

1 **Relationships between human activity and biodiversity in Europe at the national**
2 **scale: spatial density of human activity as a core driver of biodiversity erosion**

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10
11 **Abstract**

12 Many empirical studies have analyzed the relationship between human activity and the environment.
13 Some of these have focused on the potentially negative impacts of human activity on the environment.
14 Some others have tried to identify socio-political variables that could be at play in this relationship.
15 Herein, we used well-adapted statistical methods to study the relationship between human activity and
16 biodiversity in Europe at the country level; we worked with classical biodiversity indicators (two state
17 indicators, two pressure indicators and one response indicator) on the one hand, and socio-economic
18 variables on the other hand. We found strong relationships between economic variables and pressure
19 indicators (related to soil sealing) as well as state indicators (related to the proportion of extinct and
20 threatened species). However, there was no relationship between economic variables and the response
21 indicator (related to the proportion of protected area). Though we did find significant relationships
22 between some sociological variables and biodiversity indicators, the best models all included
23 economic variables. These results cast a new light on an old issue: first, they reveal the pertinence of a
24 set of variables related to the spatial density of human activity – either through economic growth or
25 population levels; they also show that the impact of the spatial density of human activity on

26 biodiversity indicators tends to decelerate – but not to decrease – as the spatial density of human
27 activity increases. These results reveal the need for further studies involving these metrics.

28 **Keywords:** species imperilment; land sealing; protected areas; endangered species; economic growth;
29 human population; social trust; indicators

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31

32 Introduction

33 Ecological science has long included analyzes at the macro scale (see Arrhenius, 1921; Willis, 1922;
34 and references in Brown, 1999; Gaston and Blackburn, 1999). Yet, this practice has only recently
35 been formalized into a research program – called macroecology – with a strong emphasis on an
36 empirical statistical approach to global patterns (Brown, 1999). This research program was inspired
37 by (i) the recognition of human pressures at a scale so large they cannot simply be analyzed from
38 smaller scale approaches (Brown, 1999; Gaston and Blackburn, 1999); (ii) the realization that
39 empirical approaches to identifying patterns are as crucial in ecology as in other scientific disciplines
40 (Peters, 1991; Brown, 1999; Gaston and Blackburn, 1999); and (iii) the increasing availability of
41 databases at this macro scale (Brown, 1999). Quite surprisingly, although macroecology has extended
42 its scope in terms of databases and scales, and has recognized the interest of the empirical approach, it
43 remains centered on ecological objects (including geographical objects such as latitudinal gradients
44 and topography). Indeed, neither of the two syntheses by Brown (1999) and Gaston and Blackburn
45 (1999) include any reference to economic or demographic indicators as explanatory variables – other
46 than their role in motivating the emergence of macroecology.

47 Extending macroecology to socio-economic drivers and variables is all the more welcome since this
48 could provide thought-provoking links to the social sciences. Indeed, the interplay between human
49 pressures and ecological objects is under active investigation in the field of economics. Concern about
50 the impact of economic activity on the environment began to rise in the 1950s, with the foundation of

51 environmental economics as an independent field of economics; this movement accelerated in the late
52 1960s, after Garrett Hardin formalized the notion of the “tragedy of the commons”. Early empirical
53 studies mostly focused on environmental objects which were physical parameters (CO₂, NO_x,
54 SO₂...) rather than ecological phenomena. In an attempt to test the relationships between economic
55 development and a wide array of environmental variables, Shafik (1994) pointed out that relationships
56 can be very different according to the variables under study, and that no obvious pattern exists. Some
57 of his results gave credit to the idea of a bell-shaped curve relating economic development and
58 pollution, known as the Environmental Kuznets Curve, which was first introduced by Selden and
59 Song (1994) and has since given rise to numerous attempts to identify macro-relations between
60 environmental quality and aggregate economic parameters.

61 Since the 1990s, the issue of the impact of economic activity on biodiversity has been growing, in
62 both ecology (Wright, 1990) and economics (Krautkraemer, 1995). In one of the earliest cross-
63 national studies focusing on biodiversity, Asafu-Adjaye (2003) tested the impact of variables related
64 to human activity on several biodiversity variables (essentially the number of mammals, birds and
65 vascular plants). As in other studies, he found different responses depending on the biodiversity
66 metrics used. For example, there were significant impacts of human population density (HPD) and of
67 ratio of protected area on species richness metrics (respectively negative and positive impacts). Per
68 capita gross domestic product (GDPc) and ratio of artificialized or agricultural land had significant
69 negative impacts on the average annual percentage change in the number of known mammal species.
70 He also introduced institutional factors (economic freedom, black markets), but these variables had a
71 strongly significant relationship only for the species richness of vascular plants. As in many other
72 studies, the impacts tended to be higher for low-income countries, although the estimators were very
73 noisy.

74 Focusing on the link between HPD and biodiversity, Luck (2007) reviewed the published empirical
75 literature through a meta-analysis. Although the published literature was skewed geographically and
76 taxonomically, he found positive correlations between HPD and various biodiversity metrics – mainly
77 related to species richness: the level of biodiversity was greater in densely populated zones, which
78 was possibly due to correlations between the two metrics and other parameters such as ecosystem

79 productivity or solar energy availability. In contrast, there were some indications of more negative
80 relationships between HPD and species extinction, but the evidence was judged weak (Luck 2007).
81 Another series of results (Mikkelsen et al., 2007; Holland et al., 2009) indicated that income
82 inequality was a significant positive indicator of the proportion of globally threatened species, though
83 only Holland et al. (2009) found that the logarithm of GDPc was a significantly negative indicator,
84 with HPD having no significant relationship. On the whole, these results partly suggest that human
85 activity *per se* might not be the most fundamental driver of biodiversity erosion.

86

87 The way human activity influences biodiversity might depend on much more than the level of
88 economic activity or population size. Sociological and cultural factors may well be at play. First,
89 national or regional cultures may be characterized by social values that are more or less favorable to
90 the protection of biodiversity. Casual observation suggests that for a given level of human presence,
91 there are very different attitudes across countries towards the quality of the environment. These
92 differences in attitudes could significantly influence the quality of ecosystems at a macro level. Many
93 studies can be found in the Convention for Biological Diversity (<https://www.cbd.int/>) that highlight
94 the role of social values. Secondly, biodiversity protection may also be influenced by the general
95 functioning of society. This is the object of the so-called “social capital” research program (Coleman,
96 1988; Dasgupta, 2000). In the same way the supra-national studies quoted above have tried to relate
97 economic and environmental variables, social scientists have tried to prove that sociological indicators
98 – in particular indicators of social values – influence economic development (Zak and Knack, 2001;
99 Bjørnskov, 2006). The main indicators used in such studies are proxies for trust and participation in
100 associations (see Callois and Schmitt, 2009, for a review of available indicators). Thirdly, one may
101 wonder if there are not even more fundamental drivers of sociological characteristics. Hofstede (1980)
102 built a 4-dimensional framework (later enlarged to six dimensions) to characterize national cultures.
103 He claimed that these dimensions capture the anthropological features driving values and attitudes in
104 society. The six dimensions are: power distance (i.e. acceptance of hierarchical power), individualism,
105 uncertainty avoidance, masculinity, long-term orientation and hedonism. Using Hofstede’s
106 framework, Chambers and Hamer (2012) found that individuality and uncertainty avoidance are the

107 main dimensions promoting economic growth. To our knowledge, few cross-country studies take into
108 account such sociological or anthropological factors when explaining biodiversity (Asafu-Ajaye,
109 2003; Holland et al., 2009).

110 The aim of this paper is to deepen the understanding of the relationships between human activities
111 and biodiversity variables by developing and comparing statistical models that link socio-economic
112 indicators with biodiversity indicators at a national scale. We include not only classically targeted
113 socio-economic variables but also more sociologically or anthropologically oriented variables. By
114 comparing different types of socio-economic variables, we hope to identify the most relevant drivers
115 of the human impacts on biodiversity and improve our understanding of their underlying mechanisms.
116 With this general goal in mind, our main hypotheses were as follows:

117

118 i. Regarding response variables, a better understanding of biodiversity indicator
119 responses to socio-economic variables can be achieved by using not only indicators of
120 the state of biodiversity but also metrics that might be the more proximal causes of
121 these variations or metrics that might be explained by the state of biodiversity (as e.g.
122 in Luck, 2007; Butchart et al., 2010). Our general hypothesis is that human activity
123 does indeed have some impact on these different variables related to biodiversity. Our
124 approach can therefore be interpreted within the Drivers-Pressures-State-Impact-
125 Response (DPSIR) framework developed by the European Environmental Agency
126 (see for instance Gari et al., 2015; Dietz 2017 for a discussion of the origin and
127 evolution of the DPSIR framework and its applications). We are not only studying the
128 relationships between Drivers of change (here, socio-economic variables) and the
129 State of biodiversity, but also between these Drivers and potentially more proximal
130 causes of change than the Drivers – coined Pressures – or responses to Pressures
131 and/or States of biodiversity, here associated with the notion of Response indicator.
132 We selected the proportion of extinct species and the proportion of threatened species
133 as State indicators, the proportion of protected area as the Response indicator and the
134 proportion of sealed land and its increase as Pressure indicators.

