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Abstract

The relation between the environment and human activity has been the subject of many empirical studies. Complexities such as which indicators related to human activity best represent biodiversity, or time lags between socio-economic activities and biodiversity, remain unclear. This paper tackles these issues based on statistical analysis of the relationship between human activity and biodiversity at the country level in Europe. We used well-adapted statistical models to explain variations in two state indicators, two pressure indicators, and one response indicator representing biodiversity. We focused on (i) the relative efficiency of the various indicators of human activity (notably human population density, human appropriation of net primary productivity, and gross domestic product per area) in predicting the biodiversity indicators, and (ii) possible time lags between metrics representing human activity and biodiversity. Results indicate that gross domestic product per area and human population density best predict the indicators for the biodiversity state, whereas human population density best predicts the indicators of biodiversity pressure. Although the indicators for biodiversity pressure best related to present-day human activity metrics, biodiversity state reveals a time lag of approximately one century. Results suggest that drivers (human population density, density of economic activity) and pressures (land sealing) should serve as primary foci for biodiversity policies. Because of the long time lags (~ one century) between these drivers and the state of biodiversity, policies regarding biodiversity should integrate a long-term view.

Keywords: species imperilment; sprawl; threatened species; socio-economic drivers; time lag

Introduction

The Intergovernmental Science–Policy Platform on Biodiversity and Ecosystem Services (IPBES) assessment on the state of biodiversity and ecosystems in the European region, published in 2018, reported that trends remain negative overall, with potential consequences for the economy and society (IPBES, 2018). The IPBES reached the same conclusion one year later at the global scale (IPBES, 2019). These negative trends related to five direct drivers of biodiversity change (or pressures). They are, in descending order of impact: (1) changes in land and sea use; (2) direct exploitation of organisms; (3) climate change; (4) pollution and (5) invasive alien species. Yet, the underlying societal causes of these pressures were related to indirect drivers of change, notably to governance issues, technological innovation and demographic and economic factors. Economic activity may impact biodiversity through different mechanisms. Pollution may cause various types of harm to indigenous species. Human presence and/or travel can disturb animal activity and, consequently, interfere with ecosystem processes. Encroachment of land due to urbanization and infrastructure can reduce the size of habitats to a critical level or fragment them, rendering metapopulations less viable. In the long term, the encroachment of land can also impoverish the gene pool through isolation, leading to population extinction. Which mechanisms are the most important in explaining the decline in biodiversity is not obvious. Studying which variable representing human activity correlates most to biodiversity, however, can help identify the appropriate types of corrective actions to target.

In this research, we therefore sought to identify the socio-economic variables that best correlate to variables indicating current levels of biodiversity at the country scale, and the time lags between the two sets of variables. We chose to examine the country scale, as have many previous studies (e.g., Hoffmann, 2004; Konickova et al., 2006; Clause and York, 2008; Dullinger et al., 2013; Gosselin & Callois, 2018), because some of the data for analysis are more readily available at this scale—for example, proportion of threatened and extinct species and gross domestic product. Additionally, the national scale is still the most relevant for many policies concerning biodiversity and socio-economic issues. More precisely, we addressed the following questions:

(i) What are the kinetics of the impact of human activity on biodiversity? Following Dullinger et al. (2013), in hypothesizing time-lag effects between indicators of human activity and those of biodiversity, we posited that past values of socio-economic variables would better explain current variations in biodiversity state indicators .

(ii) Which models involving indicators of human activity best explain the values of biodiversity indicators? We hypothesized that simpler, un-transformed or merely log-transformed, models would be at least as efficient as more complex socio-economic models.

(iii) What variables representing human activity best explain the variations in the biodiversity indicators—for example, those depending on their proximal link with biodiversity or more general variables of human activity? We hypothesized that the human appropriation of net primary production or the proportion of sealed area, which are potentially more directly related to biodiversity, would better explain the variations of biodiversity indicators than, for example, human population density, especially for the indicators of biodiversity state.

The literature relating the state of biodiversity to socio-economic drivers and pressures is now well developed. Findings indicate that drivers such as Gross Domestic Product (GDP) per capita (GDPc; Clausen and York, 2008), human population density (HPD; Brown and Laband, 2006; McKee et al., 2013; Driscoll et al., 2018), the spread of transportation infrastructure (Konvicka et al., 2006) or income inequality (Mikkelson et al., 2007; Holland et al., 2009) correlate with various measures of biodiversity.

Focusing on the link between human population density (HPD) and biodiversity, Luck (2007) reviewed the published empirical literature through a meta-analysis. The author concluded that, despite the geographic and taxonomic skew in the published literature, a positive correlation is apparent between HPD and various biodiversity metrics – mainly related to species richness. That is, the level of biodiversity is greater in densely populated zones. This correlation, however, may be due to the relation between HPD and these biodiversity metrics on the one hand, and other parameters such as ecosystem productivity or energy availability on the other. Some evidence was also apparent of negative relationships between HPD and other biodiversity metrics related to species extinction, but it was weak (Luck, 2007).

In analyzing how three variables related to economic growth (GDPc, HPD and a metric related to land use intensity—human appropriation of net primary productivity (HANPP)) are related to the proportion of threatened species in European countries, Dullinger et al. (2013) proposed an explanation for the weak evidence reported by Luck (2007). That is, the relationship between current economic and biodiversity variables could be weak because the metrics of biodiversity respond to economic variables with a time lag. Dullinger et al. (2013) proposed that the relationship would become much stronger if the metrics of biodiversity were related to past economic variables. This proposal echoes the well-known notion of extinction debt in ecology (Tilman et al., 1994; Kuussaari et al., 2009), as well as the pioneer ecological studies that identified time lags in the relationship between habitat quantity and configuration and biodiversity (Chamberlain et al., 2000 ; Lindborg and Eriksson, 2004 ; Menéndez et al., 2006 ; Metzger et al., 2009). Most of the latter studies were centered on habitat. Yet, the drivers of variations in past habitat could have even greater time lags for affecting biodiversity (Essl et al., 2015), since the time lags between the initial driver and the habitat pressure should add up to the time lags between habitat and biodiversity.

Even though this reasoning provided a new line of analysis, Gosselin (2015) questioned this conclusion on the basis of inadequate statistical tools. When more accurate statistical tools were used to take into account data pseudo-replication and over-dispersion, the significant relationships mostly disappeared, or at least became much less significant. Gosselin and Callois (2018) analyzed the data of Dullinger et al. (2013) together with data on extinct species, biodiversity pressure indicators (land sealing) and response indicators (the proportion of protected areas) in Europe and related them to diverse socio-economic drivers. They found a positive impact on the proportion of threatened and extinct species due to the density of "human activity" (either measured as human population density or as the gross domestic product per unit area of land, GDPa, and especially their logarithm transforms). These results were based on relationships between current socio-economic variables and current biodiversity indicators. Yet, one of the biodiversity indicators used in this study represented past events (the proportion of extinct species), and two indicators related to the accumulation of past decisions (proportion of sealed area and proportion of reserves). Also, for a fourth indicator (proportion of threatened species), past values of socio-economic variables likely predict states of biodiversity better than current values due to time lag effects (cf. supra). Identifying these time lags is a pressing question, according to the International Science-Policy Platform on Biodiversity and Ecosystem Services (e.g. IPBES, 2018). Furthermore, Gosselin and Callois (2018) did not incorporate human appropriation of net primary production (HANPP), another metric used by Dullinger et al. (2013). Yet, this metric is an integrated socio-ecological indicator of land-use intensity (Haberl et al., 2013), which is closely related to population density (Krausmann et al., 2009). As such, HANPP has potential to more proximally explain the impact of human activity on biodiversity, and may therefore better explain its variations (Haberl, 1997; Haberl et al., 2004; Vačkář et al., 2016). Finally, Gosselin and Callois (2018) did not include simpler models with the two core human activity variables (HPD and GDPa), which might better explain variations in biodiversity indicators than more complicated models.

Material and methods

Biodiversity indicators

This study sought to relate relevant indicators of biodiversity throughout Europe to economic variables at various dates. We chose indicators that fit the Driving forces, Pressure, State, Impact, Response (DPSIR) framework, in line with Butchart et al. (2010). Even though we did not estimate the DPSIR framework explicitly, we chose five biodiversity indicators positioned in the DPSIR diagram (http://www.eea.europa.eu/publications/TEC25), for which data are readily available at national level, as follows (cf. Table SM2 for summary statistics):

i. Two Pressure indicators related to land sealing: percent of surface area in the country sealed in 2009 (denoted as SEAL) and annual increase in sealing between 2006 and 2009 expressed as a percentage (denoted as iSEAL);

ii. Two indicators of the State and dynamics of Biodiversity: the proportion of extinct and of threatened species in each country for nine different taxonomic groups (vascular plants, bryophytes, mammals, birds, freshwater fishes, reptiles, amphibians, dragonflies and grasshoppers);

iii. One Response indicator, referring here to societal response (as defined in the DPSIR framework): the percentage of terrestrial area in each country corresponding to protected areas (combining four different types of protected areas as defined by the International Union for Conservation of Nature).

