On the time lag between human activity and biodiversity in Europe at the national scale

Frédéric Gosselin, Jean-Marc Callois

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3 Frédéric Gosselin[1] and Jean-Marc Callois[2]

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5 [1]INRAE, UR EFNO, Domaine des Barres, F-45290 Nogent-Sur-Vernisson, France.

6 Corrsponding author. ORCID Number : 0000-0003-3737-106X. Mail:

7 frederic.gosselin@inrae.fr.

8 [2] ORCID number : 0000-0002-3358-5725. Mail: jm.callois@gmail.com.

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13 **Abstract**

14 The relation between the environment and human activity has been the subject of many

15 empirical studies. Complexities such as which indicators related to human activity best

16 represent biodiversity, or time lags between socio-economic activities and biodiversity,

17 remain unclear. This paper tackles these issues based on statistical analysis of the relationship

18 between human activity and biodiversity at the country level in Europe. We used well-adapted

19 statistical models to explain variations in two state indicators, two pressure indicators, and one

20 response indicator representing biodiversity. We focused on (i) the relative efficiency of the

21 various indicators of human activity (notably human population density, human appropriation

22 of net primary productivity, and gross domestic product per area) in predicting the

23 biodiversity indicators, and (ii) possible time lags between metrics representing human

24 activity and biodiversity. Results indicate that gross domestic product per area and human

25 population density best predict the indicators for the biodiversity state, whereas human

26 population density best predicts the indicators of biodiversity pressure. Although the

27 indicators for biodiversity pressure best related to present-day human activity metrics,

28 biodiversity state reveals a time lag of approximately one century. Results suggest that drivers

29 (human population density, density of economic activity) and pressures (land sealing) should

30 serve as primary foci for biodiversity policies. Because of the long time lags (~ one century)

31 between these drivers and the state of biodiversity, policies regarding biodiversity should

32 integrate a long-term view.

33 **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

59 more readily available at this scale—for example, proportion of threatened and extinct species

60 and gross domestic product. Additionally, the national scale is still the most relevant for many

61 policies concerning biodiversity and socio-economic issues. More precisely, we addressed the

62 following questions:

63   (i)   What are the kinetics of the impact of human activity on biodiversity? Following

64   Dullinger et al. (2013), in hypothesizing time-lag effects between indicators of

65   human activity and those of biodiversity, we posited that past values of socio-

66   economic variables would better explain current variations in biodiversity state

67   indicators .

68   (ii)   Which models involving indicators of human activity best explain the values of

69   biodiversity indicators? We hypothesized that simpler, un-transformed or merely

70   log-transformed, models would be at least as efficient as more complex socio-

71   economic models.

72   (iii)   What variables representing human activity best explain the variations in the

73   biodiversity indicators—for example, those depending on their proximal link with

74   biodiversity or more general variables of human activity? We hypothesized that

75   the human appropriation of net primary production or the proportion of sealed

76   area, which are potentially more directly related to biodiversity, would better

77   explain the variations of biodiversity indicators than, for example, human

78   population density, especially for the indicators of biodiversity state.

79 The literature relating the state of biodiversity to socio-economic drivers and pressures is now

80 well developed. Findings indicate that drivers such as Gross Domestic Product (GDP) per

81 capita (GDPc; Clausen and York, 2008), human population density (HPD; Brown and

82 Laband, 2006; McKee et al., 2013; Driscoll et al., 2018), the spread of transportation

83   infrastructure (Konvicka et al., 2006) or income inequality (Mikkelson et al., 2007; Holland et

84   al., 2009) correlate with various measures of biodiversity.

85   Focusing on the link between human population density (HPD) and biodiversity, Luck (2007)

86   reviewed the published empirical literature through a meta-analysis. The author concluded

87   that, despite the geographic and taxonomic skew in the published literature, a positive

88   correlation is apparent between HPD and various biodiversity metrics – mainly related to

89   species richness. That is, the level of biodiversity is greater in densely populated zones. This

90   correlation, however, may be due to the relation between HPD and these biodiversity metrics

91   on the one hand, and other parameters such as ecosystem productivity or energy availability

92   on the other. Some evidence was also apparent of negative relationships between HPD and

93   other biodiversity metrics related to species extinction, but it was weak (Luck, 2007).

94

95   In analyzing how three variables related to economic growth (GDPc, HPD and a metric

96   related to land use intensity—human appropriation of net primary productivity (HANPP)) are

97   related to the proportion of threatened species in European countries, Dullinger et al. (2013)

98   proposed an explanation for the weak evidence reported by Luck (2007). That is, the

99   relationship between current economic and biodiversity variables could be weak because the

100   metrics of biodiversity respond to economic variables with a time lag. Dullinger et al. (2013)

101   proposed that the relationship would become much stronger if the metrics of biodiversity were

102   related to past economic variables. This proposal echoes the well-known notion of extinction

103   debt in ecology (Tilman et al., 1994; Kuussaari et al., 2009), as well as the pioneer ecological

104   studies that identified time lags in the relationship between habitat quantity and configuration

105   and biodiversity (Chamberlain et al., 2000 ; Lindborg and Eriksson, 2004 ; Menéndez et al.,

106   2006 ; Metzger et al., 2009). Most of the latter studies were centered on habitat. Yet, the

107   drivers of variations in past habitat could have even greater time lags for affecting

108 biodiversity (Essl et al., 2015), since the time lags between the initial driver and the habitat

109 pressure should add up to the time lags between habitat and biodiversity.

110 Even though this reasoning provided a new line of analysis, Gosselin (2015) questioned this

111 conclusion on the basis of inadequate statistical tools. When more accurate statistical tools

112 were used to take into account data pseudo-replication and over-dispersion, the significant

113 relationships mostly disappeared, or at least became much less significant. Gosselin and

114 Callois (2018) analyzed the data of Dullinger et al. (2013) together with data on extinct

115 species, biodiversity pressure indicators (land sealing) and response indicators (the proportion

116 of protected areas) in Europe and related them to diverse socio-economic drivers. They found

117 a positive impact on the proportion of threatened and extinct species due to the density of

118 "human activity" (either measured as human population density or as the gross domestic

119 product per unit area of land, GDPa, and especially their logarithm transforms). These results

120 were based on relationships between current socio-economic variables and current

121 biodiversity indicators. Yet, one of the biodiversity indicators used in this study represented

122 past events (the proportion of extinct species), and two indicators related to the accumulation

123 of past decisions (proportion of sealed area and proportion of reserves). Also, for a fourth

124 indicator (proportion of threatened species), past values of socio-economic variables likely

125 predict states of biodiversity better than current values due to time lag effects (cf. supra).