135 ii. Concerning explanatory variables, we considered both economic indicators of human
136 activity and sociological and anthropological variables. Regarding the latter, we
137 hypothesized that sociological and anthropological variables could act as primary
138 drivers and thus would partly explain variations in biodiversity. As for the economic
139 indicators of human activity, we used classical metrics related to economic growth
140 and human population but we also hypothesized that Gross Domestic Product (GDP)
141 should be scaled not per inhabitant but per area (square kilometer) to better reveal its
142 relationship with biodiversity indicators. Indeed, past analyses – including those
143 related to the Kuznets curve – have almost exclusively used the classical indicator,
144 GDP per capita (GDPc) (three exceptions are Panayotou, 1997; Kaufmann et al.,
145 1998; Liu et al. 2005). We suggest that GDP per area is a more logical indicator.
146 Indeed, the level of pressure on biodiversity should first appear in relation to an area,
147 rather than in relation to an inhabitant. For example, the level of wealth produced per
148 inhabitant, whether high or low, may be irrelevant for biodiversity, provided human
149 population density (HPD) is low. In contrast, pressures such as the level of resource
150 extraction per unit area, waste generation per unit area or proportion of sealed area
151 are directly linked with GDP per area (Panayotou, 1997).
152

153 **Material and methods**

154 **Biodiversity indicators**

155 The aim of our work was to relate relevant biodiversity indicators to socio-economic variables
156 throughout Europe. We chose five indicators that are readily available at national level, as follows:

157 i. Two Pressure indicators related to soil sealing (or imperviousness): the percentage of
158 surface area in the country sealed in 2009 (denoted as SEAL), and the annual increase
159 in sealing between 2006 and 2009 expressed as a percentage (denoted as iSEAL) ;

- 160 ii. Two indicators of the State of biodiversity: the proportion of extinct and threatened
161 species (denoted as Extinct and Threatened respectively) in each country for ten
162 different taxonomic groups (vascular plants, bryophytes, mammals, birds, freshwater
163 fishes, reptiles, amphibians, dragonflies, grasshoppers and trees);
- 164 iii. One Response indicator: the percentage of protected terrestrial area in each country
165 (combining the four different International Union for Conservation of Nature (IUCN)
166 types of protected areas).

167

168 The two Pressure indicators were provided by the European Environmental Agency
169 (<http://www.eea.europa.eu/data-and-maps/indicators/imperviousness-change/assessment>). Soil sealing
170 or imperviousness is a classical land use indicator. It can proxy the degree of land-cover change due
171 to urban or industrial development and related increases in transport infrastructure. Since habitat loss
172 is an undisputed cause of biodiversity erosion (Fahrig, 2003), sealing is often used as a Pressure
173 indicator for biodiversity.

174 Concerning State of biodiversity indicators, we chose (i) the proportion of extinct species
175 (corresponding to the IUCN Categories or Extinct in the Wild) in each country and for different
176 taxonomic groups to indicate a **past** “state” of biodiversity; and (ii) the proportion of threatened
177 species in each country and for different taxonomic groups to indicate the **current** state of
178 biodiversity. These proportions indicate the part of biodiversity that has eroded (for extinct species) or
179 that is still eroding (for threatened species) over time. They are therefore classically used at the
180 territory level as indicators of biodiversity State. We did not select species richness or the total
181 number of extinct or threatened species, because the two variables are very likely to share dependency
182 on territory area and other environmental variables with socio-economic variables, thus obscuring any
183 relationship they might have with those socio-economic variables (cf. Luck, 2007 in the case of HPD,
184 and Dullinger et al., 2013). We used data from Essl et al. (2013) for both threatened and extinct
185 species as well as the total number of species for different taxonomic and ecological groups to
186 calculate the proportions of extinct and threatened species in each country. The lists for extinct and
187 threatened species correspond to national Red Lists (see SM for additional comments). Essel et. al.’s

188 data set incorporates ten ecological or taxonomic groups: vascular plants, bryophytes, mammals,
189 birds, freshwater fishes, reptiles, amphibians, dragonflies and grasshoppers. We added similar data for
190 trees from Forest Europe et al. (2011, Table A4.9).
191 Finally, as the Response variable, we considered the proportion of protected area. Indeed, creating
192 protected areas is a classical component of the public policies designed to improve the state of
193 biodiversity and reduce some of the pressures on it (e.g. intensification of resource management or
194 land sealing). As an example, CBD Aichi target 11 aims to protect at least 17% of the terrestrial area.
195 We used the IUCN data on protected areas for terrestrial ecosystems by EuroStat in 2013. The four
196 IUCN categories of protected areas that we analyzed were: categories Ia and Ib (Strict Nature Reserves
197 and Wilderness Areas respectively), which we combined in Category I; Category II, corresponding to
198 National Parks; Category III, for reserves around Natural Monuments or Features; and Category IV,
199 for Habitat or Species Management Areas.
200 The five different indicators defined above are classically used in territorial reporting. They have, for
201 example, been proposed as general indicators of biodiversity in France ([http://indicateurs-
202 biodiversite.naturefrance.fr](http://indicateurs-biodiversite.naturefrance.fr)).

203 **Explanatory variables**

204 We chose our explanatory variables among socio-economic variables, that were potential Drivers in a
205 DPSIR framework. We first tested two classical indicators of human activity: gross domestic product
206 (GDP) and human population density (HPD). As explained in the introduction, we not only tested
207 GDP per capita but GDP per area as well because we conjectured that the spatial density of economic
208 activity would have a greater significance than simple per capita economic development. GDP per
209 area is a simple way to calculate an ecological footprint, as defined in the seminal work of Ehrlich and
210 Holdren (1971). We tested the role of HPD by combining it with GDP per capita (as in Holland et al.,
211 2009 and Dullinger et al., 2013). In addition, we examined rural and urban population density
212 separately; this distinction allowed us to investigate the possible role of heterogeneity in human
213 pressure, which has seldom been done for biodiversity. We supposed that the pressure human
214 population exerts on biodiversity indicators should be scaled by area to facilitate a comparison among

215 territories; therefore, although some authors retained total population size (Brown and Laband, 2006;
216 McKinney, 2002a – but see: McKinney, 2002b), we focused on HPD, as many previous studies have
217 done (cf. synthesis in Luck, 2007; Holland et al., 2009).

218 We also included sociological factors, which, to our knowledge, had never before been taken
219 into account. We tested a structured array of variables, belonging to three main categories as
220 explained in the Introduction:

- 221 - Fundamental Cultural attributes (hereafter FC), which include six variables taken from
222 Hofstede (1980), related to power distance, individualism, uncertainty avoidance,
223 masculinity, long-term orientation and hedonism.
- 224 - Social Capital indicators (SC), from the UNDP database, which include general social
225 trust, community functioning, and trust in the national government
226 (<http://hdr.undp.org/fr/data>).
- 227 - Indicators of concern for the environment (EC), including the proportion of the
228 population declaring voluntary work in environmental associations, the proportion of the
229 population claiming they trust these associations, the proportion of the population
230 claiming that “man should reign over nature”, and the proportion of the population
231 claiming that “interference with nature is often disastrous”. For these variables, we used
232 2008 European Values Study data (<http://www.europeanvaluesstudy.eu/>).

233 The three categories (FC, SC and EC) occur along a gradient, ranging from fundamental attributes
234 driving human behavior to specific measurements of environmental concern. We used the three
235 categories to try to identify the most fundamental drivers of human activity’s impact on biodiversity.
236 We hypothesized that, if the Hofstede variables (FC) were the most relevant explanatory variables,
237 this would imply that human impact on nature is deeply rooted in national cultures. If environmental
238 concern (EC) proxies were the most relevant, a policy promoting environmental awareness might be
239 able to quickly improve biodiversity. If the intermediate category of social capital (SC) turned out to
240 be the most relevant, policies promoting sociability and good institutions would seem to be the most
241 appropriate for improving biodiversity.

