negative residuals. Among former Soviet states, only Russia yielded a standardized residual greater or less than 1 (1.32). It thus appears that at least part of the 1990s depression in isodar intercepts was associated with deaths and human displacement occurring in Eastern Africa. An important lesson is that regional conflicts and human events can modify global patterns. Statistically, this is no surprise because all data points in a regression are treated equally. But if we were to concentrate our attention on the emergent global pattern, then we might easily misinterpret the scale of the effect and make false recommendations.

DISCUSSION

Patterns in isodars and biodiversity conservation

My analyses reveal three striking patterns. First, isodar intercepts underwent a mostly steady increase during the Anthropocene while the slope slowly declined. Human populations continue to aggregate in cities where, relative to rural populations, growth including migration is higher.

Second, human isodars calculated from 1980 data were reasonable indicators of future threats to mammalian biodiversity but not for avian species. Third, even so, the bulk of evidence on the cause of declining biodiversity points a direct accusatory finger at humanity and the human enterprise.

Although intercepts of the human isodars increased during the Anthropocene, their acceleration shifted downward in 1992. The new trajectory was complete by 2001, four years prior to the global deceleration in land-use change reported by Winkler et al. (2021) when the number of humans living in rural environments stabilized (Fig. 1B). The isodar slope has no similar bend. The net result is that the global rural population is now more-or-less stable while urban populations continue to increase (Fig. 1B).

Whatever the cause of the 1990 decadal anomaly, the isodar intercept entered a new trajectory in 2001. A quick perusal of equation (2) reveals the reason—the carrying capacity of cities has declined relative to that of rural habitat. The relative difference between the numbers of humans living in cities versus those in the countryside has declined, but the intercept and population sizes in both habitats continue to increase. Carrying capacity is simply the ratio of maximum population growth divided by its rate of decline with density. Any factor that changes either term, such as reduced rural emigration in ever more urbanized nations, or reduced family size, will modify carrying capacity. Regardless of cause, the isodar informs us that the difference in growth dynamics between urban and rural habitats changed in 2001.

Why didn't isodars better predict future threats to biodiversity?

It is somewhat surprising that, given their promise in the earlier Morris and Kingston (2002) analysis, predictions on future threats to biodiversity, most especially birds, did not match reality. Much of the explanation lies in understanding how isodars changed through time. Isodar slopes based on the complete data were approximately unity, and intercepts zero, until 1988. Human occupation of rural habitats became more-or-less stable thereafter, and noticeably so beginning in 2001. The 1980 isodar's ability to predict threats to biodiversity in 2020 could not anticipate decadal shifts in the distribution of humans between urban and rural habitats. Nor could it foresee the convergence of CO₂ emissions between high- and low-emitting nations (Fig. 3).

There is a second and more insidious reason for the isodar's "failure": the quality of nations' data on human abundance and energy use are far superior to those on threats to biodiversity. Moreover, temporal variation in the reliability of nations' biodiversity threats will necessarily reduce our ability to forecast future risks. Before rejecting isodars as leading indicators of future threats, we must first ensure that biodiversity data are as accurate and reliable as those on human distribution and energy use.

Where isodars "fail," related metrics of the human enterprise covary strongly with the Living Planet Index. The pattern is most obvious at the global scale where each binary indicator, except per capita CO₂, is essentially a perfect opposing match with the LPI. The conclusion is inescapable. Human populations are responsible, directly and indirectly, for the current and future global decline in Earth's biodiversity. Attempts to conserve biodiversity will fail unless they address that reality.

AN ESSAY ON FUTURE BIODIVERSITY

Planning a future that preserves biodiversity

Any reasonable plan aimed at conserving biodiversity requires evaluation of the plan's future consequences. Potential consequences are typically assessed by some form of comparative

analysis among alternatives. At the global scale, such analyses increasingly focus on the shared socioeconomic reference pathway (SSP) framework (Kriegler et al., 2014; O'Neill et al., 2014; Popp et al., 2017; Chen et al., 2020; Leclère et al., 2020). The SSP framework merges climate scenarios modeled through representative concentration pathways (RCPs; Van Vuuren et al., 2011) with socioeconomic (assumed to include biodiversity) alternatives that can integrate uncertainty in efforts to mitigate and adapt to climate change (O'Neill et al., 2014; Van Vuuren et al., 2014). The four RCPs represent low (RCP2.6 [2.6 W/m²]) to high (RCP8.5 [8.5 W/m²]) climate-change scenarios in 2100 consistent with current understanding of underlying causes, including human population growth, GDP, energy consumption, and land use, as well as greenhouse gas emissions and concentrations (Van Vuuren et al., 2011).