126 Identifying these time lags is a pressing question, according to the International Science-

127 Policy Platform on Biodiversity and Ecosystem Services (e.g. IPBES, 2018). Furthermore,

128 Gosselin and Callois (2018) did not incorporate human appropriation of net primary

129 production (HANPP), another metric used by Dullinger et al. (2013). Yet, this metric is an

130 integrated socio-ecological indicator of land-use intensity (Haberl et al., 2013), which is

131 closely related to population density (Krausmann et al., 2009). As such, HANPP has potential

132 to more proximally explain the impact of human activity on biodiversity, and may therefore

133   better explain its variations (Haberl, 1997; Haberl et al., 2004; Vačkář et al., 2016). Finally,

134   Gosselin and Callois (2018) did not include simpler models with the two core human activity

135   variables (HPD and GDPa), which might better explain variations in biodiversity indicators

136   than more complicated models.

137

Material and methods

139   **Biodiversity indicators**

140   This study sought to relate relevant indicators of biodiversity throughout Europe to economic

141   variables at various dates. We chose indicators that fit the Driving forces, Pressure, State,

142   Impact, Response (DPSIR) framework, in line with Butchart et al. (2010). Even though we

143   did not estimate the DPSIR framework explicitly, we chose five biodiversity indicators

144   positioned in the DPSIR diagram (http://www.eea.europa.eu/publications/TEC25), for which

145   data are readily available at national level, as follows (cf. Table SM2 for summary statistics):

146   i.   Two Pressure indicators related to land sealing: percent of surface area in the country

147   sealed in 2009 (denoted as SEAL) and annual increase in sealing between 2006 and

148   2009 expressed as a percentage (denoted as iSEAL);

149   ii.   Two indicators of the State and dynamics of Biodiversity: the proportion of extinct

150   and of threatened species in each country for nine different taxonomic groups

151   (vascular plants, bryophytes, mammals, birds, freshwater fishes, reptiles, amphibians,

152   dragonflies and grasshoppers);

153   iii. One Response indicator, referring here to societal response (as defined in the DPSIR

154   framework): the percentage of terrestrial area in each country corresponding to

155   protected areas (combining four different types of protected areas as defined by the

156   International Union for Conservation of Nature).

157 Data for this study came from the European Environmental Agency (two Pressure indicators),

158 Eurostat (Response indicator) and Essl et al. (2013) (two State indicators). We did not

159 consider trees as a separate taxonomic group because, at least for some countries, trees were

160 incorporated into evaluations of vascular plants. Our analyses therefore already accounted for

161 them in the vascular plant taxonomic group.

162 **Socio-economic variables**

163 We considered the economic variables in the study as potential drivers of the five Pressure-

164 State-Response (PSR) indicators described above. This approach agrees with the notion of

165 indirect drivers defined by the IPBES (https://www.ipbes.net/models-drivers-biodiversity-

166 ecosystem-change). We focused attention on two classical indicators of human activity: gross

167 domestic product (GDP) and human population density (HPD). We tested GDP per area

168 (GDPa) as well as GDP per capita (GDPc) because Gosselin and Callois (2018) found that the

169 density of economic activity (GDPa) had a stronger relationship with biodiversity indicators

170 than economic development per capita (GDPc). We also included the variable built by

171 Dullinger et al. (2013) to estimate human land use intensity: human appropriation of net

172 primary production (HANPP), which is another measure of the spatial density of human

173 activity likely closest to the indicators for PSR biodiversity. Table SM1 provides the list of

174 socio-economic variables from years 1900, 1950 and 2000, found in Dullinger et al. (2013).

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176 This study considered a list of 22 countries. These countries are the same as those in Dullinger

177 et al. (2013): Austria, Belgium, Bulgaria, the Czech Republic, Denmark, Finland, France,

178 Germany, Greece, Hungary, Italy, the Netherlands, Norway, Poland, Portugal, the Republic of

179 Ireland, Romania, Slovakia, Spain, Sweden, Switzerland and the United Kingdom.

Statistical models and hypotheses

180

181   Following Brown and Laband (2006) and Gosselin and Callois (2018), the strategy in

182 this study was based on the estimation and comparison of several simple statistical models.

183 We did not mix different metrics into a single, global metric, nor did we estimate a single

184 statistical, multiple regression model that would have included all the variables. We thus

185 avoided technical and interpretative problems of correlations between variables. We followed

186 a three-step strategy to identify the best socio-economic variables in terms of predictive power

187 and analyze their relationships with biodiversity indicators.

188   First, we addressed the first hypothesis by estimating and comparing the first seven

189 models described in Table 1 (*Null*, *Economic*, *Log Economic*, *Kuznets*, *Log Kuznets*, *Area*

190 *Kuznets* and *Log Area Kuznets*) among the three different periods (1900, 1950 and 2000). The

191 2000 versions of these models are very close to the corresponding models in Gosselin and

192 Callois (2018). These models were among the best for which historic data were available.

193 *Economic* refers to models including both GDPc and HPD, two of the main indirect drivers of

194 change according to the IPBES (2019). The *Kuznets* models included different versions of

195 GDP, as well as its square, to account for quadratic relationships with GDP and to allow for

196 possible bell-shaped relationships with GDP, a shape known as the Environmental Kuznets

197 Curve (Selden and Song, 1994). Except for the null model, each model incorporated two

198 socio-economic variables related to a specific theme. We chose to limit the number of

199 variables in the models since we only had a limited number of countries in the data set (22

200 countries) for this study. Therefore, we included at most two socio-economic variables per

201 model, following the n/10 guideline of Harrell (2001, p. 61) on the relationship between

202 sample size n and number of estimated hyperparameters. The resulting models were slightly

203 over-parametrized for state indicators (with 21 hyper-parameters estimated compared to a

204 maximum of 19.8 according to Harrell's rule). They were somewhat more over-parametrized

205 for response indicators (12 hyper-parameters compared to a maximum of 8.8 according to

206 Harrell's rule), and much more overparametrized for pressure indicators (5 hyperparameters

207 compared to 2.2 according to Harrell's rule). Our general hypotheses were that explanatory

208 models with 1900 or 1950 data would better explain the Proportion of Extinct species, the

209 Proportion of Sealed areas and the Proportion of Threatened species, since we expected a

210 rather strong time lag for the effects on Biodiversity, similar to the reasoning in Dullinger et

211 al. (2013).

212   In the second step, we compared the best model for each indicator from the first step

213 with simplified univariate explanatory models, *HPD*, *Log HPD*, *GDPa* and *Log GDPa,* for

214 1900, 1950 and 2000 data. This procedure determined, first, whether the relationships could

215 be reduced to such simple univariate models, and second, included less over-parametrized

216 models. We also considered *HANP*P and *Log HANPP* models at the different time periods (cf.