242

243 The list of socio-economic variables together with their sources and a summary of their values are
244 provided in Tables 1 and SM1 . Correlations between explanatory variables are displayed in Figure
245 SM1 in the Supplementary Materials section. Some patterns emerge from these figures that helped us
246 shape the statistical models we tested. In particular, we initially intended to fit a model including GDP
247 per unit area and (total or urban) HPD. Yet the correlation between these variables was so high that
248 we did not use them together within the same model. Two other clearly noticeable associations
249 occurred: there were a strong positive correlation (i) between Environmental Association membership
250 (MEMB.2008) and the two above-mentioned metrics (GDPa, HPD or HPDu); and (ii) between GDP
251 per capita and social capital variables (TRUTSP & COMMUN), which was expected.
252 The overall list of countries we considered was the same as the one in Essl et al. (2013), and included
253 38 European countries plus Israel. However, the actual countries included in the tests depended on the
254 availability of the socio-economic data (cf. infra). Moreover, to avoid the peculiarities of very small
255 areas, we did not take very small countries (Cyprus, Malta and Luxembourg) into account, as e.g.
256 Dullinger et al. (2013) did.

257 **Statistical models and hypotheses**

258 As in Brown and Laband (2006), our modeling strategy was based on the estimation and
259 comparison of several simple statistical models. We did not combine different metrics into a single,
260 global metric nor did we estimate a single statistical, multiple regression model that would have
261 included all the variables; we thus avoided technical and interpretative problems related to
262 correlations between variables. Instead, we estimated and compared the twelve main models described
263 in Table 2. Except for the null model, each model incorporated two socio-economic variables related
264 to a specific theme as explanatory variables. We chose to limit the number of variables in our models
265 since we only had a limited number of countries in our data set (23 for Pressure indicators, 24 for
266 species State indicators, 22 for Response indicators; cf. Harrell (2001)'s guidelines on the relationship
267 between sample size and number of explanatory variables).

268 We included an economic model (*eco*) with HPD and GDP per capita (GDPc) as explanatory
269 variables (as in Dullinger et al. (2013),but without land use intensity, which was not available for all

270 the countries in our extended data set). We also included a Kuznets model based on the Kuznets curve
 271 hypothesis which posits that the relationship between environmental State and GDP is quadratic. For
 272 the Kuznets curve, we tested two forms: *Kuznets*, the classical one, involving GDP per capita (GDPc),
 273 and a new form, *Kuznetsa*, involving GDP per area (GDPa). We then included a more precise HPD
 274 model (*demo*) that separated urban HPD from rural HPD. Since some explanatory variables had no
 275 clearly symmetrical distribution, we also fitted a version of these models with the logarithm of the
 276 explanatory variables (*leco*, *lKuznets*, *lKuznetsa* and *ldemo*; see Table 2) . These models of human
 277 presence/activity were complemented by models based on sociological attributes. We included one
 278 model based on Hostede’s fundamental cultural attributes (*FC*) , one model for social capital
 279 indicators (*SC*) – Trust in other People and Trust in the Government; and two models related to
 280 concern for the environment (*EC*), one based on participation and confidence in Environmental NGOs
 281 (*NGO*) and one based on Environmental Related Values (*ERV*; cf. Tables 1 & SM1). For the *FC*
 282 variables, we selected two dimensions: “long-term orientation” and “hedonism”. The first reflects a
 283 preference for the present, which is a fundamental parameter in economic behavior while the second
 284 concerns the focus given to material goods.

285

Name of variable	Explanation, unit and source	Main model including the variable	Summary of variations of the variable
GDPc	Gross Domestic Product per inhabitant in 2013 (unit: Euros PPS; source: Forest Europe 2015, Table 1, p.243)	Eco & Kuznets	Untransformed: 23517 (\pm 10423) [3500; 49600] Log: 9.95 (\pm 0.54) [8.16; 10.81]
GDPa	Gross Domestic Product per 10 ha in 2013 (unit:	Kuznets	Untransformed: 32847 (\pm 38647)

	Euros PPS; source: Forest Europe 2015, Table 1, p.243)		[917; 173767] Log: 9.82 (\pm 1.15) [6.82; 12.07]
GDPc^2	Gross Domestic Product per inhabitant in 2013 (unit: Euros PPS; source: Forest Europe 2015, Table 1, p.243)	Eco & Kuznets	Untransformed: 658053667 (\pm 551967811) [12250000; 2460160000] Log(GDPc)^2: 99.24 (\pm 10.45) [66.60; 116.89]
GDPa^2	Gross Domestic Product per 10 ha in 2013 (unit: Euros PPS; source: Forest Europe 2015, Table 1, p.243)	Kuznets	Untransformed: 2.52e+09 (\pm 6.02e+09) [8.41e+05; 3.02e+10] Log(GDPa)^2: 97.80 (\pm 22.29) [46.52; 145.58]
HPD	Population density	Eco	Untransformed: 123 (\pm 106) [9; 498] Log: 4.48 (\pm 0.89) [2.20; 6.21]
HPDu	Urban population density	Demo	Untransformed: 93 (\pm 99) [7; 445]

			Log: 4.12 (\pm 0.93) [1.90; 6.10]
HPDr	Rural population density	Demo	Untransformed: 31 (\pm 20) [1; 64] Log: 3.07 (\pm 1.10) [-0.22; 4.15]
H.LT	Long-term orientation (source: Hofstede 1980)	FC	59.7 (\pm 17.6) [24; 83]
H.HED	Hedonism (source: Hofstede 1980)	FC	38.8 (\pm 19.4) [13; 70]
TRUSTP	Trust in other people (%) (source: UNDP 2013)	SC	27.4 (\pm 15.8) [7; 74]
TRUSTG	Trust in the national government (%) (source: UNDP 2013)	SC	38.0 (\pm 16.1) [13; 77]
MEMB.2008	Rate of membership in environmental associations (source: European Values Study 2008)	Environmental NGOs	5.3 (\pm 6.7) [1; 36]
CONFAE.2008	Trust in environmental associations (%) (source: European Values Study 2008)	Environmental NGOs	56.3 (\pm 12.7) [25; 76]
REIGN.2008	Opinion that “man should reign over	Environment Related Values	33.4 (\pm 12.1) [17; 60]

	nature” (%) (source: European Values Study 2008)		
INTERF.2008	Opinion that “interference with nature is often disastrous” (%) (source: European Values Study 2008)	Environment Related Values	88.3 (\pm 6.2) [66; 96]

286 Table 1. List of socio-economic variables included in the main statistical models (cf. Table 2). The
287 summary of the variations of the variables across countries includes the mean (\pm the standard
288 deviation) and in square brackets the minimum and maximum. Variations come from the model for
289 extinct species (these summary statistics do not include the repetition of data when a single country is
290 included repeatedly in the analysis).

291

Model name	1 st main explanatory variable	2 nd main explanatory variable
Null	-	-
Economic (eco)	GDPc	HPD
Economic – log (leco)	log(GDPc)	log(HPD)
Kuznets (Kuznets)	GDPc	GDPc ²
Kuznets – log (lKuznets)	log(GDPc)	log(GDPc) ²
Kuznets- area (Kuznetsa)	GDPa	GDPa ²

Kuznets – log area (IKuznetsa)	log(GDPa)	log(GDPa)^2
“Demography” (demo)	HPDu	HPDr
“Demography” – log (ldemo)	log(HPDu)	log(RPOd)
Fundamental Culture (FC)	H.LT	H.HED
Social Capital (SC)	TRUSTP	TRUSTG
Environmental NGOs (NGOs)	in NGOsMEMB.2008	CONFAE.2008in NGOs
Environment Related Values (ERV)	REIGN.2008	INTERF.2008

292 Table 2. The twelve main statistical models estimated with their names and the main explanatory
293 variables they contain. The meaning of the variables as well as information on their values can be
294 found in Table 1.

295

296 **Statistical methods**

297 We used statistical methods with a priori relevant probabilistic properties relative to our data. Based
298 on the lessons learned on partly similar data from Gosselin (2015), we paid careful attention to the
299 potential over-dispersion of data as well as to the inclusion of random country effects. Indeed, in all
300 our statistical models for State and Response indicators, we simultaneously analyzed different
301 categories (i.e. either taxonomic groups or types of protected areas). This means that the same
302 countries can correspond to several different values of the response variable; if this is not taken into

303 account, it can potentially violate the independence hypothesis of the statistical models (Gosselin,
304 2015). A random country effect, which was assumed to follow a Gaussian distribution with a zero
305 mean and an estimated standard deviation, was therefore introduced for State and Response
306 indicators.