Data for this study came from the European Environmental Agency (two Pressure indicators), Eurostat (Response indicator) and Essl et al. (2013) (two State indicators). We did not consider trees as a separate taxonomic group because, at least for some countries, trees were incorporated into evaluations of vascular plants. Our analyses therefore already accounted for them in the vascular plant taxonomic group.

Socio-economic variables

We considered the economic variables in the study as potential drivers of the five Pressure-State-Response (PSR) indicators described above. This approach agrees with the notion of indirect drivers defined by the IPBES (https://www.ipbes.net/models-drivers-biodiversity-ecosystem-change). We focused attention on two classical indicators of human activity: gross domestic product (GDP) and human population density (HPD). We tested GDP per area (GDPa) as well as GDP per capita (GDPc) because Gosselin and Callois (2018) found that the density of economic activity (GDPa) had a stronger relationship with biodiversity indicators than economic development per capita (GDPc). We also included the variable built by Dullinger et al. (2013) to estimate human land use intensity: human appropriation of net primary production (HANPP), which is another measure of the spatial density of human activity likely closest to the indicators for PSR biodiversity. Table SM1 provides the list of socio-economic variables from years 1900, 1950 and 2000, found in Dullinger et al. (2013).

This study considered a list of 22 countries. These countries are the same as those in Dullinger et al. (2013): Austria, Belgium, Bulgaria, the Czech Republic, Denmark, Finland, France, Germany, Greece, Hungary, Italy, the Netherlands, Norway, Poland, Portugal, the Republic of Ireland, Romania, Slovakia, Spain, Sweden, Switzerland and the United Kingdom.

Statistical models and hypotheses

Following Brown and Laband (2006) and Gosselin and Callois (2018), the strategy in this study was based on the estimation and comparison of several simple statistical models. We did not mix different metrics into a single, global metric, nor did we estimate a single statistical, multiple regression model that would have included all the variables. We thus avoided technical and interpretative problems of correlations between variables. We followed a three-step strategy to identify the best socio-economic variables in terms of predictive power and analyze their relationships with biodiversity indicators.

First, we addressed the first hypothesis by estimating and comparing the first seven models described in Table 1 (*Null*, *Economic*, *Log Economic*, *Kuznets*, *Log Kuznets*, *Area Kuznets* and *Log Area Kuznets*) among the three different periods (1900, 1950 and 2000). The 2000 versions of these models are very close to the corresponding models in Gosselin and Callois (2018). These models were among the best for which historic data were available. *Economic* refers to models including both GDPc and HPD, two of the main indirect drivers of change according to the IPBES (2019). The *Kuznets* models included different versions of GDP, as well as its square, to account for quadratic relationships with GDP and to allow for possible bell-shaped relationships with GDP, a shape known as the Environmental Kuznets Curve (Selden and Song, 1994). Except for the null model, each model incorporated two socio-economic variables related to a specific theme. We chose to limit the number of variables in the models since we only had a limited number of countries in the data set (22 countries) for this study. Therefore, we included at most two socio-economic variables per model, following the n/10 guideline of Harrell (2001, p. 61) on the relationship between sample size *n* and number of estimated hyperparameters. The resulting models were slightly over-parametrized for state indicators (with 21 hyper-parameters estimated compared to a maximum of 19.8 according to Harrell's rule). They were somewhat more over-parametrized for response indicators (12 hyper-parameters compared to a maximum of 8.8 according to Harrell's rule), and much more overparametrized for pressure indicators (5 hyperparameters compared to 2.2 according to Harrell's rule). Our general hypotheses were that explanatory models with 1900 or 1950 data would better explain the Proportion of Extinct species, the Proportion of Sealed areas and the Proportion of Threatened species, since we expected a rather strong time lag for the effects on Biodiversity, similar to the reasoning in Dullinger et al. (2013).

In the second step, we compared the best model for each indicator from the first step with simplified univariate explanatory models, *HPD*, *Log HPD*, *GDPa* and *Log GDPa*, for 1900, 1950 and 2000 data. This procedure determined, first, whether the relationships could be reduced to such simple univariate models, and second, included less over-parametrized models. We also considered *HANP*P and *Log HANPP* models at the different time periods (cf. Table 1). We expected these two last models to reveal more proximal causes of variations in the indicators, especially for the two State Indicators. For these two indicators, we also included hierarchical versions of the univariate explanatory models described above. We then added a taxonomic random effect on the slope, thus estimating the mean slope across taxonomic groups as well as the standard variation across taxonomic groups of this slope. This procedure yielded models with a number of parameters similar to the models in the first step. This process allowed the relationship to vary across taxonomic groups instead of being fixed to a mean response as in the previous models.

In the final step related to the third hypothesis, and only for the two State indicators of biodiversity, we compared the best model involving present explanatory variables from the first two steps with a model including the current proportion of sealed area (SEAL). This procedure determined whether SEAL could serve as a more proximal indicator of the current biodiversity state.

Figure SM1 in the Supplementary Materials section (see also Supplementary Materials in Dullinger et al., 2013 for associated graphics) displays the correlations between explanatory variables. We found mildly strong correlations among the group of GDPc variables at different dates, and stronger correlations among HANPP variables and among the group formed by GDPa and HPD variables. The latter two groups had squared Pearson correlations of at least 0.7. These correlations prevented us from formulating models including both GDPa and HPD, or the same variable at different dates.

Statistical methods

We paid careful attention to the potential over-dispersion of data as well as to the inclusion of random country effects, following Gosselin (2015). We therefore introduced a random country effect into the models involving repeated values per country. We assumed this effect to follow a Gaussian distribution with a zero mean and an estimated standard deviation, This approach allowed inclusion of indeterminacy between country-level explanatory variables and other, unknown, country-level determinants. We used this random country effect, for example, for the two State indicators, which provided proportions of Extinct and Threatened species for different taxonomic groups within each country. For the proportion of extinct or threatened species, we used a logit link function and a beta-binomial distribution to model the number of extinct and threatened species as a proportion of the number of native species and native minus extinct species, respectively. Each taxonomic group had separate estimated intercept and extra-binomial variation fixed parameters. For the proportion of protected areas and the percentage of sealed area and its increment, we used the zero-inflated beta distribution. This distribution is a direct sub-product of the zero-inflated cumulative beta distribution, proposed to analyze plant cover class data (Herpigny and Gosselin, 2015). For sealed areas, we fitted a separate model for area and increment (SEAL and iSEAL) and therefore did not include a random country effect in the corresponding models. We framed the models within a Bayesian setting. For the proportion of protected areas, each category of protected area had separate estimated intercept and variance fixed parameters, but the parameter for zero inflation was the same for the different categories.

We used the Stan program embedded in R 3.3.2 through the rstan library (Stan Development Team 2015) to estimate the models described above. The priors of the hyper-parameters were mostly non-informative, except for the proportion of extinct species that required an upper bound at exp(10) for dispersion levels in order to obtain converging results. All the explanatory variables were centered and scaled to ensure a residual standard deviation of the variable around one while keeping clear control over the level of scaling.

The models were compared in terms of predictive capacity with the leave-one-out Information Criterion (LOOIC; Vehtari et al., 2016). For State and Response indicators, we used the marginal version of the LOOIC (Gosselin and Callois, 2018, 2019).

We investigated the estimators of the socio-economic parameters with an eye toward the statistical significance and magnitude of the relationships. For statistical significance, we used Bayesian quantiles based on beta random draws (Gosselin, 2011). This paper includes only those cases with a p-value below 5%. To judge the magnitude of Odds-ratios, we analyzed the effect of an increase of one standard deviation at the linear combination level (on the log of odds ratios) for each socio-economic variable, according to guidelines adapted from Daniels et al. (1983) (see Table 5 legend for more details). These ratios are adapted to the framework for magnitude analysis proposed in ecology (e.g., Camp et al., 2008; Barbier et al., 2009).