217 Table 1). We expected these two last models to reveal more proximal causes of variations in

218 the indicators, especially for the two State Indicators. For these two indicators, we also

219 included hierarchical versions of the univariate explanatory models described above. We then

220 added a taxonomic random effect on the slope, thus estimating the mean slope across

221 taxonomic groups as well as the standard variation across taxonomic groups of this slope.

222 This procedure yielded models with a number of parameters similar to the models in the first

223 step. This process allowed the relationship to vary across taxonomic groups instead of being

224 fixed to a mean response as in the previous models.

225   In the final step related to the third hypothesis, and only for the two State indicators of

226 biodiversity, we compared the best model involving present explanatory variables from the

227 first two steps with a model including the current proportion of sealed area (SEAL). This

228 procedure determined whether SEAL could serve as a more proximal indicator of the current

229 biodiversity state.

230   Figure SM1 in the Supplementary Materials section (see also Supplementary Materials

231   in Dullinger et al., 2013 for associated graphics) displays the correlations between

232   explanatory variables. We found mildly strong correlations among the group of GDPc

233   variables at different dates, and stronger correlations among HANPP variables and among the

234   group formed by GDPa and HPD variables. The latter two groups had squared Pearson

235   correlations of at least 0.7. These correlations prevented us from formulating models

236   including both GDPa and HPD, or the same variable at different dates.

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238

239   **Statistical methods**

240   We paid careful attention to the potential over-dispersion of data as well as to the inclusion of

241   random country effects, following Gosselin (2015). We therefore introduced a random

242   country effect into the models involving repeated values per country. We assumed this effect

243   to follow a Gaussian distribution with a zero mean and an estimated standard deviation, This

244   approach allowed inclusion of indeterminacy between country-level explanatory variables and

245   other, unknown, country-level determinants. We used this random country effect, for

246   example, for the two State indicators, which provided proportions of Extinct and Threatened

247   species for different taxonomic groups within each country. For the proportion of extinct or

248   threatened species, we used a logit link function and a beta-binomial distribution to model the

249   number of extinct and threatened species as a proportion of the number of native species and

250   native minus extinct species, respectively. Each taxonomic group had separate estimated

251   intercept and extra-binomial variation fixed parameters. For the proportion of protected areas

252   and the percentage of sealed area and its increment, we used the zero-inflated beta

253   distribution. This distribution is a direct sub-product of the zero-inflated cumulative beta

254   distribution, proposed to analyze plant cover class data (Herpigny and Gosselin, 2015). For

255 sealed areas, we fitted a separate model for area and increment (SEAL and iSEAL) and

256 therefore did not include a random country effect in the corresponding models. We framed the

257 models within a Bayesian setting. For the proportion of protected areas, each category of

258 protected area had separate estimated intercept and variance fixed parameters, but the

259 parameter for zero inflation was the same for the different categories.

260 We used the Stan program embedded in R 3.3.2 through the rstan library (Stan Development

261 Team 2015) to estimate the models described above. The priors of the hyper-parameters were

262 mostly non-informative, except for the proportion of extinct species that required an upper

263 bound at $\exp(10)$ for dispersion levels in order to obtain converging results. All the

264 explanatory variables were centered and scaled to ensure a residual standard deviation of the

265 variable around one while keeping clear control over the level of scaling.

266 The models were compared in terms of predictive capacity with the leave-one-out

267 Information Criterion (LOOIC; Vehtari et al., 2016). For State and Response indicators, we

268 used the marginal version of the LOOIC (Gosselin and Callois, 2018, 2019).

269 We investigated the estimators of the socio-economic parameters with an eye toward

270 the statistical significance and magnitude of the relationships. For statistical significance, we

271 used Bayesian quantiles based on beta random draws (Gosselin, 2011). This paper includes

272 only those cases with a p-value below 5%. To judge the magnitude of Odds-ratios, we

273 analyzed the effect of an increase of one standard deviation at the linear combination level (on

274 the log of odds ratios) for each socio-economic variable, according to guidelines adapted from

275 Daniels et al. (1983) (see Table 5 legend for more details). These ratios are adapted to the

276 framework for magnitude analysis proposed in ecology (e.g., Camp et al., 2008; Barbier et al.,

277 2009).

278 Finally, to gauge the adequacy of the statistical models in relation to the data, we used

279 sampled posterior goodness-of-fit p-values (Gosselin, 2011). These values are based on

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280   normalized quantile residuals (Dunn and Smyth, 1996), with discrepancy functions similar to

281   Herpigny and Gosselin (2015) and Godeau et al. (2020). We first diagnosed the distributions

282   of the residuals or the random effects by using their mean, variance, skewness and kurtosis as

283   discrepancy functions. Then, to diagnose potentially ill-modelled relationships for the mean or

284   variance, we used discrepancy functions based on correlations with Hoeffding's D statistic

285   (Harrell, 2001). These functions determined the links between (i) the residuals and the fitted

286   values, (ii) the residuals and each of the explanatory variables, and (iii) the square of the

287   residuals and the fitted values. Hoeffding's D statistic can detect correlations that include

288   linear and non-linear relationships, and increasing or decreasing as well as non-increasing and

289   non-decreasing relationships. Finally, we used two discrepancy functions to diagnose any

290   spatial autocorrelation of country random effects (if they were included in the model) or

291   residuals (if random effects were not included). We fitted a generalized least squares (gls)

292   model with an exponentially decaying spatial autocorrelation (Pinheiro and Bates, 2000)on

293   country random effects or residuals (functions corExp and gls in the nlme library with a

294   nugget), then considered the range and nugget of the gls model as the two final discrepancy

295   functions. These p-values allowed, in sum, diagnosis of the adequacy of the probability

296   distributions used, the adequate specification of the non-linear relationship between

297   explanatory variables and data, the correct specification of variance, the absence of additional

298   spatial autocorrelation and, in cases where the model included country random effects, the

299   adequacy of the probability distribution of the random effect. Given usage of around ten

300   discrepancy functions per model, we only investigated cases with p-values below 0.005.

301   These p-values were applied to the best model associated with each biodiversity variable.

302   **Results**

303   Overall, with Proportion of Protected Areas as a dependent variable, none of the main

304   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

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330   proportion of Extinct species, and was close to the best models for the proportion of

331   Threatened species (Table SM5).

332   Graphical representations of the relationships also indicated a better link with 1900

333   than 2000 economic variables for Extinct and Threatened species and the reverse for SEAL

334   and iSEAL (Figure 1). Considering the associated estimators (Table 5), results were overall

335   less obvious with only slight differences either in estimator significance (p-value) or in the

336   mean estimated effect of adding 1 standard deviation to the variable (first column). The only

337   strong difference in terms of magnitude was with iSEAL. The models fitted the study data

338   adequately since we did not detect any discrepancy between the data and the best models at a

339   significance level fixed at p<0.005.