307 For the proportion of extinct or threatened species, we used a beta-binomial distribution to model the
308 number of extinct or threatened species. In this model, the logit of the proportion of threatened or
309 extinct species was equal to the linear combination incorporating the country random effect, the
310 taxonomic group fixed effect and the effect of other socio-economic variables (cf. *infra*). We also
311 modelled a dispersion parameter for the beta-binomial distribution – one different level of dispersion
312 per taxonomic group.

313 For the proportion of protected area and the percentage of sealed soil area (SEAL) and its increment
314 (iSEAL), we used a zero-inflated beta distribution, which is a direct sub-product of the zero-inflated
315 cumulative beta distribution that Herpigny and Gosselin (2015; MTUnlimited2 version) proposed to
316 analyze plant cover class data. Here too, the logit of the mean proportion of protected areas or sealed
317 area was equal to the same linear combinations as above. For the proportion of protected area, the
318 type of protected area (among the four IUCN categories mentioned above) replaced the taxonomic
319 group. For sealed area, we fitted a separate model for the two indicators (SEAL and iSEAL) and
320 therefore did not include a random country effect in the corresponding models. Also, a dispersion
321 parameter was estimated for each type of protected area (and globally for SEAL and iSEAL). Finally,
322 a single extra parameter was estimated to model the probability of zeros, as proposed in Herpigny and
323 Gosselin (2015; parameter d).

324 We processed all the analyses with R software v. 3.3.2 (R Core Team, 2016). We used the Stan
325 program embedded in R through the rstan library (Stan Development Team 2015) to estimate the
326 above models. The priors of the hyper-parameters were mostly non-informative, except for the
327 proportion of extinct species for which we had to introduce an upper bound at $\exp(10)$ for dispersion
328 levels in order to obtain converging results. All the explanatory variables were centered and manually
329 scaled to ensure a residual standard deviation of the variable of around 1 while keeping a clear control
330 on the level of scaling for magnitude analyses. We ran between 200,000 and 350,000 iterations of

331 three Markov chain trajectories. The warm-up period was 20,000. The thinning parameter was either
332 10 or 30 (for Extinct). This ensured us a minimum of 10,000 (for Protected Area models) and around
333 25,000 (for Extinct, Threatened, SEAL and iSEAL) independent values of the parameters. With this
334 setting, the models converged very well for the proportion of species, SEAL, iSEAL and well for the
335 proportion of protected areas (Gelman-Rubin Rhat statistic below 1.01 and 1.03 respectively; Gelman
336 et al., 2004).

337 The models were compared with the Leave-one out Information Criterion (LOOIC) of Vehtari
338 et al. (2016). For State and Response indicators, we used the marginal version of the LOOIC for
339 reasons discussed by Millar (2009, 2017) and because the country random effect introduced a number
340 of parameters that was of the same order of magnitude as the number of observations.

341 The estimators of the socio-economic parameters were also investigated, with an eye to
342 statistical significance and the magnitude of the relationships. For statistical significance, we used
343 Bayesian quantiles based on beta random draws as in Gosselin (2011); we comment only those cases
344 with a p-value below 5%. To judge the magnitude of Odds-ratios adapted to the magnitude analysis
345 framework proposed in ecology by e.g. Camp et al. (2008) and Barbier et al. (2009), we analyzed the
346 effect of an increase of one standard deviation at the linear combination level (on the log of odds
347 ratios) for each socio-economic variable according to guidelines adapted from Daniels et al. (1983)
348 (see Table 4 legend for more details).

349 In a more explorative phase, for the socio-economic variables that were part of a larger set
350 (FC Values and Environment Related Values in Table SM1) but that were not included in our main
351 models in Table 2, we fitted models including the whole set of variables. We also tested models
352 involving other economic variables, including income inequality (the last four variables in Table
353 SM1). We fitted these extra models to be sure that no important relationships had been missed. For
354 these extra models, we only reported the socio-economic effects that were highly significant (p-values
355 below 0.001 or with an absolute value of mean/standard error ratio above 3.3).

356 Also, to check whether proportion of endemic species should be considered as a covariate in
357 models with proportion of extinct and threatened species, as suggested by the results of Holland et al.
358 (2009), we fitted the Null model with the proportion of endemic species as a covariate. The resulting

359 models either had a poorer LOOIC than the Null model (for threatened species) or a lower LOOIC but
360 with significant effects in the unexpected, negative direction (for extinct species) so we did not
361 include them in the analyses.

362

363 Finally, to gauge the adequacy of statistical models in relation to the data, we used sampled
364 posterior goodness-of-fit p-values (Gosselin, 2011). These p-values allowed us in particular to
365 diagnose (i) the adequacy of the probability distributions used, (ii) the correlation between normalized
366 randomized quantile residuals (Dunn and Smyth, 1996) or their squared value and explanatory
367 variables or the mean of observed variables (to diagnose the link function and the specification of
368 variance) – as in Hergigny and Gosselin (2015) –, and (iii) the spatial autocorrelation of the
369 normalized randomized quantile residuals. Given that we used around ten discrepancy functions per
370 model, only p-values below 0.005 were investigated with graphics, much as in Harrell (2001). These
371 p-values are based on normalized transforms of data as in Gosselin (2011) and were applied to the
372 best model associated with each biodiversity variable.

373

374 Results

375 On the whole, with proportion of protected area as a dependent variable, none of the main
376 socio-economic models was better than the Null model (Tables 3). The estimated relationships were
377 all non-significant (Table SM3).

Model name	Extinct species	Threatened species	Protected Areas	SEAL	iSEAL
Null	31,11	31,26	<u>0,00</u>	46,86	19,93

eco	5,93	24,43	10,89	18,26	<u>0,00</u>
leco	2,01	2,46	8,82	<u>0,00</u>	0,61
Kuznets	27,39	25,47	7,61	42,09	17,91
IKuznets	32,59	29,41	4,89	48,01	19,70
Kuznetsa	<u>0,00</u>	<u>0,00</u>	14,82	12,95	4,80
IKuznetsa	0,10	1,78	6,97	6,58	5,03
demo	6,89	18,53	18,85	17,16	0,82
ldemo	1,35	9,85	5,38	1,41	3,57
FC	2,78	9,83	6,58	40,82	22,14
SC	26,35	15,32	6,02	52,64	24,38
NGOs	29,95	38,41	8,12	39,10	15,05
ERV	20,36	38,27	3,50	44,85	22,32

378

379 Table 3. Statistical comparison of models. Difference in Leave-one out Information Criterion

380 (LOOIC) values with the LOOIC of the best model for the different explanatory models fitted (by

381 column). The lower the LOOIC, the better the model. The best model is underlined and models with a

382 LOOIC within 6 units of the best model – i.e. relatively close to the best model – are in bold (as

383 suggested in Millar, 2009). Only the models pertaining to the same target variable (models within one
 384 column) can be compared. See Tables 1 and 2 for the content of the models.

385
 386

Variable name	Summary statistics of the estimator	p-value	Summary impact in log odds ratio of an increase of 1 standard deviation of the variable
GDPc/10000 in eco	0.039 (0.101)	0.34679	00
HPD/100 in eco	0.325 (0.085)	0.00019	00+
log(GDPc/10000) in leco	0.272 (0.199)	0.08037	00
log(HPD/100) in leco	0.434 (0.116)	0.00024	0+
GDPc/10000 in Kuznets	0.313 (0.142)	0.01274	0
$(\text{GDPc}/10000)^2$ in Kuznets	-0.158 (0.091)	0.03674	

log(GDPc/10000) in lKuznets	0.413 (0.263)	0.0578	00
log(GDPc/10000) ² in lKuznets	-0.102 (0.285)	0.36477	
GDPa/50000 in Kuznetsa	0.71 (0.191)	0.00032	0+
(GDPa/50000) ² in Kuznetsa	-0.153 (0.098)	0.05587	0
log(GDPa/50000) in lKuznetsa	0.296 (0.115)	0.0044	0+
log(GDPa/50000) ² in lKuznetsa	0.09 (0.078)	0.11922	
HPDu/100 in demo	0.34 (0.086)	0.00019	00+
HPDr/100 in demo	0.278 (0.487)	0.27778	00
log(HPDu/100) in ldemo	0.443 (0.104)	0.00013	0+
log(HPDr/100) in ldemo	-2.138 (4.242)	0.30231	
H.LT/10 in FC	0.23 (0.057)	0.00024	0+
H.HED/10 in FC	0.174 (0.05)	0.00068	00+
TRUSTP in SC	-0.16 (0.096)	0.04626	0
TRUSTG in SC	0.246 (0.093)	0.00461	0+
MEMB.2008 in NGOs	0.174 (0.079)	0.0139	00

CONFAE.2008 in NGOs	-0.011 (0.091)	0.44712	00
REIGN.2008 in ERV	-0.165 (0.095)	0.03734	00
INTERF.2008 in ERV	-0.467 (0.169)	0.0039	00-