Finally, to gauge the adequacy of the statistical models in relation to the data, we used sampled posterior goodness-of-fit p-values (Gosselin, 2011). These values are based on normalized quantile residuals (Dunn and Smyth, 1996), with discrepancy functions similar to Herpigny and Gosselin (2015) and Godeau et al. (2020). We first diagnosed the distributions of the residuals or the random effects by using their mean, variance, skewness and kurtosis as discrepancy functions. Then, to diagnose potentially ill-modelled relationships for the mean or variance, we used discrepancy functions based on correlations with Hoeffding's D statistic (Harrell, 2001). These functions determined the links between (i) the residuals and the fitted values, (ii) the residuals and each of the explanatory variables, and (iii) the square of the residuals and the fitted values. Hoeffding's D statistic can detect correlations that include linear and non-linear relationships, and increasing or decreasing as well as non-increasing and non-decreasing relationships. Finally, we used two discrepancy functions to diagnose any spatial autocorrelation of country random effects (if they were included in the model) or residuals (if random effects were not included). We fitted a generalized least squares (gls) model with an exponentially decaying spatial autocorrelation (Pinheiro and Bates, 2000)on country random effects or residuals (functions corExp and gls in the nlme library with a nugget), then considered the range and nugget of the gls model as the two final discrepancy functions. These p-values allowed, in sum, diagnosis of the adequacy of the probability distributions used, the adequate specification of the non-linear relationship between explanatory variables and data, the correct specification of variance, the absence of additional spatial autocorrelation and, in cases where the model included country random effects, the adequacy of the probability distribution of the random effect. Given usage of around ten discrepancy functions per model, we only investigated cases with p-values below 0.005. These p-values were applied to the best model associated with each biodiversity variable.

Results

Overall, with Proportion of Protected Areas as a dependent variable, none of the main socio-economic models had better predictive capacity than the Null model (Table 2). For the proportion of Extinct species, the 1900-data versions of the Log Area Kuznets, Area Kuznets, Economic and Log Economic (Table 1) models involving different combinations of three measures of human activity clearly yielded the models with the best predictive capacity (Table 2). The human activities were gross domestic product per area (GDPa), gross domestic product per capita (GDPc) and human population density (HPD). A logical ranking was also apparent over time, with 1950 models being better than 2000 models and worse than 1900 models. For Threatened species, a similar result emerged, except that the Economic model had worse predictive capacity than the other socio-economic models. The 1950 and 2000 models were somewhat closer to 1900 models than for Extinct species. Yet, we observed the same ranking, with 1900 yielding better models than either 1950 or 2000 (Table 2). For the share of sealed land (SEAL) and its dynamic (iSEAL), the analysis produced the reverse result, since 2000 models with economic variables were best (Table 2). The 1950 models were close to the best models for both SEAL and iSEAL, though the order of ranking was 2000, 1950, 1900.

Comparing these socio-economic models with simpler, univariate explanatory models (Tables 3 & 4), we found that the univariate model with Log GDPa in 1900 was best, both for Extinct and Threatened species. For Threatened species only, the log of human population density (Log HPD) in 1900 was close to this best model. For SEAL and iSEAL, HPD in 2000 (log-transformed for SEAL but not for iSEAL) was the best univariate variable, even yielding the best model for SEAL (Table SM3). Both for state and pressure indicators, the indicator of human appropriation of primary production (HANPP; Dullinger et al., 2013) did not provide models with better predictive capacity than the best univariate or multivariate models (Tables 3 & 4). When restricting to the relationship of present socio-economic driver variables to the two State biodiversity indicators and comparing them with the relationship between SEAL and these same indicators, we found that SEAL had better predictive properties for the proportion of Extinct species, and was close to the best models for the proportion of Threatened species (Table SM5).

Graphical representations of the relationships also indicated a better link with 1900 than 2000 economic variables for Extinct and Threatened species and the reverse for SEAL and iSEAL (Figure 1). Considering the associated estimators (Table 5), results were overall less obvious with only slight differences either in estimator significance (p-value) or in the mean estimated effect of adding 1 standard deviation to the variable (first column). The only strong difference in terms of magnitude was with iSEAL. The models fitted the study data adequately since we did not detect any discrepancy between the data and the best models at a significance level fixed at $p<0.005$.

Discussion

The finding of no relationship between socio-economic variables with the Response indicator (i.e. the proportion of protected areas in European countries; Table 2) contrasts with previous literature. In a summary of results, Luck (2007) reported a negative relationship between human population density (HPD) and protected areas. The metrics considered for protected areas, however, varied from area proportion to absolute area, which was not the case in the present study, as only area proportion was used. The absence of a statistical relationship may be the outcome of conflicting mechanisms. On the one hand, economic activity and population density raise pressures for land sealing .On the other hand, they may also trigger social demand for protected areas as a reaction to the consequences of land sealing.

Second, the importance of 2000 economic drivers in explaining the Pressure indicators (Tables 2 and 5) suggests their closer relationship to the current level of human population density or activity than to those in 1900. This finding was contrary to our expectations for SEAL, which we expected would integrate the cumulative effects of land sealing over many generations and therefore more relevant to economic variables representing the past. Yet, the study of urbanization during the 20th century shows that the link between human activity and land encroachment operates quite quickly. For example, in post-World War II industrial countries, land use changed radically within a time span of a few decades., Colsaet et al. (2018) reported that the most indisputable causal factors were income and population growth. This is consistent with our results (Tables 3, 5 and SM3), which show the foremost contribution of current population density on land sealing indicators.

The better explanatory power of the 1900 socio-economic variables and particularly the Kuznets-like models for the current proportion of extinct species should not come as a surprise. Current extinctions reflect past events – although on a relatively unknown time scale –, which themselves are related to past pressures. We therefore expected close relationships between the proportion of extinctions and socio-economic values in 1900 or 1950. It was a priori unclear, however, whether 1900 or 1950 variables would serve as better predictors. The results, with 1900 models clearly having better predictive capacity than 1950 models (Table 2), suggest, apparently for the first time, that the causes of current extinction levels are rooted further in the past. The results echo those of Konvicka et al. (2006), however, who found a correlation between butterfly extinctions and railway densities that was interpretable as an indicator of early industrialization.

The similar trends for the proportion of threatened species—i.e. models involving 1900 values of socio-economic variables better predicted the current proportion of threatened species than those involving 2000 values—were more surprising. These results follow the global message of Dullinger et al. (2013), but for more adequate statistical models and different variables (gross domestic product per capita (GDPc) and gross domestic product per area (GDPa) in Dullinger at al., 2013 and this study, respectively). We therefore confirm the trend for a long-term effect of socio-economic development on the state of biodiversity, and a time lag in the relationship. Results from this study, however, do not allow precise estimate of the length of this time lag nor explanations for this phenomenon, although the time lag is apparently shorter for Threatened than for Extinct species. These empirical results are in line with the concept of extinction debt proposed by Tilman et al. (1994), substantiated by e.g. Vellend et al. (2006) and reviewed by Kuussaari et al. (2009). Findings of macro-level relationships in this study suggest that the relationship between economic drivers and biodiversity erosion may reflect such extinction debt.

Results of this study also confirm Gosselin and Callois (2018), in that the two State indicators of biodiversity are mostly related with models that include either Human Population Densities (HPD) or Gross Domestic Product per area (GDPa) (Table 3).. The results also confirm the conclusions of Gosselin and Callois (2018)on the interest of these metrics as biodiversity-driver indicators, though with a logarithm transformation and a time lag of approximately one century. The results are also consistent with previous findings where HPD was significantly associated to the proportion of Threatened or Extinct species or related quantities (Hoffmann, 2004, McPherson and Nieswiadomy, 2005, Luck, 2007 and, to some extent, Pandit and Laband, 2007 and McKee et al., 2013). They also echo McKee and Chambers (2011) on the identification of GDPa rather than mere GDP as a robust variable significantly related with the number of Threatened species. These previous studies, however, did not use HPD or GDPa in 1900 but rather more recent values of HPD or GDPa. In terms of magnitude, starting with proportions of extinct species and threatened species of 3.00% and 30.0% respectively, doubling GDPa in 1900 in the study models would increase these proportions to 4.15% (±0.26%) and 33.5% (±1.1%), respectively (based on estimates in Table 5). We therefore consider these effects very significant and of intermediate strength.

These results lead to a main conclusion that Log GDPa in 1900 is an accurate driver indicator for the two State indicators, and Log HPD in 2000 for the two Pressure indicators.

Additionally, SEAL could represent a relevant present pressure indicator for the two State indicators, since it provided relationships with either equivalent (for Threatened species) or better (for Extinct species) predictive quality than the other socio-economic variables in 2000 (Table SM5). This conclusion is consistent with the considerable body of work on the impact of land encroachment and urbanization on biodiversity. Louwagie et al. (2017) showed how the process of land sealing reduces biodiversity at different levels. Given our previous results, we conjecture that past land sealing might be an even better Pressure indicator than past GDPa for current proportions of Extinct and Threatened species. This conjecture also agrees with Konvicka et al. (2006), who reported that the density of railway lines was the best socio-economic predictor of past butterfly extinctions in European states. In contrast, the density of highways was not as strongly and consistently related to past butterfly extinctions. The authors interpret this result as an indication that “butterfly losses are attributable to persistent patterns of economic history rather than to the recent situation”

Generalizing the results of this study to broader indicators of biodiversity yields conclusions even more pessimistic than previously reported at global levels (e.g., Butchart et al., 2010; Tittensor et al., 2014). Since the processes that reflect in the Pressure indicators (and Driver indicators in our case) are still continuing to increase, and given the time-lag between these processes and the State of biodiversity, one should not expect the State indicators to improve before many decades, if the relationships remain unchanged. This analysis using indicators reveals that biodiversity, like climate change, apparently has a strong temporal inertia in its interactions with its drivers, which highlights the urgent need for protective measures.