340   **Discussion**

341   The finding of no relationship between socio-economic variables with the Response

342   indicator (i.e. the proportion of protected areas in European countries; Table 2) contrasts with

343   previous literature. In a summary of results, Luck (2007) reported a negative relationship

344   between human population density (HPD) and protected areas. The metrics considered for

345   protected areas, however, varied from area proportion to absolute area, which was not the case

346   in the present study, as only area proportion was used. The absence of a statistical relationship

347   may be the outcome of conflicting mechanisms. On the one hand, economic activity and

348   population density raise pressures for land sealing .On the other hand, they may also trigger

349   social demand for protected areas as a reaction to the consequences of land sealing.

350   Second, the importance of 2000 economic drivers in explaining the Pressure indicators

351   (Tables 2 and 5) suggests their closer relationship to the current level of human population

352   density or activity than to those in 1900. This finding was contrary to our expectations for

353   SEAL, which we expected would integrate the cumulative effects of land sealing over many

354 generations and therefore more relevant to economic variables representing the past. Yet, the

355 study of urbanization during the 20th century shows that the link between human activity and

356 land encroachment operates quite quickly. For example, in post-World War II industrial

357 countries, land use changed radically within a time span of a few decades., Colsaet et al.

358 (2018) reported that the most indisputable causal factors were income and population growth.

359 This is consistent with our results (Tables 3, 5 and SM3), which show the foremost

360 contribution of current population density on land sealing indicators.

361   The better explanatory power of the 1900 socio-economic variables and particularly

362 the Kuznets-like models for the current proportion of extinct species should not come as a

363 surprise. Current extinctions reflect past events – although on a relatively unknown time scale

364 –, which themselves are related to past pressures. We therefore expected close relationships

365 between the proportion of extinctions and socio-economic values in 1900 or 1950. It was a

366 priori unclear, however, whether 1900 or 1950 variables would serve as better predictors. The

367 results, with 1900 models clearly having better predictive capacity than 1950 models (Table

368 2), suggest, apparently for the first time, that the causes of current extinction levels are rooted

369 further in the past. The results echo those of Konvicka et al. (2006), however, who found a

370 correlation between butterfly extinctions and railway densities that was interpretable as an

371 indicator of early industrialization.

372   The similar trends for the proportion of threatened species—i.e. models involving

373 1900 values of socio-economic variables better predicted the current proportion of threatened

374 species than those involving 2000 values—were more surprising. These results follow the

375 global message of Dullinger et al. (2013), but for more adequate statistical models and

376 different variables (gross domestic product per capita (GDPc) and gross domestic product per

377 area (GDPa) in Dullinger at al., 2013 and this study, respectively). We therefore confirm the

378 trend for a long-term effect of socio-economic development on the state of biodiversity, and a

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379   time lag in the relationship. Results from this study, however, do not allow precise estimate of

380   the length of this time lag nor explanations for this phenomenon, although the time lag is

381   apparently shorter for Threatened than for Extinct species. These empirical results are in line

382   with the concept of extinction debt proposed by Tilman et al. (1994), substantiated by e.g.

383   Vellend et al. (2006) and reviewed by Kuussaari et al. (2009). Findings of macro-level

384   relationships in this study suggest that the relationship between economic drivers and

385   biodiversity erosion may reflect such extinction debt.

386   Results of this study also confirm Gosselin and Callois (2018), in that the two State

387   indicators of biodiversity are mostly related with models that include either Human

388   Population Densities (HPD) or Gross Domestic Product per area (GDPa) (Table 3).. The

389   results also confirm the conclusions of Gosselin and Callois (2018)on the interest of these

390   metrics as biodiversity-driver indicators, though with a logarithm transformation and a time

391   lag of approximately one century. The results are also consistent with previous findings where

392   HPD was significantly associated to the proportion of Threatened or Extinct species or related

393   quantities (Hoffmann, 2004, McPherson and Nieswiadomy, 2005, Luck, 2007 and, to some

394   extent, Pandit and Laband, 2007 and McKee et al., 2013). They also echo McKee and

395   Chambers (2011) on the identification of GDPa rather than mere GDP as a robust variable

396   significantly related with the number of Threatened species. These previous studies, however,

397   did not use HPD or GDPa in 1900 but rather more recent values of HPD or GDPa. In terms of

398   magnitude, starting with proportions of extinct species and threatened species of 3.00% and

399   30.0% respectively, doubling GDPa in 1900 in the study models would increase these

400   proportions to 4.15% ($\pm$0.26%) and 33.5% ($\pm$1.1%), respectively (based on estimates in Table

401   5). We therefore consider these effects very significant and of intermediate strength.

402   These results lead to a main conclusion that Log GDPa in 1900 is an accurate driver

403   indicator for the two State indicators, and Log HPD in 2000 for the two Pressure indicators.

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404   Additionally, SEAL could represent a relevant present pressure indicator for the two State

405   indicators, since it provided relationships with either equivalent (for Threatened species) or

406   better (for Extinct species) predictive quality than the other socio-economic variables in 2000

407   (Table SM5). This conclusion is consistent with the considerable body of work on the impact

408   of land encroachment and urbanization on biodiversity. Louwagie et al. (2017) showed how

409   the process of land sealing reduces biodiversity at different levels. Given our previous results,

410   we conjecture that past land sealing might be an even better Pressure indicator than past

411   GDPa for current proportions of Extinct and Threatened species. This conjecture also agrees

412   with Konvicka et al. (2006), who reported that the density of railway lines was the best socio-

413   economic predictor of past butterfly extinctions in European states. In contrast, the density of

414   highways was not as strongly and consistently related to past butterfly extinctions. The

415   authors interpret this result as an indication that "butterfly losses are attributable to persistent

416   patterns of economic history rather than to the recent situation"

417   Generalizing the results of this study to broader indicators of biodiversity yields

418   conclusions even more pessimistic than previously reported at global levels (e.g., Butchart et

419   al., 2010; Tittensor et al., 2014). Since the processes that reflect in the Pressure indicators

420   (and Driver indicators in our case) are still continuing to increase, and given the time-lag

421   between these processes and the State of biodiversity, one should not expect the State

422   indicators to improve before many decades, if the relationships remain unchanged. This

423   analysis using indicators reveals that biodiversity, like climate change, apparently has a strong

424   temporal inertia in its interactions with its drivers, which highlights the urgent need for

425   protective measures.