387

388 Table 4. Proportion of extinct species. Summary of the estimators of the socio-economic variables in
389 the twelve main models (all models in Table 2 except the null model) for the proportion of extinct
390 species. For magnitude analyses (last column), the results of the analyses were conclusive if 95% of
391 the odds ratio effects were in the interval $[-0.1; 0.1]$ (denoted as 000 and qualified as a strongly
392 negligible relationship), $[-0.5; 0.5]$ (denoted as 00 and qualified as a moderately negligible
393 relationship), $[-1; 1]$ (denoted as 0 and qualified as a weakly negligible relationship), $[0.1; +\infty[$
394 (denoted as + and qualified as a weakly positive relationship), $[0.5; +\infty[$ (denoted as ++ and qualified
395 as a moderately positive relationship), $[1; +\infty[$ (denoted as +++ and qualified as a strongly positive
396 relationship), $]-\infty; -0.1]$ (denoted as - and qualified as a weakly negative relationship), $]-\infty; -0.5]$
397 (denoted as -- and qualified as a moderately negative relationship) and $]-\infty; -1]$ (denoted as --- and
398 qualified as a strongly negative relationship) (as in e.g. Daniels 1983). Results were inconclusive with
399 respect to magnitude analyses if the last column was void. See Tables 1 and 2 for the content of the
400 models and the definition of the explanatory variables.

401

402

403

Variable name	Summary statistics of the estimator	p-value	Summary impact in log odds ratio of an increase of 1 standard deviation of the variable
GDPc/10000 in eco	0.097 (0.084)	0.12161	00
HPD/100 in eco	0.143 (0.078)	0.03224	00
log(GDPc/10000) in leco	0.283 (0.148)	0.02691	00
log(HPD/100) in leco	0.259 (0.087)	0.00266	00+
GDPc/10000 in Kuznets	0.223 (0.096)	0.01127	00
(GDPc/10000) ² in Kuznets	-0.093 (0.06)	0.06117	
log(GDPc/10000) in IKuznets	0.34 (0.182)	0.03235	00
log(GDPc/10000) ² in IKuznets	-0.019 (0.19)	0.46242	
GDPa/50000 in Kuznetsa	0.623 (0.153)	0.00022	0+

(GDPa/50000) ² in Kuznetsa	-0.237 (0.081)	0.00258	0-
log(GDPa/50000) in IKuznetsa	0.29 (0.091)	0.00208	0+
log(GDPa/50000) ² in IKuznetsa	-0.027 (0.066)	0.32468	
HPDu/100 in demo	0.132 (0.078)	0.04234	00
HPDr/100 in demo	0.703 (0.419)	0.04708	00
log(HPDu/100) in Idemo	0.255 (0.087)	0.00355	00+
log(HPDr/100) in Idemo	1.363 (4.081)	0.36571	
H.LT/10 in FC	0.13 (0.047)	0.00412	00
H.HED/10 in FC	0.12 (0.043)	0.00342	00
TRUSTP in SC	-0.156 (0.068)	0.01296	00
TRUSTG in SC	0.156 (0.066)	0.01137	00
MEMB.2008 in NGOs	0.063 (0.064)	0.15124	00
CONFAE.2008 in NGOs	0.06 (0.071)	0.19241	00
REIGN.2008 in ERVERV	-0.108 (0.077)	0.07665	00
INTERF.2008 in ERVERV	-0.037 (0.145)	0.39607	00

405 Table 5. Proportion of threatened species. Summary of the estimators of the socio-economic variables
406 in the twelve main models (all models in Table 2 except the null model) for the proportion of
407 threatened species. See Table 4 legend for the meaning of the signs used for magnitude analysis (last
408 column). See Tables 1 and 2 for the content of the models and the definition of the explanatory
409 variables.

410

411 We observed more significant relationships for the proportion of threatened species, for which
412 the models with economic variables (*Ieco*, *Kuznetsa* & *IKuznetsa* models) were the best models –
413 indeed, far better than the null model (Tables 3 & 5). Significant relationships (second column of
414 Table 5) involved GDP (both per capita GDPc and per area GDPa), HPD (and urban HPDu) as well as
415 social variables related to Fundamental Cultural values (long-term orientation and hedonism variables
416 in the FC model, and Trust in other people (TRUSTP) and Trust in the national government
417 (TRUSTG) in the SC model. Among these, only the relationships related to GDPa in the *Kuznets*-type
418 models and those related to log-transformed HPD or urban HPD (HPDu) were non-negligible (last
419 column of Table 5). All these relationships were positive except for the quadratic terms in the
420 *Kuznets*-type models and Trust in other people (TRUSTP), which were negative.

421 Clear relationships were found for the proportion of extinct species as well (Tables 3 & 4): the
422 best models (the models with economic variables and the Fundamental Cultural FC model) were
423 clearly better than the null model: relationships were more significant, and there were more positive
424 or negative non-negligible relationships (last column of Table 4) than for the proportion of threatened
425 species. The two FC variables (long-term orientation H.LT and hedonism H.HED) had a positive non-
426 negligible relationship with the proportion of extinct species – as did GDPa, HPD, HPDu and Trust in
427 Government (TRUSTG) – while the opinion that “interference with nature is often disastrous”
428 (INTERF.2008) had a negative non-negligible relationship (Table 4). In addition, some other
429 variables displayed a weak but still significant relationship: various GDPc metrics (positive
430 relationships, except for one negative relationship for the square of GDPC in *Kuznets*); Trust in
431 People (TRUSTP; negative relationship); membership in environmental associations (MEMB.2008;
432 positive relationship); and belief that “man should reign over nature” (REIGN.2008; negative effect).

433 Lastly, the models with the proportion of Sealed area (SEAL) as the dependent variable
434 suggested that the log-transformed versions of the economic and demographic models (leco and
435 ldemo) had the best explanatory capacity (Table 3). Non-negligible positive relationships were found
436 with the logarithm of the HPD variables as well as with GDPa, Fundamental Cultural H.LT and
437 H.HED variables and membership in environmental associations (MEMB.2008). Non-negligible
438 negative relationships were found with the square terms of GDPc and GDPa in the *Kuznets*-type
439 models (Table 6). The dynamics of sealed areas (iSEAL; Tables 3 and 7) gave rather similar results to
440 those from the models with the proportion of extinct species (except that the FC models lost
441 explanatory power and that economic and demographic models had good explanatory power whether
442 they were log-transformed or not). HPD and HPDu were highly significant and had a non-negligible
443 positive impact, which was also observed for GDPa.

444

Variable name	Summary statistics of the estimator	p-value	Summary impact in log odds ratio of an increase of 1 standard deviation of the variable
GDPc/10000 in eco	0.007 (0.072)	0.45115	00
HPD/100 in eco	0.446 (0.052)	0.00005	0+
log(GDPc/10000) in leco	0.277 (0.131)	0.01693	00

log(HPD/100) in leco	0.767 (0.088)	0.00005	0++
GDPc/10000 in Kuznets	0.331 (0.13)	0.00448	0+
(GDPc/10000) ² in Kuznets	-0.247 (0.084)	0.00066	--
log(GDPc/10000) in IKuznets	0.452 (0.259)	0.03379	00
log(GDPc/10000) ² in IKuznets	-0.716 (0.41)	0.03131	--
GDPa/50000 in Kuznetsa	0.899 (0.135)	0.00005	0++
(GDPa/50000) ² in Kuznetsa	-0.163 (0.065)	0.00729	0-
log(GDPa/50000) in IKuznetsa	0.545 (0.098)	0.00005	0+
log(GDPa/50000) ² in IKuznetsa	0.042 (0.06)	0.23333	
HPDu/100 in demo	0.438 (0.053)	0.00005	0+
HPDr/100 in demo	0.597 (0.405)	0.06555	00
log(HPDu/100) in Idemo	0.73 (0.068)	0.00005	0++
log(HPDr/100) in Idemo	-0.012 (0.05)	0.38822	00

H.LT/10 in FC	0.208 (0.072)	0.00312	0+
H.HED/10 in FC	0.182 (0.062)	0.00285	0+
TRUSTP in SC	-0.035 (0.08)	0.32184	00
TRUSTG in SC	0.034 (0.092)	0.34344	00
MEMB.2008 in NGOs	0.43 (0.113)	0.0021	0+
CONFAE.2008 in NGOs	0.09 (0.075)	0.11056	00
REIGN.2008 in ERV	-0.24 (0.094)	0.00529	00-
INTERF.2008 in ERV	-0.317 (0.158)	0.03082	00

445

446 Table 6. Proportion of Sealed Area. Summary of the estimators of the socio-economic variables in the
447 twelve main models (all models in Table 2 except the null model) for the proportion of Sealed Area.