Patterns of biodiversity loss are obviously more complex than reflected in the simple statistical models used in this paper. Yet, based on goodness-of-fit p-values, the lack of departures from the data indicates that the models are not too simple for the data at hand. In fact, they might be too complex, especially for the two pressure indicators, as revealed by the analyses of the number of parameters estimated relative to the amount of data used (see Statistical Models and Hypotheses section). The results for the two pressure indicators should be taken with care, as they may stem from over-fitted models (Harrell, 2001). Additional analyses, for example with extended data sets with more countries or at smaller spatial scales, with diachronic data sets (e.g. McKee et al., 2013), or using a more integrated framework ,such as structural equation modelling, would be useful.

Policy implications

Although results from this study may suggest that current policy measures may only have effects on biodiversity after decades at best, these results nevertheless provide policymakers with precious knowledge. Understanding how these systems have long time lags should help policymakers better assess the actions they take. They may integrate in their monitoring evaluations of biodiversity policies, for example, the notion that a policy may have no noticeable effect on extinction or threatened species metrics in the short term. One or two decades may not suffice. As results from this study confirm that human population density and especially GDP per area driver biodiversity, and that land sealing may be an important pressure to consider, biodiversity preservation should infuse all economic activity, and not be restricted to local actions such as protected areas.

Conclusion

In conclusion, the analysis presented above enable clear answers to the research questions posed in this paper. First, even at a coarse (country) scale and with a small sample, a clear lagged relationship is apparent between the State of biodiversity and the gross domestic product per area (GDPa). This finding is consistent with the first hypothesis. Considering the different results for Extinct and Threatened species, the typical time lag is apparently about one century, though the time lag between Drivers (human presence and economic activity) and Pressure (land encroachment) appears much shorter.

Second, in accordance with the second hypothesis, simple models with human population density and GDPa improved modelling predictive capacity for three pressure and state indicators out of four. These results confirm the intuition that human activity as a whole impacts biodiversity, and that more complex models do not necessarily add substantial predictive power.

Third, the variables representing human activity that best explain variations in biodiversity were Log GDPa in 1900 for the two State indicators, and Log HPD in 2000 for the two Pressure indicators. In contrast with our expectations, including human appropriation of primary productivity did not improve the predictive capacity of the models over these more indirect measures of human activity. In line with our hypothesis, the above results further suggest that the causality between past human activity and the current state of biodiversity may be mediated by human pressure on the land through land encroachment.

These results suggest that human population density, density of economic activity, and land sealing should serve as primary foci for environmental policies. Because of the short-term view often common for policymaking, such findings steer toward the preservation of natural lands as high priority toward effective mitigation of the loss of biodiversity. Future additional analyses with diachronic data at much finer spatial levels would refine further the estimation of time lags to help guide such policies.

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Data accessibility (put here because our names are in it)

The code and data that support the findings of this study are openly available in Zenodo at https://zenodo.org/record/3240962#.XPt6W4gzZPY (doi: 10.5281/zenodo.3240961).

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Model name	1st explanatory variable	2nd explanatory variable
Null	-	-
Economic	GDPc	HPD
Log Economic	log(GDPc)	log(HPD)
Kuznets	GDPc	GDPc^2
Log Kuznets	log(GDPc)	log(GDPc)^2
Area Kuznets	GDPa	GDPa^2
Log Area Kuznets	log(GDPa)	log(GDPa)^2
GDPa	GDPa	–
Log GDPa	log(GDPa)	–
HPD	HPD	–
Log HPD	log(HPD)	–
HANPP	HANPP	–
Log HANPP	log(HANPP)	–

Table 1. The thirteen main statistical models estimated with their names and the explanatory variables they contain. GDPc refers to Gross Domestic Product per capita, GDPa to Gross Domestic Product per area, HPD to Human Population Density, HANPP to Human Appropriation of Primary Productivity. Further details on these variables can be found in Table SM1.

Model name	Extinct species	Threatened species	Protected Areas	SEAL	iSEAL
Null	39.47	25.26	**0.00**	44.51	18.34
Economic.2000	18.51	26.24	6.75	17.45	**0.00**
Economic.1950	9.67	21.47	**4.51**	13.20	**2.17**
Economic.1900	**2.54**	16.81	**4.66**	23.26	8.84
Log Economic.2000	16.64	10.66	**5.29**	**0.00**	**4.87**
Log Economic.1950	7.82	6.91	**4.69**	**2.65**	6.07
Log Economic.1900	**0.98**	**4.92**	**4.55**	14.92	9.03
Kuznets.2000	51.70	34.38	**5.75**	48.00	20.62
Kuznets.1950	42.14	39.89	**4.07**	49.05	22.35
Kuznets.1900	17.44	29.48	6.54	43.84	23.31
Log Kuznets.2000	51.78	41.30	7.46	48.02	20.77
Log Kuznets.1950	37.60	42.44	**3.01**	48.35	21.91
Log Kuznets.1900	17.87	29.78	**3.72**	42.90	23.00
Area Kuznets.2000	19.52	12.87	9.39	22.76	8.65
Area Kuznets.1950	12.46	**5.45**	7.89	27.95	18.51
Area Kuznets.1900	**0.75**	**0.00**	13.64	26.13	19.83
Log Area Kuznets.2000	18.53	7.73	**4.71**	20.18	10.84
Log Area Kuznets.1950	7.90	**5.23**	**4.04**	19.21	15.77
Log Area Kuznets.1900	**0.00**	**2.51**	6.72	20.14	15.47

Table 2. Statistical comparison of the socio-economic main models considered at either 1900, 1950 and 2000 (rows) to predict different biodiversity indicators (columns). Difference in Leave-one-out Information Criterion (LOOIC) values with the LOOIC of the best model fitted for the different explanatory models (by column). The lower the LOOIC, the better the model. The best model is underlined and models with a LOOIC relatively close to the best model– i.e. within six units of the best model – are in bold (as suggested in Millar, 2009). Only the models pertaining to the same target variable (models in the same column) are comparable. See Tables 1 and SM1 for the content of the models. For the first three columns, the marginal version of the LOOIC is used.

Model name	Simpler models	Hierarchical models
Null	39.47	-
Economic.1900	2.54	-
Log Economic.1900	**0.98**	**-**
Area Kuznets.1900	**0.75**	**-**
Log Area Kuznets.1900	**0.00**	**--**
HPD.1900	9.04	20.66
Log HPD.1900	9.04	8.48
GDPa.1900	6.37	5.88
Log GDPa.1900	**-1.11**	**-4.15**
Log GDPa.1950	3.83	3.75
Log GDPa.2000	14.45	14.04
HANPP.1900	17.20	17.96
lHANPP.1900	7.06	3.48

Table 3. Statistical comparison of the ability of additional univariate explanatory models (rows) to predict the proportion of Extinct species, both with simple models (one effect shared by all taxonomic groups; first column) and hierarchical models (effect varying among taxonomic groups as a random effect; second column). The difference between Leave-one-out Information Criterion (LOOIC) of the model and the LOOIC of the best model in Table 2 for the proportion of Extinct species is indicated. The lower the LOOIC, the better the model. The best model is underlined and models with a LOOIC within six units of the best model – i.e. relatively close to the best model – are in bold. Models in both columns can be compared

since they pertain to the same target variable. See Tables 1 and SM1 for the content of the models.