426   Patterns of biodiversity loss are obviously more complex than reflected in the simple

427   statistical models used in this paper. Yet, based on goodness-of-fit p-values, the lack of

428   departures from the data indicates that the models are not too simple for the data at hand. In

429   fact, they might be too complex, especially for the two pressure indicators, as revealed by the

430   analyses of the number of parameters estimated relative to the amount of data used (see

431   Statistical Models and Hypotheses section). The results for the two pressure indicators should

432   be taken with care, as they may stem from over-fitted models (Harrell, 2001). Additional

433   analyses, for example with extended data sets with more countries or at smaller spatial scales,

434   with diachronic data sets (e.g. McKee et al., 2013), or using a more integrated framework

435   ,such as structural equation modelling, would be useful.

436   **Policy implications**

437   Although results from this study may suggest that current policy measures may only have

438   effects on biodiversity after decades at best, these results nevertheless provide policymakers

439   with precious knowledge. Understanding how these systems have long time lags should help

440   policymakers better assess the actions they take. They may integrate in their monitoring

441   evaluations of biodiversity policies, for example, the notion that a policy may have no

442   noticeable effect on extinction or threatened species metrics in the short term. One or two

443   decades may not suffice. As results from this study confirm that human population density

444   and especially GDP per area driver biodiversity, and that land sealing may be an important

445   pressure to consider, biodiversity preservation should infuse all economic activity, and not be

446   restricted to local actions such as protected areas.

447   **Conclusion**

448   In conclusion, the analysis presented above enable clear answers to the research questions

449   posed in this paper. First, even at a coarse (country) scale and with a small sample, a clear

450   lagged relationship is apparent between the State of biodiversity and the gross domestic

451   product per area (GDPa). This finding is consistent with the first hypothesis. Considering the

452   different results for Extinct and Threatened species, the typical time lag is apparently about

453   one century, though the time lag between Drivers (human presence and economic activity)

454   and Pressure (land encroachment) appears much shorter.

455

456   Second, in accordance with the second hypothesis, simple models with human population

457   density and GDPa improved modelling predictive capacity for three pressure and state

458   indicators out of four. These results confirm the intuition that human activity as a whole

459   impacts biodiversity, and that more complex models do not necessarily add substantial

460   predictive power.

461

462   Third, the variables representing human activity that best explain variations in biodiversity

463   were Log GDPa in 1900 for the two State indicators, and Log HPD in 2000 for the two

464   Pressure indicators. In contrast with our expectations, including human appropriation of

465   primary productivity did not improve the predictive capacity of the models over these more

466   indirect measures of human activity. In line with our hypothesis, the above results further

467   suggest that the causality between past human activity and the current state of biodiversity

468   may be mediated by human pressure on the land through land encroachment.

469

470   These results suggest that human population density, density of economic activity, and land

471   sealing should serve as primary foci for environmental policies. Because of the short-term

472   view often common for policymaking, such findings steer toward the preservation of natural

473   lands as high priority toward effective mitigation of the loss of biodiversity. Future additional

474   analyses with diachronic data at much finer spatial levels would refine further the estimation

475   of time lags to help guide such policies.

476

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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637

638

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)	–

639   Table 1. The thirteen main statistical models estimated with their names and the explanatory

640   variables they contain. GDPc refers to Gross Domestic Product per capita, GDPa to Gross

641   Domestic Product per area, HPD to Human Population Density, HANPP to Human

642   Appropriation of Primary Productivity. Further details on these variables can be found in

643   Table SM1.

644

Model name	Extinct species	Threatened species	Protected Areas	SEAL	iSEAL
Null	39.47	25.26	**<u>0.00</u>**	44.51	18.34
Economic.2000	18.51	26.24	6.75	17.45	**<u>0.00</u>**
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**	**<u>0.00</u>**	**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**	**<u>0.00</u>**	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	**<u>0.00</u>**	**2.51**	6.72	20.14	15.47

645

646   Table 2. Statistical comparison of the socio-economic main models considered at either 1900,

647   1950 and 2000 (rows) to predict different biodiversity indicators (columns). Difference in

648   Leave-one-out Information Criterion (LOOIC) values with the LOOIC of the best model

649   fitted for the different explanatory models (by column). The lower the LOOIC, the better the

650   model. The best model is underlined and models with a LOOIC relatively close to the best

651   model– i.e. within six units of the best model – are in bold (as suggested in Millar, 2009).

652   Only the models pertaining to the same target variable (models in the same column) are

653   comparable. See Tables 1 and SM1 for the content of the models. For the first three columns,

654   the marginal version of the LOOIC is used.

655

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**	**<u>-4.15</u>**
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

656 Table 3. Statistical comparison of the ability of additional univariate explanatory models

657 (rows) to predict the proportion of Extinct species, both with simple models (one effect shared

658 by all taxonomic groups; first column) and hierarchical models (effect varying among

659 taxonomic groups as a random effect; second column). The difference between Leave-one-out

660 Information Criterion (LOOIC) of the model and the LOOIC of the best model in Table 2 for

661 the proportion of Extinct species is indicated. The lower the LOOIC, the better the model. The

662 best model is underlined and models with a LOOIC within six units of the best model – i.e.

663 relatively close to the best model – are in bold. Models in both columns can be compared

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

665   models.

666

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	**_-1.17_**	**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

667   Table 4. Statistical comparison of the ability of additional univariate explanatory models

668   (rows) to predict the proportion of Threatened species, both with simple models (one effect

669   shared by all taxonomic groups; first column) and hierarchical models (effect varying among

670   taxonomic groups as a random effect; second column). The difference between Leave-one-out

671   Information Criterion (LOOIC) of the model and the LOOIC of the best model in Table 2 for

672   the proportion of Threatened species is indicated. The lower the LOOIC, the better the model.

673   The best model is underlined and models with an LOOIC within six units of the best model –

674   i.e. relatively close to the best model – are in bold. Models in both columns can be compared

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

676   models.

677

678

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+

679

680   Table 5. Analysis of the estimators of the best socio-economic variables at different dates for

681   the four Biodiversity indicators that are sensitive to these variables. For magnitude analyses

682   (last column), the results of the analyses of adding one standard variable of the best variate on

683   odds ratios were conclusive if 95% of the odds ratio effects were in the interval $\left[-0.1;\ 0.1\right]$

684   (denoted as 000 and qualified as a strongly negligible effect), $\left[-0.5;\ 0.5\right]$ (denoted as 00 and

685   qualified as a moderately negligible effect), $\left[-1;\ 1\right]$ (denoted as 0 and qualified as a weakly

686   negligible effect), $[0.1; +\infty)$ (denoted as + and qualified as a weakly positive effect),

687     $[0.5; +\infty)$ (denoted as ++ and qualified as a moderately positive effect), $[1; +\infty)$ (denoted as

688   +++ and qualified as a strongly positive effect) (as in e.g. Daniels 1983). Estimators are given

689   for the best univariate model (first) and then for the other models with the same variable but at

690   different dates. GDPa refers to Gross Domestic Product per area, HPD to Human Population

691   Density (log-transformed if an "l" is added at the beginning of the name of the variable). For

692   Extinct species, the best model is the hierarchical model, from which we consider the mean

693   effect across the nine taxonomic groups; estimators by Taxon are provided in Table SM4.