448 See Table 4 legend for the meaning of the signs used for magnitude analysis (last column). See Tables
449 1 and 2 for the content of the models and the definition of the explanatory variables.

450

451

452

Variable name	Summary statistics of the estimator	p-value	Summary impact in log odds ratio of an increase of 1 standard deviation of the variable
---------------	-------------------------------------	---------	---

GDPc/10000 in eco	-0.02 (0.071)	0.39303	00
HPD/100 in eco	0.326 (0.056)	0.00005	00+
log(GDPc/10000) in leco	0.133 (0.145)	0.17557	00
log(HPD/100) in leco	0.483 (0.101)	0.00005	0+
GDPc/10000 in Kuznets	0.188 (0.102)	0.0306	00
(GDPc/10000) ² in Kuznets	-0.161 (0.074)	0.00847	-
log(GDPc/10000) in lKuznets	0.285 (0.202)	0.07194	00
log(GDPc/10000) ² in lKuznets	-0.513 (0.339)	0.05544	
GDPa/50000 in Kuznetsa	0.437 (0.144)	0.00282	0+
(GDPa/50000) ² in Kuznetsa	-0.019 (0.071)	0.39134	00
log(GDPa/50000) in lKuznetsa	0.339 (0.095)	0.00028	0+
log(GDPa/50000) ² in lKuznetsa	0.015 (0.069)	0.39856	

HPDu/100 in demo	0.301 (0.056)	0.00007	00+
HPDr/100 in demo	0.575 (0.395)	0.06912	00
log(HPDu/100) in Idemo	0.441 (0.081)	0.00002	0+
log(HPDr/100) in Idemo	-0.002 (0.066)	0.46199	00
H.LT/10 in FC	0.089 (0.066)	0.0872	00
H.HED/10 in FC	0.065 (0.056)	0.12368	00
TRUSTP in SC	-0.016 (0.068)	0.40567	00
TRUSTG in VSC	0.004 (0.074)	0.47225	00
MEMB.2008 in NGOs	0.317 (0.104)	0.00746	0+
CONFAE.2008 in NGOs	0.068 (0.062)	0.13418	00
REIGN.2008 in ERV	-0.144 (0.077)	0.02876	00
INTERF.2008 in ERV	-0.184 (0.143)	0.10071	00

453

454 Table 7. Increment of the proportion of dynamic of Sealed Area. Summary of the estimators of the
455 socio-economic variables in the twelve main models (all models in Table 2 except the null model) for
456 the increment between 2006 and 2009 of the proportion of Sealed Area. See Table 4 legend for the
457 meaning of the signs used for magnitude analysis (last column). See Tables 1 and 2 for the content of
458 the models and the definition of the explanatory variables.

459

460 The only *additional* variable (in Table SM1) that was found to be very significant according
461 to our standards for additional variables was the opinion that “freedom is more important than
462 equality” (FREED.2008), which was positively associated with the proportion of Sealed area
463 (SEAL,cf. Table SM4).

464

465 Generally, we did not detect any very significant discrepancy between the data and the best model by
466 using posterior goodness-of-fit p-values for the proportion of protected area, sealed area, increase in
467 sealed area or extinct species. Skewness of normalized data ($p < 0.001$) revealed a significant
468 discrepancy, however, for the best model for Threatened.

469

470 Discussion

471 Patterns of biodiversity loss are, of course, more complicated than shown in the simple models we
472 fitted. Our results highlight a new potential indicator for the ecological footprint, gross domestic
473 product per area (GDPa), which appears to robustly explain the two indicators of State of biodiversity
474 we analyzed (the proportions of extinct and threatened species). Our results also indicate the
475 prominent role of human population density (HPD), especially when log-transformed, except for the
476 proportion of protected area.

477 Empirical Findings

478 Surprisingly, we did not find any strong relationship between the proportion of protected area and our
479 socio-economic variables. Indeed, none of these relationships was significant, even at the 5% level
480 (Table SM3). This is in contrast with the results summarized by Luck (2007) who reported a negative
481 relationship between human population density (HPD) and protected areas – however, the metrics
482 Luck considered for protected areas, from area proportion to absolute area, were not all consistent
483 with area proportion as used in our study.

484 In an extensive study, Blaikie and Brookfield (2013) advocated the need to implement land
485 management practices that would avoid land degradation induced by human activities. Following this
486 seminal work, a vast amount of literature was published on the issue of land degradation or land
487 sealing, which mostly studied the factors determining the degree of land degradation (Salvati and
488 Zitti, 2009; Kizos et al, 2016). There are fewer studies about the impact of soil sealing on biodiversity
489 at a macro (cross-country) level. Our results reveal the same trends as those reported by Luck (2007)
490 for HPD and protected areas (see above): our best models involved HPD, HPDu or GDPa (Table 3)
491 and the effects of HDP and HPDu were significant and mildly strongly positive (Tables 6 & 7).
492 If previous references are scarce on the link between socio-economic variables and the Pressure and
493 Response indicators we used, the literature is more abundant on our two State indicators – the
494 proportion of threatened species and, to an even greater extent, the proportion of extinct species.
495 Indeed, regarding the statistical models for the proportion of threatened species, our results are very
496 much in agreement with those of Gosselin (2015) in terms of the statistical significance of the
497 relationships for economic variables. Our model *eco* is a simplified version of the models in Gosselin
498 (2015). As did Gosselin (2015), we found that, for threatened species, these models are not
499 particularly better than the null model as judged from their LOOIC value (cf. Table 3). Noticeably, a
500 similar model with log-transformed variables yielded much better results (model *leco* in Table 3). The
501 two socio-economic variables that stand out are HPD and GDPa – a relatively new metric of
502 development intensity calculated by unit of area and not per capita as usual. HPD and GDPa are
503 highly correlated (cf. Figure SM1), in agreement with Liu et al. (2005) – and their associated models
504 (IKuznetsa, Kuznetsa & leco) stand out as the best explanatory variables/models for variations in the
505 proportion of both extinct and threatened species in European countries (Tables 3, 4 and 5). Our
506 results are quite consistent with previous findings where HPD was significantly and positively
507 associated to the proportion of threatened or extinct species (Hoffmann, 2004; McPherson and
508 Nieswiadomy, 2005; Luck, 2007; Pandit and Laband, 2007). In contrast, we did not find any
509 significant relationship with income inequality, as had been reported by Holland et al. (2009) and
510 Mikkelsen et al. (2007).

511 In terms of magnitude, starting with proportions of extinct species and threatened species of 3.0 and
512 30.0% respectively, doubling HPD would correspond to increasing these proportions to 4.0 (+/-0.3) %
513 and 33.9 (+/- 1.4) % respectively, while doubling GDPa would yield 3.7 (+/-0.3) % and 34.4 (+/- 1.4)
514 % respectively. We therefore judge that these effects are of intermediate strength.

515 Our results seem to validate some sort of “Kuznets curve”, involving either the logarithm of GDPa or
516 of the very correlated HPD. This implies that human pressure on biodiversity should tend to slow
517 down as human activity – measured through either HPD or GDPa – grows. However, this does not
518 mean that the relationship between human pressure and biodiversity will turn negative for high levels
519 of human pressure since in the logarithm version of the Kuznets model with GDPa the quadratic term
520 is non-significant for the proportion of both extinct and threatened species. We therefore have no sign
521 that continuing growth will have a positive impact on biodiversity for high levels of development.

522 Of course, testing our results on a larger sample of countries would also be pertinent. However, the
523 data we used for extinct and threatened species were at the national scale (cf. Essl et al., 2013), not at
524 the global scale defined by the IUCN and used in many other publications (e.g. McKinney, 2002a,
525 2002b; Hoffmann, 2004; Clausen and York, 2008; Holland et al., 2009). Despite ongoing initiatives,
526 such national-scale red lists are, to the best of our knowledge, not yet available for an extended list of
527 countries outside Europe. It would also be interesting to include other indicators of human activity
528 than the ones studied here. Candidates include total human population (and not its density; cf.
529 McKinney, 2002a; Brown and Laband, 2006; Clausen and York, 2008), spatial concentration of
530 population (Pandit and Laband, 2007 in line with considerations in e.g. Ehrlich & Holdren, 1971), or
531 the variables devised by Hoffmann (2004) related to increases over time in HPD or GDP, or levels of
532 energy consumption.