Initial SSPs include five narratives ranging from high-paced sustainable development and land productivity (SSP 1, the so-called green road) to absence of climate policies, carbon-based energy, economic development, and slowing population growth (SSP 5). Perhaps the worst option is SSP 3, in which economic growth fuels climate-changing emissions in a world with massive inequities in wealth and opportunity. The narratives commonly include different assumptions on global population growth, income, and per capita demand on resources (e.g., Popp et al., 2017). Modeling can yield a wide range of potential outcomes such as land use and its downstream effects on conservation, climate change, and food prices (Popp et al., 2017; Chen et al., 2020), or more direct land conservation efforts to sustain biodiversity (Leclère et al., 2020).

The implicit “philosophy” underlying SSP modeling for conservation is similar to that which plagues much of conservation biology—options that mitigate effects beyond control. So it is unclear how SSP modeling can inform policies on the root problem of too many people consuming too many resources in short supply. The thoughtful and comprehensive analysis of land-use scenarios by Leclère et al. (2020), for example, included various agricultural, consumption, and conservation management scenarios but nothing directly related to controlling human populations. The same is more generally true of many well-intentioned policies aiming to protect areas on Earth’s surface for the conservation of biodiversity. All are doomed to fail unless we find a way to limit human populations and their self-reinforcing tragedy of the commons (Lloyd, 1833; Hardin, 1968, 1998; Morris, 2019).

Education, human fertility, and population growth

Three mechanisms—reproduction, death, and dispersal—dictate a population’s dynamics, human or otherwise. Migration disappears in global populations that change solely by reproduction and death. That leaves only fertility as a morally acceptable option for limiting human population growth. Although there are intriguing exceptions (Colleran and Snopkowski, 2018), such that wealth is more likely to result in higher fertility (Stulp and Barrett, 2016), human birth rates tend to decline with female income and especially so with educational attainment and access to contraceptives (e.g., Sheikh and Loney, 2018; Götmark and Andersson, 2020; Liu and Raftery, 2020 and references therein). More than 80% of the variance in female fertility by age 50 is accounted for by statistical models incorporating access to contraception and educational attainment (Vollset et al., 2020). Such patterns are useful in forecasting future population and economic consequences expected from education and contraceptive use, but the underlying links to the evolution of human life history remain mostly correlational. Moreover, there are good reasons to anticipate contrary long-term reversals such as the ability of religiosity to counteract expected reductions in total fertility (Hackett et al., 2015; Götmark and Andersson, 2020). There is also no guarantee that reduced human population size will necessarily result in less consumption, less use of resources and space, or slow down the loss of biodiversity.

The true villain of biodiversity

The way that isodars change through time reveals the underlying threat to biodiversity: the omnipresent tyranny of cities. Their defining features are a human tragedy of the commons (Morris, 2019) and a massive appropriation of rural area exceeding their own by three orders of magnitude (Folke et al., 1997). The scourge of biodiversity is less likely associated with the Greek *Anthropos* (human) than it is by the Greek *Polis* (city). The human isodar tells us that the Poliscene began in 1958, after which the isodar intercept (log scale) was no longer significantly less than zero.

It is not just cities that are a problem, but as well the exodus to the suburbs whose climate and environmental impacts exceed that of their adjacent city cores (Teicher et al., 2021). We can surmise that the rise of suburbia also emerged through human habitat selection. So it is within habitat selection that we must search for a solution. Can we make high-density cities more attractive without increasing their spatial nexus?

Saviors of biodiversity?

There are true wildernesses around the world that, if simply left alone, will endure as wildernesses.

—E.O. Wilson (2016: 175)

If biodiversity is to persist in any form such as we know it, then we must provide space for non-human life (Rosenzweig et al., 2012; Wilson, 2016). Those spaces can be realized only if cities devise strategies that make high-density living more attractive, efficient, and sustainable; they must reduce their rural demands for energy, food, and resources. There is no shortage of solutions, only a dearth of knowledge, leadership, and vision. Clean mass transit, zero-emission buildings, solar collectors, and alternative materials reduce energy demand. Vertical urban agriculture (Kalantari et al., 2017) supplies fresh produce, and combined with local manufacturing, reduces transportation. Attractive cities, particularly those with embedded wild areas, quench their citizens' thirst for nature, reconcile our coexistence with other species (Rosenzweig, 2003), and provide respites for biodiversity. And by being more attractive, immigration can reduce rural expansion and industrialization. But cities must do so cooperatively without further promoting the tragedy of the commons by competing with others for resources, jobs, and wealth.