694

695   (a) Extinct species

696
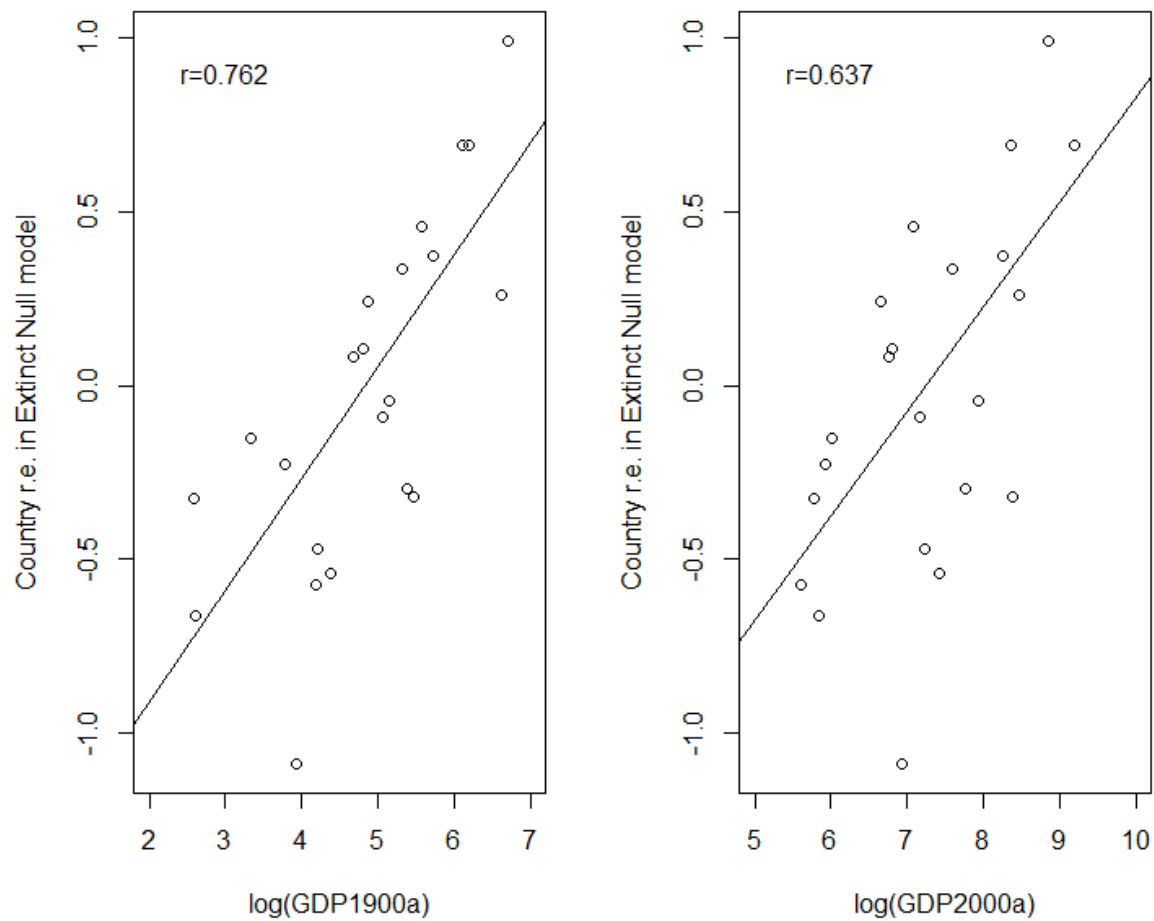
697

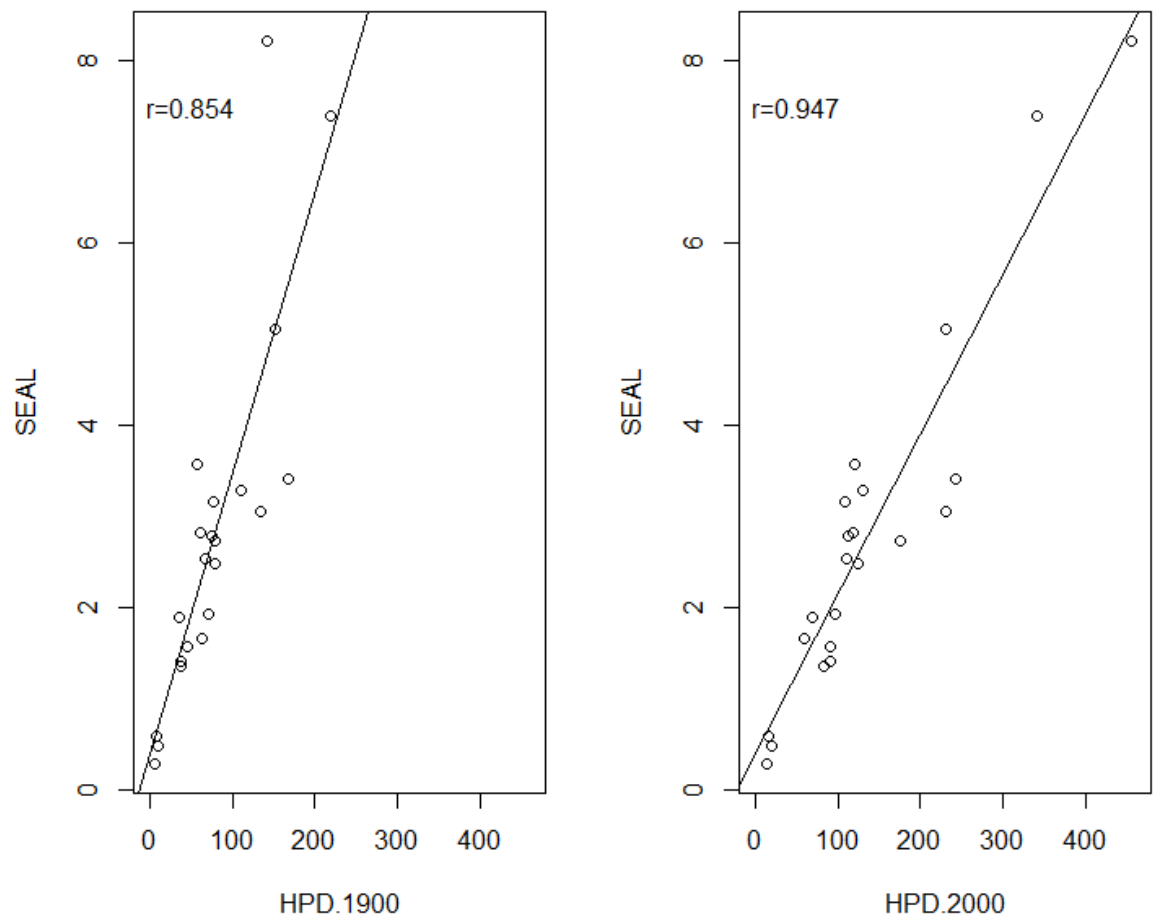698   (b) Threatened Species

699
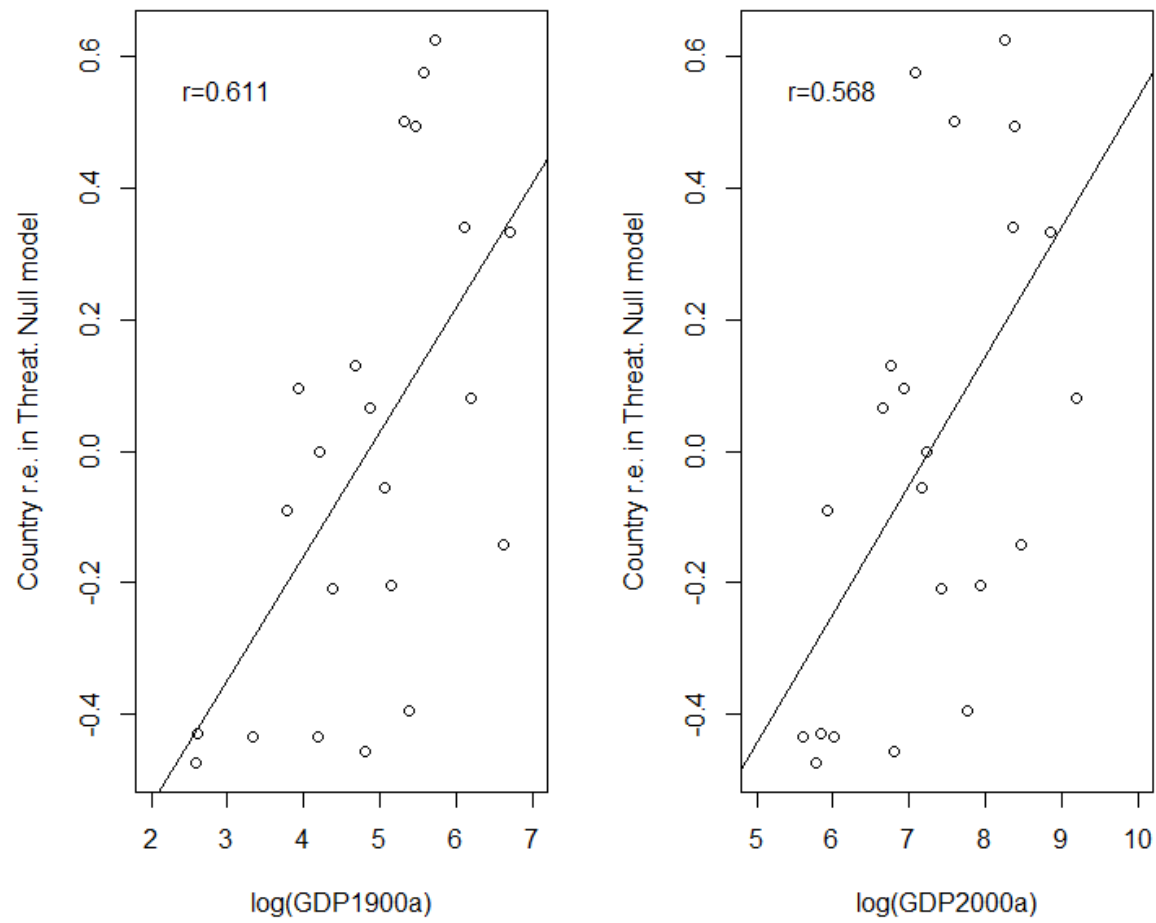