533 **Potential Mechanisms**

534 Our results clarify the potential mechanisms behind biodiversity erosion at the country level. Indeed,
535 the high number of theoretical models attempting to explain the Environmental Kuznets Curve (EKC)
536 make it difficult to discriminate among mechanisms (Dinda, 2004; Kijima et al., 2010). The lack of

537 robustness for empirical results on EKC, as well as the curve's loose theoretical foundations, have led
538 several authors to suggest giving up the search for relations between aggregate data and focusing
539 instead on the processes at play in each national situation (Stern 2004). In this vein, integrative
540 models have been developed to take into account a variety of contextual parameters (e.g Verboom et
541 al., 2007). The search for macro-relations goes on, however, in the context of growth theory. For
542 example, Brock and Taylor (2010) show that the EKC and many empirical results can be derived as
543 an extension of a basic growth model by adding a pollution compartment. Our results using GDP per
544 area provide a strong argument that economic activity is a major driving force for biodiversity
545 erosion.

546 Even if our models with sociological variables have a lower predictive power than our best economic
547 models, two fundamental cultural (FC) variables seemed to have a robust effect: "Long-term
548 orientation" (H.LT) and "Hedonism" (H.HED). Both had a positive sign for the two State indicators
549 and for the sealed area Pressure indicator – with non-negligible relationships for the proportion of
550 extinct species and sealed area –, thus indicating that these variables negatively impact biodiversity
551 indicators related to past trends (extinct species and sealed area) more than they do indicators related
552 to current trends (threatened species and increment in sealed area). While this result is not surprising
553 for hedonism, which could translate into a preference for material goods over preserving nature, it is
554 more surprising for "long-term orientation". In fact, both seeking profit (hedonism) and investing
555 (long-term) are core values of capitalism. Consequently, the causal chain seems to run from
556 fundamental cultural values (FC) to economic growth, then to biodiversity.

557

558 Interpersonal trust (TRUSTP) reaches significant negative estimates for both biodiversity State
559 indicators; an increase in Interpersonal trust leads to a decrease in biodiversity erosion. This result is
560 interesting because trust is also generally considered to be a key component of social capital, which
561 promotes economic growth. The fact that interpersonal trust is also positively associated with
562 biodiversity suggests that a high-quality social life acts positively on concern for the environment.
563 Surprisingly, trust in government (TRUSTG) is positively associated with biodiversity erosion
564 (whereas, classically, it is also positively correlated with economic activity). One explanation could

565 be that collective action (or a demand for action on the part of the government) may act either in favor
566 of the environment or against it, in order to promote economic interests, for instance.

567

568 Membership in environmental associations (MEMB.2008) was often positively associated with
569 biodiversity erosion or land sealing. This could reflect a reaction to a deteriorated state of the
570 environment, rather than signal the existence of fundamental environmental values (this variable
571 might therefore be classified as a Response indicator in the DPSIR scheme). The belief that
572 interference with nature is often disastrous (INTERF.2008) was negatively associated with
573 biodiversity erosion only for extinct species, suggesting a weak relationship between environmental
574 concern and biodiversity. Lastly, and surprisingly, the belief that “man should reign over nature”
575 (REIGN.2008) was positively associated with some indicators of biodiversity, i.e. associated with less
576 soil sealing or a lower proportion of extinct species, suggesting that “reign over nature” may convey a
577 protective, stewardship view, and not only an extractive one.

578

579 **Policy implications**

580 The main driver of biodiversity erosion seems to be economic activity. Our results suggest that the
581 spatial density of economic activity (economic growth; variable GDPa) or human population (variable
582 HPD) in particular are key variables that are positively related to land sealing levels – interpreted here
583 as a pressure on biodiversity – and to both past and current biodiversity erosion. Echoing e.g. Ehrlich
584 and Holdren (1971), our results clearly indicate that the spatial density of human activity should be
585 part of political analyses related to biodiversity. Variables related to spatial density of human activity
586 should integrate systems of biodiversity indicators.

587

588 Our results may seem discouraging: it is difficult to promote policies which discourage economic
589 growth in a period of economic crisis. However, information and education can alter social and
590 cultural attitudes, for example by lowering “hedonism”, which our results show to be detrimental to

591 biodiversity. Brahic and Rambonilaza (2015) have shown, for example, that providing visitors with
592 information on the quality of forest ecosystems significantly alters the value they attribute to these
593 ecosystems. Education and information often involve associations, whose activity in turn reinforces
594 social capital and trust in other people, which, as we have seen, are conducive to both economic
595 prosperity and a better state of biodiversity. Increasing social trust should therefore be an overarching
596 government objective.

597

598 Land use appears to be a crucial aspect in both biodiversity protection and the interrelation between
599 biodiversity and economic activity. That is why ecological compensation (or biodiversity offset)
600 policies are crucial in favoring cohabitation between economic activity and ecosystem quality (Bull et
601 al., 2013). Such policies have been adopted in many countries; they impose compensation for
602 biodiversity loss on any project which negatively impacts natural habitats. If correctly designed,
603 offsetting policies can even create new jobs (restoration activities or ecological engineering,
604 alternative forms of agriculture and tourism). In practice however, they are often poorly implemented,
605 due to the difficulty of clearly evaluating ecological impacts and to the lack of effective monitoring
606 and enforcement systems.

607

608 **Conclusion**

609 Despite our small sample size, our results allow a general picture to emerge. Economic activity
610 appears to be a strong component of human pressure on biodiversity, and the spatial density of this
611 pressure – either in terms of economic growth or human population – should be taken into account.
612 Our results seem to validate the “Kuznets curve” when the spatial density of growth is considered
613 instead of per capita growth, which indicates that human pressure should tend to slow down as the
614 spatial density of human activity increases. However, we should not conclude that continuing growth
615 will have a positive impact on biodiversity, first because the decrease shown by the Kuznets curve

616 might be due to the exportation of environmental pressures to poorer countries, and second, because
617 there is no sign of negative relationships for high levels of growth in models where growth has been
618 log-transformed.

619 The role of social values is not easy to decipher, but social trust, and to some extent concern for the
620 environment, seem to favor the preservation of biodiversity. This is good news since social trust is
621 also known to positively influence economic performance, and should be a natural target for
622 policymakers. Societies that function well as a whole are more likely to sustain both prosperity and
623 the quality of the environment.

624 Overall, our results cast a new light on old issues. They call for further studies around the new metric,
625 GDP per unit area, which seems more relevant than the classical GDP per capita, studies with more
626 data or with data reflecting smaller geographical scales. Finally, relationships and potential causalities
627 should be tested within the DPSIR framework, which would require new indicators for the other
628 components in that framework.

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631

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635

636 **References:**

637 Arrhenius, O., 1921. Species and area. *J. Ecol.* 9, 95-99.

638 Asafu-Adjaye, J., 2003. Biodiversity loss and economic growth: A cross-country analysis. *Contemp.*
639 *Econ. Pol.* 21, 173-185.

640 Barbier, S., Chevalier, R., Loussot, P., Bergès, L., Gosselin, F., 2009. Improving biodiversity
641 indicators of sustainable forest management: tree genus abundance rather than tree genus richness and

642 dominance for understory vegetation in French lowland oak hornbeam forests. *For. Ecol. Manag.* 258,
643 S176-S186.

644 Bjørnskow, C., 2006. The multiple facets of social capital. *Eur. J. Political Econ.*, 22, 22-40.

645 Blaikie, P.M., Brookfield H., 2013. *Land degradation and society*. Routledge Revival, London.

646 Brahic E., Rambonilaza T., 2015. The impact of information on public preferences for forest
647 biodiversity preservation: a split-sample test with choice experiment method. *Revue d'économie*
648 *politique* 125, 152-171.

649 Brock W.A., Taylor M.S., 2010. The Green Solow model. *J. Econ. Growth* 15, 127-153.

650 Brown, J.H., 1999. Macroecology: Progress and prospect. *Oikos* 87,3-14.

651 Brown, R.M., Laband, D.N., 2006. Species imperilment and spatial patterns of development in the
652 United States. *Cons. Biol.* 20, 239-244.

653 Bull, J.W., Suttle, K.B., Gordon, A., Singh, N.J., Milner-Gulland, E.J., 2013. Biodiversity offsets in
654 theory and practice. *Oryx* 47, 369–380.

655 Butchart, S.H., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J.P. et al., 2010. Global
656 biodiversity: Indicators of recent declines. *Science* 328, 1164-1168.

657 Callois, J.M., Schmitt. B., 2009. The role of social capital components on local economic growth: the
658 case of French rural areas. *Rev. Agric. Envir. Studies* 90, 257-286.

659 Camp, R.J., Seavy, N.E., Gorresen, P.M., Reynolds, M.H., 2008. A statistical test to show negligible
660 trend: *Comment. Ecology* 89, 1469-1472.