Faced with the common perils of extinction, each city's actions to save and promote biodiversity benefits all others. When the costs of those actions are small, and shared benefits large, cooperation flourishes (Hamilton, 1964). Theory tells us that cooperation in such a system is most likely when actors (cities) reliably signal their cooperative spirit (e.g., Dawkins, 1976; Pagel, 2012). Knowing which others are cooperating reduces the likelihood of providing benefits to free riders—cooperate with cooperators. And, when the benefits are global, cooperation can snowball—everyone shares the benefits of cooperators' actions. Merged with multi-level selection (Wilson, 1975; Wilson and Wilson, 2007), small benefits to individuals can multiply into massive benefits for cooperating groups. Wise is the individual (city) who leads the charge.

There is no shortage of relevant examples. The common good of eliminating global pandemics universally exceeds the costs of cooperation. Countries that quickly control the epidemic are the first to reward their citizens with wellbeing and economic opportunities. Corporations, when allowed to do so by informed legislation, quickly copied others' demands that employees be fully vaccinated against COVID-19. Repeated polls documenting wide support for mandatory vaccinations by Canadians demonstrate that common good can trump self-interest (Britneff, 2020; Boynton, 2021; Turnbull, 2021); support by German citizens is more equivocal (Graeber et al., 2021).

Companies reducing carbon emissions advertise their public service, and are rewarded by customers who value that service. Mutual benefits emerge similarly when cities signal their cooperative intent by directing efforts toward conservation. One promising approach calls for re-designing cities with affordable (high-density) housing embedded in a network of shared open spaces to alleviate crowding and support wildlife (Haase, 2021). Those solutions must first dispense with oxymoronic policies of sustainable development and the mythical rhetoric of humans “living in harmony with nature” and “harmony with Mother Earth” (Díaz et al., 2019; Anon., 2020; Secretariat of the Convention on Biological Diversity, 2020). No species, past, present, or future has, can, or will live in harmony—each requires from others its resources, space, and safe harbor. The best that we must aim for is to minimize human influence on remaining biodiversity. Doing so requires informed and visionary leadership.

Leadership

Some optimists will point to the 196 Parties to the Convention on Biological Diversity and to the 2020 Leaders’ Pledge for Nature (Anon., 2020) to “put nature and biodiversity on a path to recovery by 2030” as exemplars of conservation leadership. Others will note that the USA has not yet ratified the Convention, that the Leaders’ Pledge lacks concrete and clearly defined courses of action, and that it is devoid of any reference to human population growth. National leaders must do more—they must provide financial and other incentives that motivate cities to cooperative action and eliminate the exodus to suburbia. They must institute policies that yield fair and equitable services and opportunities to all citizens. And they must understand Earth’s limits to humans’ use of space, resource consumption, and population growth.

Leaders need to recognize that even ambitious conservation targets surpassing the Bonn Challenge (<https://www.bonnchallenge.org/>) are, by themselves, unlikely to limit peak biodiversity losses until at least 2075 (Leclère et al., 2020). Current modeling demonstrates that “reversal” in biodiversity trends by mid-century is only possible in an aggressive scenario merging land protection and restoration with greatly intensified agricultural production and trade, a 50% reduction in food waste, and 50% substitution of animal calories by plant-based diets for the majority of humans (Leclère et al., 2020). The models do not include direct feedback on human population size—all scenarios assume that the global human population peaks at 9.4 billion in 2070 (Leclère et al., 2020), and no nation is anywhere close to achieving the required scenarios.

Worse, other scenarios, such as those proposed by the International Energy Agency (IEA), call for order-of-magnitude expansions of wind, solar, and other renewable energies (IEA, 2021), and globalized markets (which are responsible for massive land-use change since 1960; Winkler et al., 2021). Similar concerns can be raised about the IEA’s proposed pathway for increased bioenergy, notwithstanding a moderate increase in land area and its claim that it will avoid “negative impacts on biodiversity” (IEA, 2021: 77). The IEA pathway aims to protect biodiversity hotspots, but doing so is inadequate to meet the needs of myriad other species. One wonders what policies would emerge if the focus on energy was shifted toward preserving biodiversity.