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703   (c) SEAL
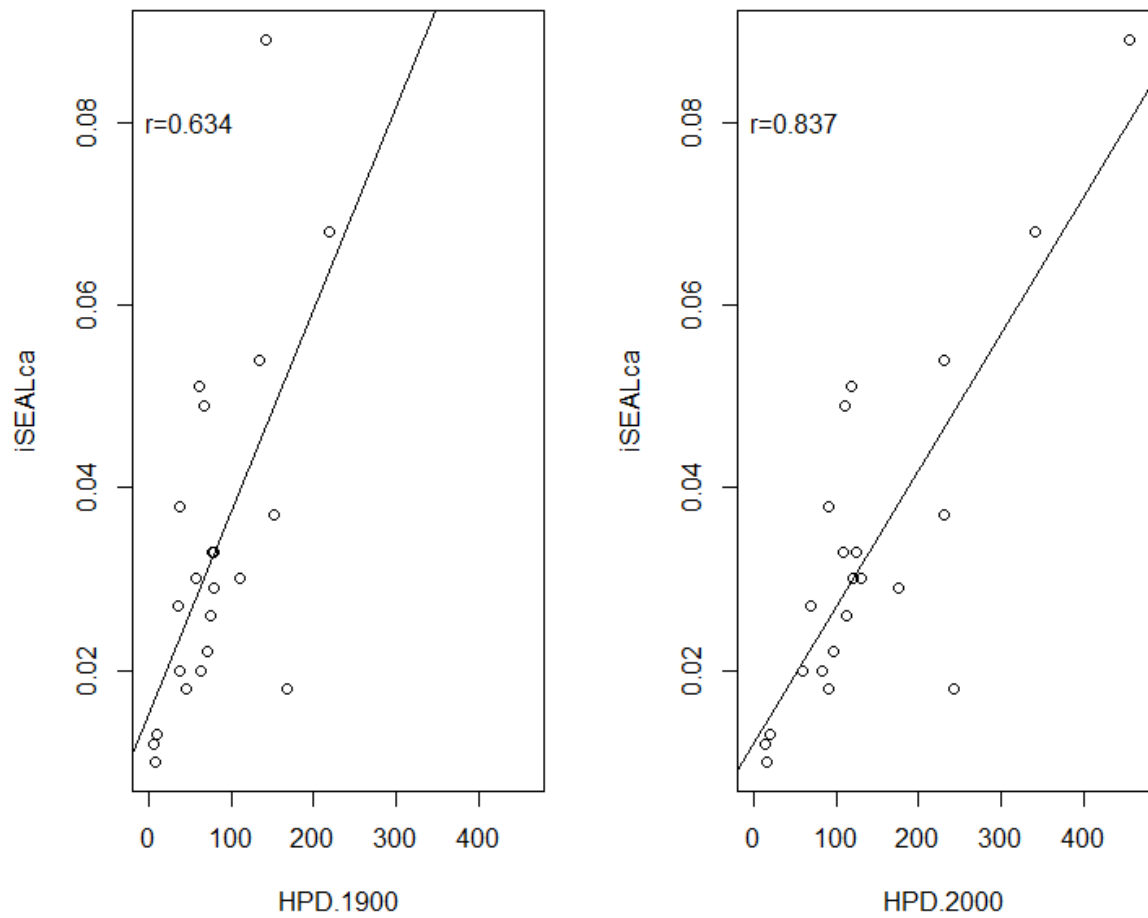
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706   (d) iSEAL