Model name	Simpler models	Hierarchical models
Null	25.26	-
Economic.1900	16.81	-
Log Economic.1900	4.92	**-**
Area Kuznets.1900	**0.00**	**-**
Log Area Kuznets.1900	**2.51**	**-**
HPD.1900	8.76	9.90
Log HPD.1900	**-1.10**	**0.03**
GDPa.1900	17.74	19.10
Log GDPa.1900	<u>**-1.17**</u>	**0.08**
Log GDPa.1950	4.95	5.54
Log GDPa.2000	6.70	8.30
HANPP.1900	25.79	26.36
lHANPP.1900	19.57	20.68

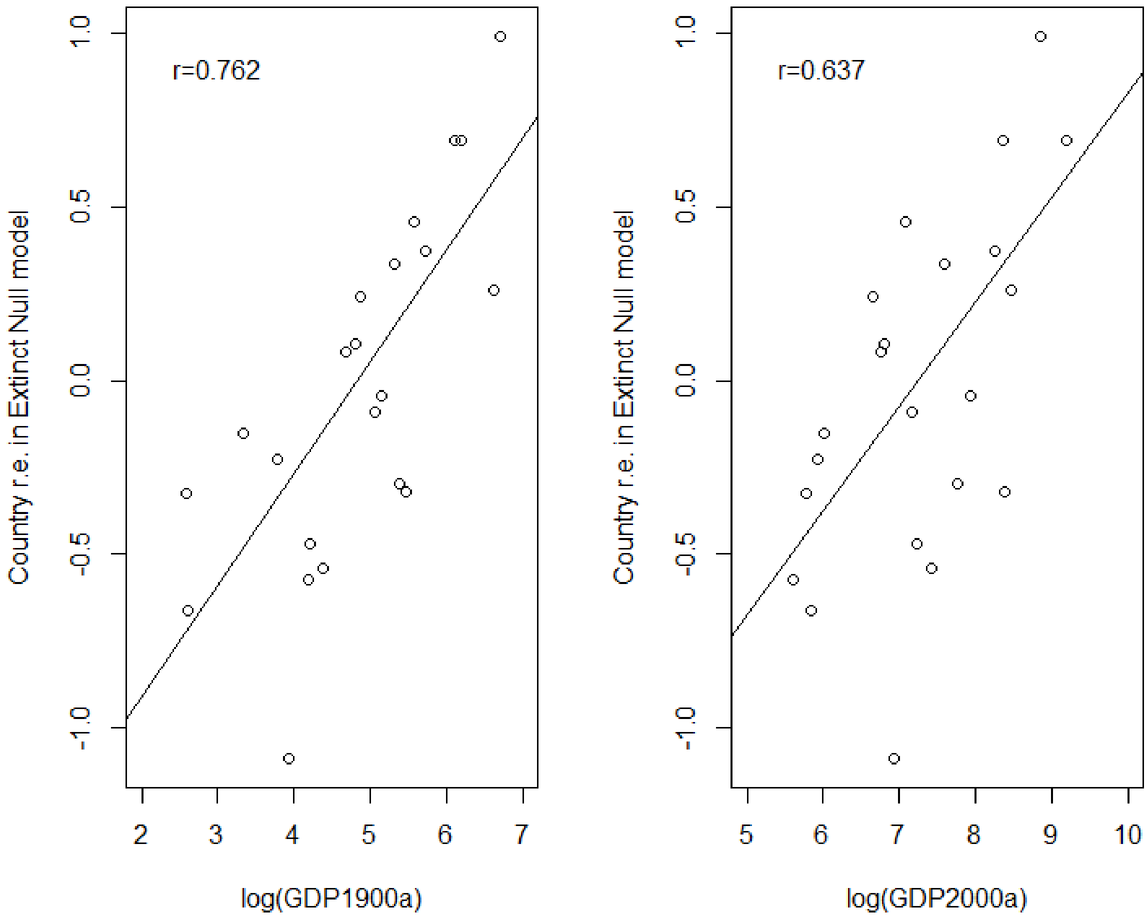
Table 4. Statistical comparison of the ability of additional univariate explanatory models (rows) to predict the proportion of Threatened species, both with simple models (one effect shared by all taxonomic groups; first column) and hierarchical models (effect varying among taxonomic groups as a random effect; second column). The difference between Leave-one-out Information Criterion (LOOIC) of the model and the LOOIC of the best model in Table 2 for the proportion of Threatened species is indicated. The lower the LOOIC, the better the model. The best model is underlined and models with an LOOIC within six units of the best model – i.e. relatively close to the best model – are in bold. Models in both columns can be compared

since they pertain to the same target variable. See Tables 1 and SM1 for the content of the models.

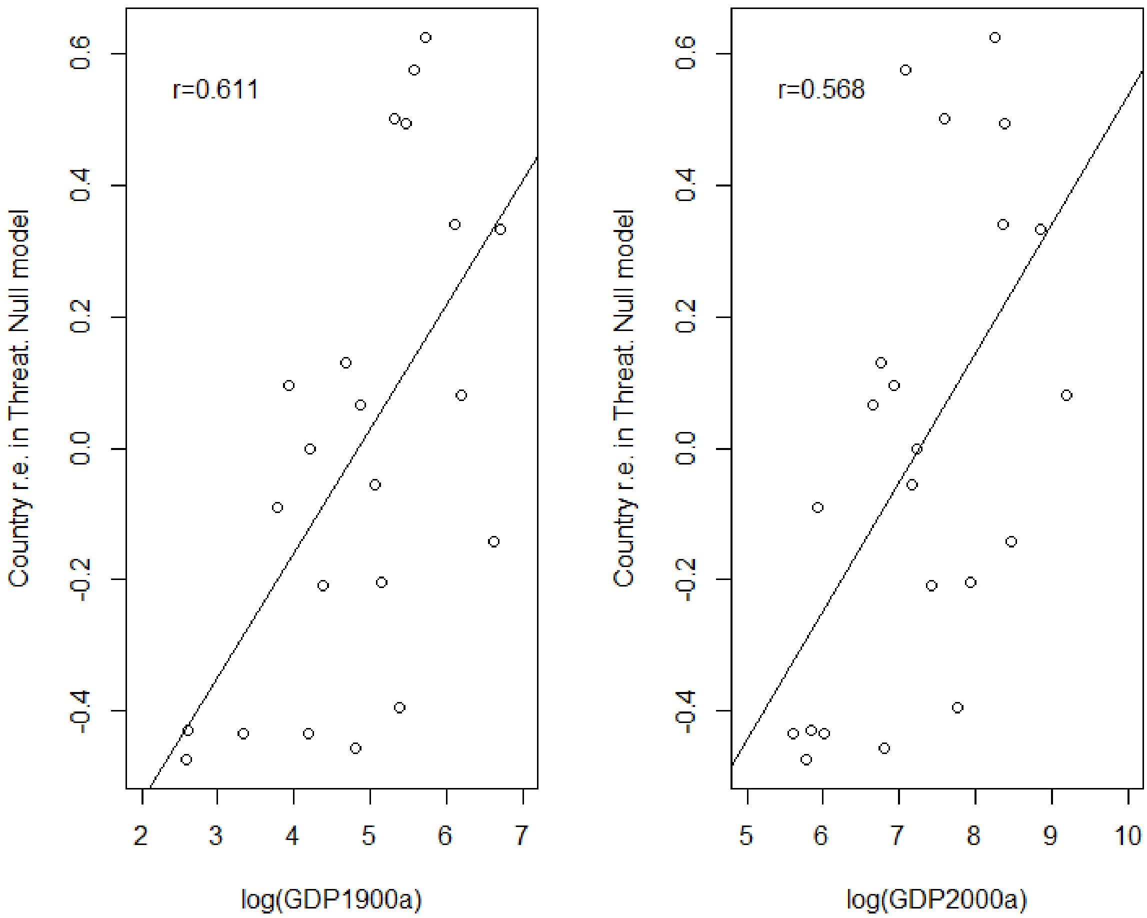
Variable name	Summary statistics of the estimator – mean (standard deviation)	p-value	Summary impact in log odds ratio of an increase of 1 standard deviation of the variable
Log GDPa.1900 for Extinct species	0.481 (0.096)	0.00003	0+
Log GDPa.1950 for Extinct species	0.467 (0.108)	0.00003	0+
Log GDPa.2000 for Extinct species	0.404 (0.121)	0.00145	0+
Log GDPa.1900 for Threatened species	0.234 (0.074)	0.00176	00+
Log GDPa.1950 for Threatened species	0.234 (0.087)	0.00441	00+
Log GDPa.2000 for Threatened species	0.238 (0.085)	0.00398	00+
Log HPD.2000 for SEAL	0.856 (0.08)	0.00005	0++
Log HPD.1950 for SEAL	0.846 (0.082)	0.00005	0++
Log HPD.1900 for SEAL	0.791 (0.107)	0.00005	0++
HPD.2000 for iSEAL	0.51 (0.107)	0.00002	++
HPD.1950 for iSEAL	0.227 (0.047)	0.00008	0+
HPD.1900 for iSEAL	0.255 (0.077)	0.0018	0+

Table 5. Analysis of the estimators of the best socio-economic variables at different dates for the four Biodiversity indicators that are sensitive to these variables. For magnitude analyses (last column), the results of the analyses of adding one standard variable of the best variate on odds ratios were conclusive if 95% of the odds ratio effects were in the interval $\left[-0.1;\ 0.1\right]$ (denoted as 000 and qualified as a strongly negligible effect), $\left[-0.5;\ 0.5\right]$ (denoted as 00 and qualified as a moderately negligible effect), $\left[-1;\ 1\right]$ (denoted as 0 and qualified as a weakly negligible effect), $[0.1;+\infty)$ (denoted as + and qualified as a weakly positive effect), $[0.5;+\infty)$ (denoted as ++ and qualified as a moderately positive effect), $[1;+\infty)$ (denoted as +++ and qualified as a strongly positive effect) (as in e.g. Daniels 1983). Estimators are given for the best univariate model (first) and then for the other models with the same variable but at different dates. GDPa refers to Gross Domestic Product per area, HPD to Human Population Density (log-transformed if an “l” is added at the beginning of the name of the variable). For Extinct species, the best model is the hierarchical model, from which we consider the mean effect across the nine taxonomic groups; estimators by Taxon are provided in Table SM4.