661 Chambers, D., Hamer, S., 2012. Culture and growth: Some empirical evidence. *Bull. Econ. Res.* 64,
662 549-564.

663 Clausen, R., York, R., 2008. Global biodiversity decline of marine and freshwater fish: A cross-
664 national analysis of economic, demographic, and ecological influences. *Social Sci. Res.* 37, 1310-
665 1320.

666 Coleman, J. S., 1988. Social capital in the creation of human capital. *Amer. J. Sociol.* 94, S95-S120.

667 Daniels, S.R., Greenberg, R.S., Ibrahim, M.A., 1983. Etiologic research in pediatric epidemiology. *J.*
668 *Pediatrics* 102, 494-504.

669 Dasgupta, P., 2000. Economic Progress and the Idea of Social Capital, in: Dasgupta, P., Serageldin, I.
670 (Eds), Social capital: A multifaceted perspective.. The World Bank, Washington DC, pp. 325-424.

671 Dietz, T., 2017. Drivers of human stress on the environment in the twenty-first century. *Annu. Rev.*
672 *Envir. Resources* 42, 189-213.

673 Dinda, S., 2004. Environmental Kuznets Curve hypothesis: A survey. *Ecol. Econ.* 49, 431-455.

674 Dullinger, S., Essl, F., Rabitsch, W., Erb, K.H., Gingrich, S. et al., 2013. Europe's other debt crisis
675 caused by the long legacy of future extinctions. *Proc. Nat. Acad. Sci. USA* 110, 7342-7347.

676 Dunn, P.K., Smyth, G.K., 1996. Randomized quantile residuals. *Journal of Computational and*
677 *Graphical Statistics* 5, 236-244.

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

679 Essl, F., Moser, D., Dirnböck, T., Dullinger, S., Milasowszky, N. et al., 2013. Native, alien, endemic,
680 threatened, and extinct species diversity in European countries. *Biol. Cons.* 164, 90-97.

681 Fahrig, L., 2003. Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology and*
682 *Systematics* 34, 487-515.

683 Forest Europe, UNECE, FAO, 2011. State of Europe's forests 2011. Status and trends in Sustainable
684 Forest Management in Europe. FOREST EUROPE Liaison Unit Oslo.

685 Forest Europe. 2015. State of Europe's forests 2015.- FAO & EFI.

686 Gari, S.R., Newton, A., Icely, J.D., 2015. A review of the application and evolution of the DPSIR
687 framework with an emphasis on coastal social-ecological systems. *Ocean Coast. Manage.* 103, 63-77.

688 Gaston, K.J., Blackburn, T.M., 1999. A critique for macroecology. *Oikos* 84, 353-368.

689 Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. *Bayesian Data Analysis*, second ed..
690 Chapman & Hall, Boca Raton.

691 Gosselin, F., 2011. A New Calibrated Bayesian Internal Goodness-of-Fit Method: Sampled Posterior
692 p-values as Simple and General p-values that Allow Double Use of the Data. *PLOS ONE* 6, e14770.

693 Gosselin, F., 2015. Reevaluating Europe's other debt with improved statistical tools. *Biodiv. Cons.*
694 24, 205-211.

695 Harrell, F.E., 2001. *Regression Modeling Strategies, With Applications to Linear Models, Logistic*
696 *Regression, and Survival Analysis*. Springer, New York, USA.

697 Herpigny, B., Gosselin, F., 2015. Analyzing plant cover class data quantitatively: customized
698 cumulative zero-inflated beta distributions show promising results. *Ecol. Informatics* 26, 18-26.

699 Hoffmann, J.P., 2004. Social and environmental influences on endangered species: a cross-national
700 study. *Sociol. Perspect.* 47, 79-107.

701 Hofstede, G., 1980. *Culture's Consequences: International Differences in Work-related Values*.
702 Thousand Oaks, CA: Sage.

703 Holland, T.G., Peterson, G.D., Gonzalez, A., 2009. A cross-national analysis of how economic
704 inequality predicts biodiversity loss. *Cons. Biol.* 23, 1304-1313.

705 Kaufmann, R.K., Davidsdottir, B., Garnham, S., Pauly, P., 1998. The determinants of atmospheric
706 SO₂ concentrations: reconsidering the environmental Kuznets curve. *Ecol. Econ.* 25, 209-220.

707 Kijima M., Nishide K., Ohyama A., 2010. Economic models for the environmental Kuznets curve: A
708 survey. *J. Econ. Dynam. Control* 34, 1187–1201.

709 Kizos, T., Tsilimigkas, G., Karampela, S., 2016. What drives built-up area expansion on islands?
710 Using soil sealing indicators to estimate built-up area patterns on Aegean islands, Greece. *Tijdschrift*
711 *voor Economische en Sociale Geografie* 108, 836-853.

712 Krautkraemer, J.A. 1995. Incentives, development and population: a growth-theoretic perspective, in:
713 Swanson, T.M. (Ed.), *The economics and ecology of biodiversity decline: the forces driving global*
714 *change*. Cambridge University Press.

715 Liu, J., Liang, S.-C. , Liu, F.-H. , Wang, R.-Q. , Dong, M., 2005. Invasive Alien Plant Species in
716 China: Regional Distribution Patterns. *Divers. Distrib.* 11, 341-347.

717 Luck, G.W., 2007. A review of the relationships between human population density and biodiversity.
718 *Biol. Rev.* 82, 607-645.

719 McKinney, M.L., 2002a. Why larger nations have disproportionate threat rates: Area increases
720 endemism and human population size. *Biodiv. Cons.* 11, 1317-1325.

721 McKinney, M.L., 2002b. Effects of national conservation spending and amount of protected area on
722 species threat rates. *Cons. Biol.* 16, 539-543.

723 McPherson, M.A., Nieswiadomy, M.L., 2005. Environmental Kuznets curve: Threatened species and
724 spatial effects. *Ecological Economics* 55, 395-407.

725 Mikkelsen, G.M., Gonzalez, A., Peterson, G.D., 2007. Economic inequality predicts biodiversity loss.
726 PLOS ONE 2, e444.

727 Millar, R.B. 2009. Comparison of hierarchical bayesian models for overdispersed count data using
728 DIC and Bayes' factors. *Biometrics* 65, 962-969.

729 Millar, R.B., 2017. Conditional vs marginal estimation of the predictive loss of hierarchical models
730 using WAIC and cross-validation. *Statistics and Computing* 28, 375-385.

731 Panayotou, T., 1997. Demystifying the environmental Kuznets curve: turning a black box into a
732 policy tool. *Envir. Develop. Econ.* 2, 465-484.

733 Pandit, R., Laband, D.N., 2007. Threatened species and the spatial concentration of humans. *Biodiv.*
734 *Cons.* 16, 235-244.

735 Peters, R.H., 1991. *A critique for ecology*. Cambridge University Press, Cambridge.

736 R Core Team, 2016. *R: A language and environment for statistical computing*. 3.3.2. R Foundation for
737 Statistical Computing, Vienna, Austria.

738 Salvati, L., Zitti, M., 2009. Assessing the impact of ecological and economic factors on land
739 degradation vulnerability through multiway analysis. *Ecological Indicators* 9, 357-363.

740 Selden T.M., Song D., 1994. Environmental quality and development: is there a Kuznets curve for air
741 pollution emissions? *J. Envir. Econ. Manag.* 27, 147-162.

742 Shafik, N., 1994. Economic development and environmental quality: An econometric analysis.
743 *Oxford Econ. Papers* 46, 757-773.

744 Stan Development Team, 2015. *Stan Modelling language User's guide and reference manual*, V2.6.2.

745 Stern, D.I., 2004. The Rise and Fall of the Environmental Kuznets Curve. *World Dev.* 32, 1419-1439.

746 Vehtari, A., Gelman, A., Gabry, J., 2016. Practical Bayesian model evaluation using leave-one-out
747 cross-validation and WAIC. *Statist. Comput.* 5, 1413-1432.

748 Verboom, J., Alkemade, R., Klijn, J., Metzger, M.J., Reijnen, R., 2007. Combining biodiversity
749 modeling with political and economic development scenarios for 25 EU countries. *Ecol. Econ.* 62,
750 267-276.

751 Willis, J. C., 1922. *Age and area: a study in geographical distribution and origin of species*.
752 Cambridge University Press, Cambridge.

- 753 Wright, D.H., 1990. Human impacts on energy flow through natural ecosystems, and implications for
754 species endangerment. *Ambio* 19, 189-194.
- 755 Zak, P. J., Knack, S., 2001. Trust and Growth. *Econom. J.* 111, 295-321.
- 756