707

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)

			[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]

720

721   Table SM1. List of economic variables included in the statistical models (cf. Table 2). The summary

722   of the variations for the variables include the mean (+/- the standard deviation) and in square brackets

723   the minimum and maximum for the variable in the model for Extinct species (these summary statistics

724   do not include the repetition of data when a single country is included repeatedly in the analysis). All

725   the data come from [Dullinger, 2013 ^ny #120369] (2013).

726

727

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]

46

	(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]

728   Table SM2. List of the biodiversity indicators used in this paper. The summary of the variations for

729   the variables include the mean (+/- the standard deviation) and in square brackets the minimum and

730   maximum for the variable.

731

732

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

733

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+

742

743 Table SM4. Analysis of the estimators of the best socio-economic variables at different dates

744 for the proportion of Extinct species, by taxonomic group. For magnitude analyses (last

745 column), the results of the analyses of adding one standard variable of the best variate on odds

746 ratios were conclusive if 95% of the odds ratio effects were in the interval $[-0.1; 0.1]$

747 (denoted as 000 and qualified as a strongly negligible effect), $[-0.5; 0.5]$ (denoted as 00 and

748 qualified as a moderately negligible effect), $[-1; 1]$ (denoted as 0 and qualified as a weakly

749 negligible effect), $[0.1; +\infty)$ (denoted as + and qualified as a weakly positive effect),

750 $[0.5; +\infty)$ (denoted as ++ and qualified as a moderately positive effect), $[1; +\infty)$ (denoted as

751 +++ and qualified as a strongly positive effect) (as in e.g. Daniels 1983). The best model was

752 the hierarchical model at date 1900. For each taxonomic group, estimated tend to decrease

753 with date, except for Birds and Reptiles, for which they tend to increase with date, and

754 vascular plants and amphibians, for which 1900 and 1950 estimators were very close and

755 greater than 2000 estimator.

756

757

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**

758

759 Table SM5. Statistical comparison of additional univariate models in 2000 (rows) to predict

760 the two state biodiversity indicators (columns). Difference in Leave-one-out Information

761 Criterion (LOOIC) values with the LOOIC of the best model with current values of socio-

762 economic variables in Table 2, for additional univariate models involving only current values

763 of variables for the proportion of Extinct and Threatened species. The lower the LOOIC, the

764 better the model. The best model is underlined and models with an LOOIC within six units of

765 the best model – i.e. relatively close to the best model – are in bold. Only the models

766 pertaining to the same target variable (column heading) are comparable. It should be noted

767 that for extinct species, the best present model was the bivariate model involving

768 untransformed SEAL and iSEAL (Difference in LOOIC of -14.18). See Tables 1 and SM1 for

769 the content of the models.

770

771

variable clustering (varclus) - with correlations
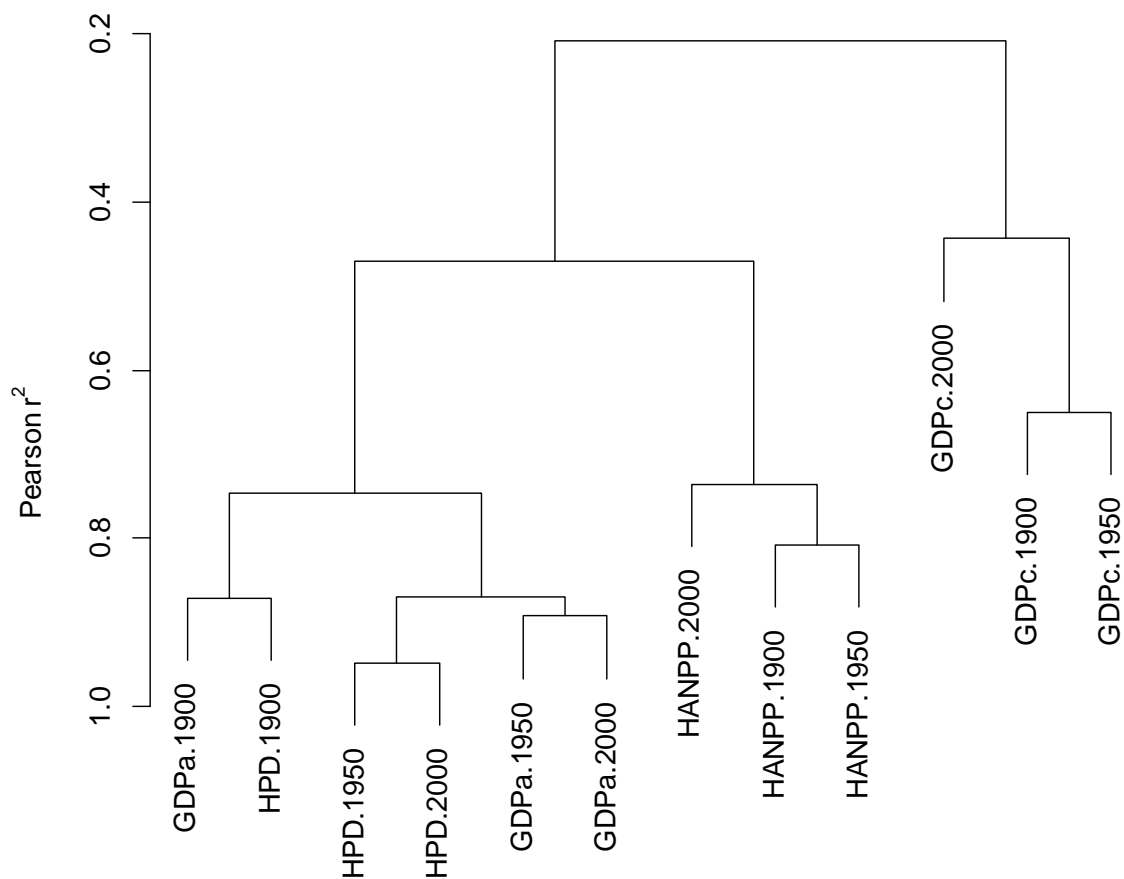
method : average

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.