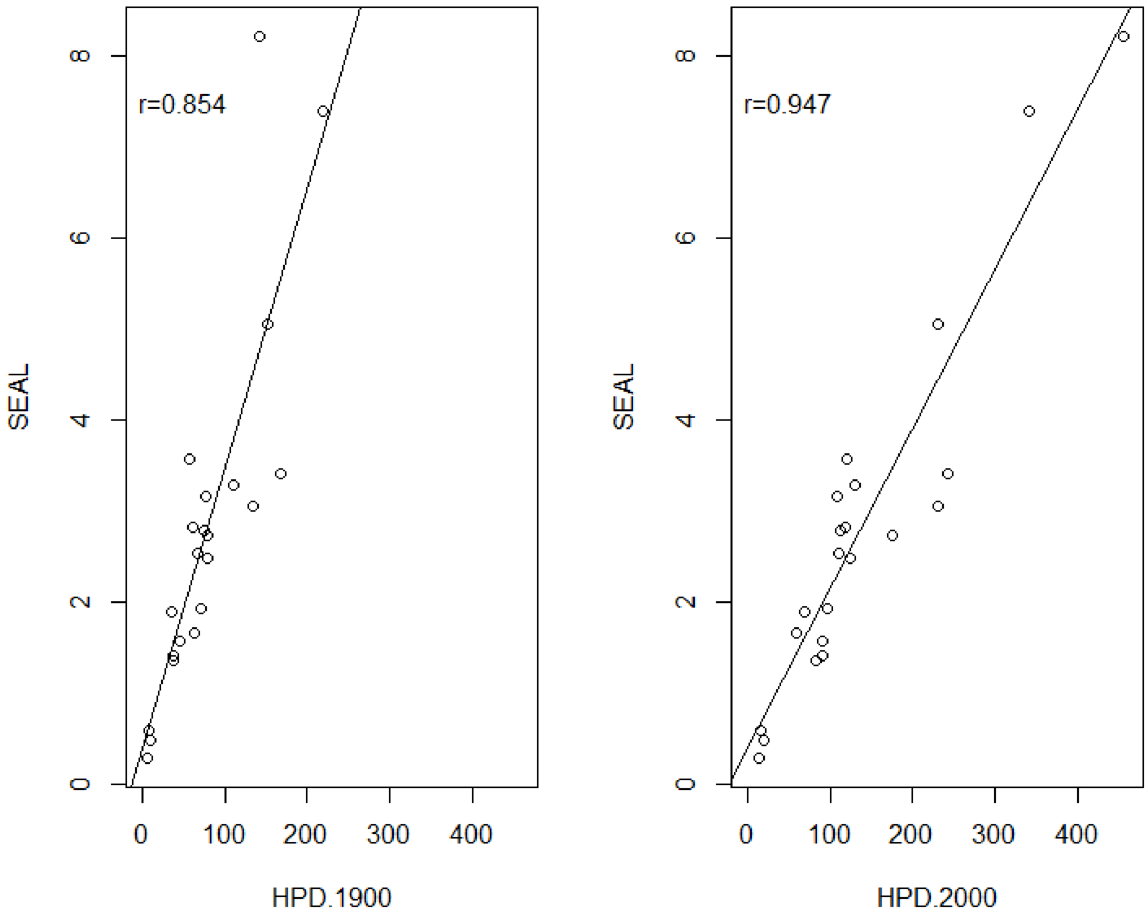
(a) Extinct species



(b) Threatened Species


r=0.611
Country r.e. in Threat. Null model
log(GDP1900a)
r=0.568
Country r.e. in Threat. Null model
log(GDP2000a)

(c) SEAL



(d) iSEAL

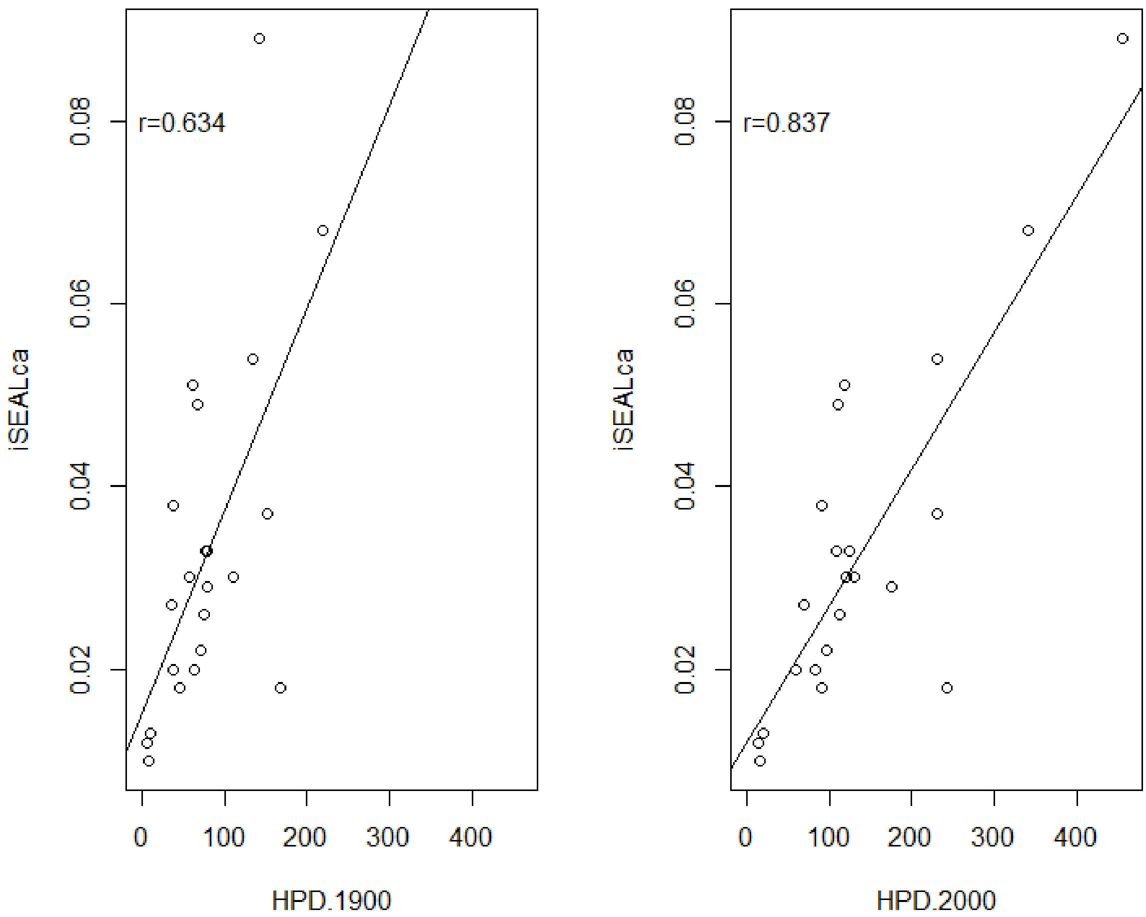


Figure 1. Graphical summary of the relationships between the best variable in 1900 (left) and in 2000 (right) and the four Biodiversity indicators showing relationships with socio-economic variables. For Extinct and Threatened species, because we have multiple observations (i.e. taxonomic groups) for each country, the numbers on the y-axis are the Mean estimates of the country random effect in the Null model. Inside each Figure, we indicate the Pearson correlation – denoted as r – between the two variables. GDPa refers to Gross Domestic Product per area, HPD to Human Population Density.