Vision: a global moratorium on space

We have to learn to think in a new way.

—Russell et al. (1955)

Unlike solutions for climate change, no single quantitative target exists to protect Earth’s biodiversity. In the case of climate change, scientists of many stripes used quantitative data and

sophisticated modeling to demonstrate that catastrophic consequences of a 2°C increase in global surface temperature can be averted only by net zero CO₂ emissions (IPCC, 2021). Identifying the implications of global warming on climate and economies, merging those effects with underlying human activities, and providing a solution gives policy-makers a single universal objective and benchmark for assessing the effectiveness of policies to achieve it. The same is true in international efforts to reduce the Sars-CoV-2 (and its variants') reproductive number below 1. Compare these clear objectives with the 20 mostly qualitative Aichi biodiversity targets set out in the Convention on Biological Diversity's strategic plan for 2011–2020, the majority of which have not been achieved and the remainder only partially so (Secretariat of the Convention on Biological Diversity, 2020). We need a different course of action, a cooperative set of international, national, regional, and local commitments to STOP further expanding our spatial web on land and sea, our consumption and displacement of wild species, and pollution of soil, water, and air. Stopping expansion will force societies to capitalize on intensive rather than extensive economies (Wilson, 2016), including nuclear and hydrogen (Brown et al., 2023). It doesn't mean that humans have to survive on less. It simply means that by living and working smarter, we do not use more. Attaining the necessary education provides an additional bonus. Synergies between policy and economy, at least in developed nations, lead to longer periods of education, older age at first reproduction (Neels et al., 2017), and the potential for reduced lifetime fecundity.

Some will argue that STOP strands assets that impede the progress of commerce. Wiser heads will understand its promise of providing the sustainable green infrastructure necessary for life on a small planet. But why STOP? Have not nations made significant progress in setting aside protected areas? Yes, but doing so protects only small or remnant ecosystems and fails to address the scale of sustainable biodiversity. Policies on protection vary and we must ask "protected from what and from whom"? And we must also ask, what do we allow of the remainder?

Much of the value and promise of STOP is scale invariance. It can, and indeed must, be practiced by individuals, communities, corporations, and governments of all sizes. It becomes global through international agreements. Each scale has its separate and interacting responsibilities, jurisdictions, and opportunities to STOP. And of course, STOP cannot rescue biodiversity on its own. It must be merged with policies and commitments on energy production, restoration, places for untouchable nature, and reconciliation. But at least it puts the brakes on incessant human expansion. And it can easily be applied by establishing global standards for non-financial reports similar to those suggested for climate change (e.g., Carney, 2021). A useful first step would include STOP as an integral reporting component by the IFRS Foundation's nascent International Sustainability Standards Board.

Practically, STOP means explicit policies that restrict further expansion into wilderness, end the conversion of farmland to city, and limit transportation and energy corridors to those currently available. It means that we STOP viewing the natural world as economic opportunity, and recognize its inseparable identity with our own. But just as importantly, STOP allows humans to choose how they will treat what has already been taken from nature. Populations of humans and domesticates can grow or decline, people can remain where they are or move, countries can limit or open immigration, industry and trade can thrive, agriculture can become more productive, nature reserves can be expanded (but never reduced). The central principle is that future actions must take place within the constraints of STOP.

STOP will surely fail if it is not linked to greater equity among nations and peoples, to realigned values (Carney, 2021), greatly improved opportunities for education and family planning, and reversing the tragic runaway competition for economic and military dominance. Social

action must not simply demand equity, it must eliminate ecological ignorance through education, value philanthropy over wealth, and replace greed with compassion. Most importantly, as we are learning from climate change and COVID-19, success emerges when we advertise a collective cooperative intent by placing common good above self-interest.

STOP, alone, will not save biodiversity. But it buys time while humanity seeks additional options, including reconsideration of nuclear energy (Brown et al., 2023), setting aside inviolate space for the rest of life (Wilson, 2016), learning to better reconcile humans' use of habitat with that of other species (Rosenzweig, 2003), and major restructuring of economic, social, natural, and political systems (Barnard et al., 2021). Nor does STOP mean that there are no options for temporary set-asides for development. Small-scale exceptions can be allowed as long as those transgressions replace all-too common practices of "mitigation" with complete restoration. Each exception must include ironclad guarantees of complete rehabilitation consistent with Wilson's maxim "do no further harm to the biosphere" (Wilson, 2016: 212). STOP provides the context: do nothing that expands your spatial web.

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