Supplementary material

Name of variable	Explanation, unit and source	Main model including the variable	Summary of variations of the variable
GDPc.2000	Gross Domestic Product per inhabitant in 2000 (unit: 100,000 International Geary–Khamis dollar)	Eco & Kuznets	Untransformed: 16.06 (± 6.63) [3.00; 24.36] Log: 2.65 (± 0.57) [1.10; 3.19]
GDPa.2000	Gross Domestic Product per 1 ha in 2000 (unit: 100,000 International Geary–Khamis dollar)	Kuznets	Untransformed: 2363.55 (± 2455.17) [273.18; 9802.31] Log: 7.27 (± 1.05) [5.61; 9.19]
GDPc.2000^2	Gross Domestic Product per inhabitant in 2000 (unit: 100,000 International Geary–Khamis dollar)	Eco & Kuznets	Untransformed: 299.87 (± 188.19) [9.01; 593.60] Log: 5.30 (± 1.15) [2.20; 6.39]
GDPa.2000^2	Gross Domestic Product per 1 ha in 2000 (unit: 100,000 International Geary–Khamis dollar)	Kuznets	Untransformed: 1.1e+07 (± 2.2e+07) [74628.41;

			9.6e+07] Log: 14.54 (± 2.11) [11.22; 18.38]
HPD.2000	Population density in 2000 (unit: inhabitants/ha)	Eco	Untransformed: 138.18 (± 106.34) [14; 454] Log: 4.62 (± 0.89) [2.64; 6.12]
HANPP.2000	Human Appropriation of Primary Productivity in 2000 (unit: %, with 100% corresponding to 1)	Eco	Untransformed: 0.43 (± 0.21) [0.058; 0.92] Log: -0.99 (± 0.59) [-2.85; -0.079]
GDPc.1950	Gross Domestic Product per inhabitant in 1950 (unit: 100,000 International Geary–Khamis dollar)	Eco & Kuznets	Untransformed: 4.25 (± 1.98) [1.65; 9.06] Log: 1.34 (± 0.47) [0.50; 2.20]
GDPa.1950	Gross Domestic Product per 1 ha in 1950 (unit: 100,000 International Geary–Khamis dollar)	Kuznets	Untransformed: 483.71 (± 502.35) [51.04; 1690.87] Log: 5.68 (± 1.04) [3.93; 7.43]
GDPc.1950^2	Gross Domestic Product per inhabitant in 1950	Eco & Kuznets	Untransformed: 21.83 (± 19.98)

	(unit: 100,000 International Geary–Khamis dollar)		[2.73; 82.16] Log: 2.69 (± 0.94) [1.00; 4.41]
GDPa.1950^2	Gross Domestic Product per 1 ha in 1950 (unit: 100,000 International Geary–Khamis dollar)	Kuznets	Untransformed: 474856.35 (± 837766.19) [2604.67; 2859048.12] Log: 11.36 (± 2.08) [7.87; 14.87]
HPD.1950	Population density in 1950 (unit: inhabitants/ha)	Eco	Untransformed: 104.59 (± 77.79) [10; 282] Log: 4.34 (± 0.90) [2.30; 5.64]
HANPP.1950	Human Appropriation of Primary Productivity in 1950 (unit: %, with 100% corresponding to 1)	Eco	Untransformed: 0.33 (± 0.18) [0.067; 0.73] Log: -1.24 (± 0.58) [-2.70; -0.31]
GDPc.1900	Gross Domestic Product per inhabitant in 1900 (unit: 100,000 International Geary–Khamis dollar)	Eco & Kuznets	Untransformed: 2.36 (± 0.94) [1.22; 4.49] Log: 0.79 (± 0.39) [0.20; 1.50]

GDPa.1900	Gross Domestic Product per 1 ha in 1900 (unit: 100,000 International Geary–Khamis dollar)	Kuznets	Untransformed: 217.81 (± 224.68) [13.34; 817.09] Log: 4.85 (± 1.15) [2.59; 6.71]
GDPc.1900^2	Gross Domestic Product per inhabitant in 1900 (unit: 100,000 International Geary–Khamis dollar)	Eco & Kuznets	Untransformed: 6.43 (± 5.05) [1.50; 20.18] Log: 1.57 (± 0.78) [0.40; 3.00]
GDPa.1900^2	Gross Domestic Product per 1 ha in 1900 (unit: 100,000 International Geary–Khamis dollar)	Kuznets	Untransformed: 95625.60 (± 180503.21) [178.06; 667634.43] Log: 9.70 (± 2.30) [5.18; 13.41]
HPD.1900	Population density in 1900 (unit: inhabitants/ha)	Eco	Untransformed: 79.05 (± 54.86) [7; 219] Log: 4.06 (± 0.92) [1.95; 5.39]
HANPP.1900	Human Appropriation of Primary Productivity in 1900 (unit: %, with 100% corresponding to 1)	Eco	Untransformed: 0.32 (± 0.17) [0.06; 0.76] Log: -1.29 (± 0.58) [-2.81; -

			0.28]

Table SM1. List of economic variables included in the statistical models (cf. Table 2). The summary of the variations for the variables include the mean (+/- the standard deviation) and in square brackets the minimum and maximum for the variable in the model for Extinct species (these summary statistics do not include the repetition of data when a single country is included repeatedly in the analysis). All the data come from [Dullinger, 2013 ^ny #120369] (2013).

Name of variable	Explanation, unit and source	Summary of variations of the variable
Extinct	Number of Extinct species for various taxonomic groups and countries (data from Essl et al. 2013)	Summary statistics for the proportion of Extinct species for each taxonomic group: Vascular Plants: 0.018 (± 0.018) [0.0016; 0.088] Bryophytes: 0.024 (± 0.02) [0.00; 0.056] Mammals: 0.035 (± 0.032) [0.00; 0.13] Birds: 0.031 (± 0.023) [0.00; 0.087] Freshwater Fishes: 0.056 (± 0.056) [0.00; 0.15] Reptiles: 0.015 (± 0.032) [0.00; 0.12] Amphibians: 0.0025 (± 0.012) [0.00; 0.056] Dragonflies: 0.035 (± 0.037) [0.00; 0.10] Grasshoppers: 0.051 (± 0.057) [0.00; 0.22]
Threatened	Number of Threatened species for various taxonomic groups and countries (data from Essl et al. 2013)	Summary statistics for the proportion of Threatened species (excluding Extinct species) for each taxonomic group: Vascular Plants: 0.22 (± 0.13) [0.065; 0.56] Bryophytes: 0.23 (± 0.097) [0.072; 0.37] Mammals: 0.23 (± 0.10) [0.10; 0.44] Birds: 0.29 (± 0.11) [0.15; 0.55] Freshwater Fishes: 0.33 (± 0.15) [0.093; 0.57] Reptiles: 0.39 (± 0.26) [0.00; 0.79] Amphibians: 0.34 (± 0.24) [0.00; 0.89] Dragonflies: 0.30 (± 0.17) [0.036; 0.57] Grasshoppers: 0.22 (± 0.11) [0.069; 0.40]
SEAL	Percent area of country considered as sealed in 2009	2.81 (± 1.98) [0.29; 8.22]

	(source: http://www.eea.europa.eu/data-and-maps/indicators/imperviousness-change/assessment)	
iSEAL	Annual percent increase in the country area that was sealed between 2006 and 2009 (source: http://www.eea.europa.eu/data-and-maps/indicators/imperviousness-change/assessment	0.033 (± 0.019) [0.01; 0.089]
PA1	Proportional area of country in IUCN Category 1	0.011 (± 0.025) [0.00; 0.086]
PA2	Proportional area of country in IUCN Category 2	0.024 (± 0.03) [0.00; 0.10]
PA3	Proportional area of country in IUCN Category 3	0.0021 (± 0.0062) [0.00; 0.029]
PA4	Proportional area of country in IUCN Category 4	0.031 (± 0.04) [0.00038; 0.16]

Table SM2. List of the biodiversity indicators used in this paper. The summary of the variations for the variables include the mean (+/- the standard deviation) and in square brackets the minimum and maximum for the variable.

Model name	SEAL	iSEAL
Null	44.51	18.34
Economic.2000	17.45	**0.00**
Log Economic.2000	**0.00**	**4.87**
Economic.1950	13.20	**2.17**
Log Economic.1950	**2.65**	6.07
GDPa.2000	24.30	**5.36**
Log GDPa.2000	18.54	8.46
HPD.2000	17.70	**0.75**
Log HPD.2000	**-2.21**	**2.54**
HPD.1950	11.76	**5.38**
Log HPD.1950	**0.07**	**5.53**
HANPP.2000	11.93	8.93
Log HANPP.2000	9.31	10.61

Table SM3. Statistical comparison of additional univariate models (rows) to predict the two pressure biodiversity indicators (columns). Difference between Leave-one-out Information Criterion (LOOIC) of the model and the LOOIC of the best model in Table 2 for the proportion of Sealed area in 2009 (SEAL) and the increase in that proportion between 2006 and 2009 (iSEAL) (columns). The lower the LOOIC, the better the model. The best model is underlined and models with an LOOIC within six units of the best model – i.e. relatively close to the best model – are in bold. Only the models pertaining to the same target variable (column heading) are comparable. See Tables 1 and SM1 for the content of the models.

Variable name	Taxon	Summary statistics of the estimator – mean (standard deviation)	p-value	Summary impact in log odds ratio of an increase of 1 standard deviation of the variable
Log GDPa.1900	Vascular Plants	0.356 (0.128)	0.00359	0+
Log GDPa.1900	Bryophytes	0.509 (0.161)	0.00061	0+
Log GDPa.1900	Mammals	0.516 (0.139)	0.00023	0+
Log GDPa.1900	Birds	0.292 (0.151)	0.0298	0
Log GDPa.1900	Fishes	0.544 (0.157)	0.00045	0+
Log GDPa.1900	Reptiles	0.299 (0.263)	0.12923	0
Log GDPa.1900	Amphibians	0.498 (0.297)	0.03758	
Log GDPa.1900	Dragonflies	0.623 (0.217)	0.00042	+
Log GDPa.1900	Grasshoppers	0.691 (0.232)	0.00008	+
Log GDPa.1950	Vascular Plants	0.391 (0.133)	0.0032	0+
Log GDPa.1950	Bryophytes	0.464 (0.159)	0.0032	0+
Log GDPa.1950	Mammals	0.488 (0.141)	0.00046	0+
Log GDPa.1950	Birds	0.336 (0.156)	0.02077	0
Log GDPa.1950	Fishes	0.536 (0.158)	0.00021	0+
Log GDPa.1950	Reptiles	0.314 (0.255)	0.10858	0
Log GDPa.1950	Amphibians	0.5 (0.268)	0.024	+
Log GDPa.1950	Dragonflies	0.585 (0.209)	0.00035	+
Log GDPa.1950	Grasshoppers	0.589 (0.203)	0.00049	+
Log GDPa.2000	Vascular Plants	0.272 (0.157)	0.04517	0

Log GDPa.2000	Bryophytes	0.446 (0.16)	0.00285	0+
Log GDPa.2000	Mammals	0.419 (0.147)	0.00285	0+
Log GDPa.2000	Birds	0.339 (0.155)	0.01933	0
Log GDPa.2000	Fishes	0.448 (0.157)	0.00224	0+
Log GDPa.2000	Reptiles	0.317 (0.213)	0.07399	0
Log GDPa.2000	Amphibians	0.418 (0.234)	0.0305	0
Log GDPa.2000	Dragonflies	0.491 (0.199)	0.00299	0+
Log GDPa.2000	Grasshoppers	0.483 (0.192)	0.00358	0+

Table SM4. Analysis of the estimators of the best socio-economic variables at different dates for the proportion of Extinct species, by taxonomic group. For magnitude analyses (last column), the results of the analyses of adding one standard variable of the best variate on odds ratios were conclusive if 95% of the odds ratio effects were in the interval $[-0.1;\ 0.1]$ (denoted as 000 and qualified as a strongly negligible effect), $[-0.5;\ 0.5]$ (denoted as 00 and qualified as a moderately negligible effect), $[-1;\ 1]$ (denoted as 0 and qualified as a weakly negligible effect), $[0.1;+\infty)$ (denoted as + and qualified as a weakly positive effect), $[0.5;+\infty)$ (denoted as ++ and qualified as a moderately positive effect), $[1;+\infty)$ (denoted as +++ and qualified as a strongly positive effect) (as in e.g. Daniels 1983). The best model was the hierarchical model at date 1900. For each taxonomic group, estimated tend to decrease with date, except for Birds and Reptiles, for which they tend to increase with date, and vascular plants and amphibians, for which 1900 and 1950 estimators were very close and greater than 2000 estimator.

Model name	Extinct species	Threatened species
Null	22.83	17.53
Log Economic.2000	0.0	2.93
Log Kuznets.2000a	1.89	**0.0**
HPD2000l	-1.68	**<u>-4.65</u>**
Log GDPa.2000	-2.21	**-1.03**
Log SEAL	**<u>-10.67</u>**	**-0.28**

Table SM5. Statistical comparison of additional univariate models in 2000 (rows) to predict the two state biodiversity indicators (columns). Difference in Leave-one-out Information Criterion (LOOIC) values with the LOOIC of the best model with current values of socio-economic variables in Table 2, for additional univariate models involving only current values of variables for the proportion of Extinct and Threatened species. The lower the LOOIC, the better the model. The best model is underlined and models with an LOOIC within six units of the best model – i.e. relatively close to the best model – are in bold. Only the models pertaining to the same target variable (column heading) are comparable. It should be noted that for extinct species, the best present model was the bivariate model involving untransformed SEAL and iSEAL (Difference in LOOIC of -14.18). See Tables 1 and SM1 for the content of the models.

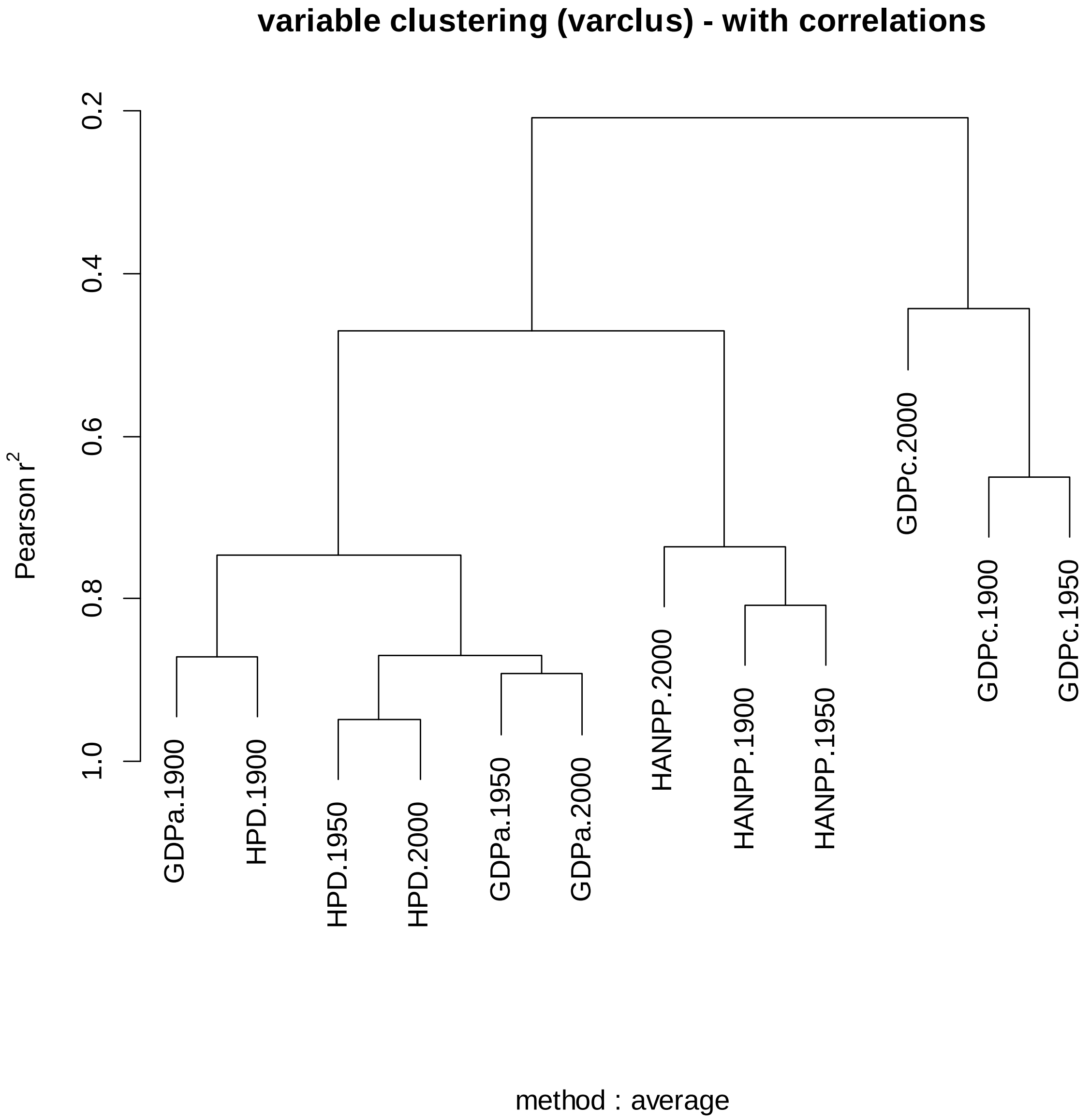


Figure SM1. Variable clustering for the explanatory variables used in the paper. The correlation metric was the Pearson correlation and the method used to summarize multiple correlations was the average method. Variables linked at a value close to one are on average closely correlated while variables linked at a value close to zero have a low level of correlation.