Europe's other debt crisis caused by the long legacy of future extinctions

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Rapid economic development in the past century has translated into severe pressures on species survival as a result of increasing land-use change, environmental pollution, and the spread of invasive alien species. However, though the impact of these pressures on biodiversity is substantial, it could be seriously underestimated if population declines of plants and animals lag behind contemporary environmental degradation. Here, we test for such a delay in impact by relating numbers of threatened species appearing on national red lists to historical and contemporary levels of socioeconomic pressures. Across 22 European countries, the proportions of vascular plants, bryophytes, mammals, reptiles, dragonflies, and grasshoppers facing medium-to-high extinction risks are more closely matched to indicators of socioeconomic pressures (i.e., human population density, per capita gross domestic product, and a measure of land use intensity) from the early or mid-, rather than the late, 20th century. We conclude that, irrespective of recent conservation actions, large-scale risks to biodiversity lag considerably behind contemporary levels of socioeconomic pressures. The negative impact of human activities on current biodiversity will not become fully realized until several decades into the future. Mitigating extinction risks might be an even greater challenge if temporal delays mean many threatened species might already be destined toward extinction.

extinction debt | socioeconomic history | time lag

The progressive impact of environmental degradation on the loss of global biodiversity (1–4) is strongly linked to key socioeconomic indicators such as human population size (5), land use (6), and gross domestic product (GDP) (7, 8). However, species populations do not necessarily respond immediately to environmental degradation but might do so with a delay (9, 10). Such time-lags between environmental forcing, population decline, and, finally, extinction create a transient disequilibrium between environmental conditions and species' abundance or range size, which has been conceptualized as "extinction debt" (9). Recent empirical research has shown that, at the scale of individual habitat patches, a delayed response of species to habitat loss and fragmentation is indeed often detectable, particularly among habitat specialists (9–11). The likelihood and magnitude of extinction debt is still contentious, however (12, 13), and seems to vary with the nature of environmental degradation and with the life history traits of the species concerned (14–18). In long-lived or less-mobile taxa (e.g., vascular plants, bryophytes, reptiles), a delayed response of populations to the deterioration and fragmentation of their habitats is especially likely and might extend over at least several decades.

If time-lags in population decline at the scale of individual habitats are a common phenomenon, the number of species facing extinction risks at larger spatial scales might easily be underestimated because many local populations of extant species might not survive in the long-term even if further environmental degradation is halted. Thus, red lists describing threatened species at either a national or global scale, which identify species extinction risks using criteria such as a reduction in population size, range size, and perceived rate of recent population or range decline (19), might be too optimistic. However, despite the recent increase in interest in the potential for temporal lags in population declines and extinction processes (8, 10, 12, 17), evidence for extinction debt has not yet been examined for a broad range of taxa at a spatial scale consistent with national or global decision-making. Given that many conservation policies in Europe (and elsewhere) are developed and implemented at regional to global scales (e.g., Ramsar Convention and Convention on Biological Diversity) and reported at the level of individual countries, assessing extinction debt at this scale would appear to be a crucial step.

Here, we provide such an assessment by analyzing national red lists (NRL) of threatened species of seven taxonomic groups (vascular plants, bryophytes, mammals, fish, reptiles, dragonflies, and grasshoppers) from 22 European countries (Tables S1 and S2) in relation to the magnitude of contemporary as well as historic drivers of environmental degradation. Red lists provide an objective framework for the classification of the broadest range of species according to their extinction risk based on the current trend in population size, geographic range, and area of occupancy (19). We focus on Europe because this is the only continent where NRLs have become recently available, and are regularly updated, for a range of taxonomic groups across more than 20 countries using standard approaches to the listing of threatened species. Our analysis is based on a rationale similar to the one used in Essl et al. (5) for evaluating delays in alien species invasions: if NRLs provide an accurate estimate of the number of species at risk under the current magnitude of human pressures on biodiversity, these numbers should best correlate with the spatial variation in contemporary levels of these drivers. If, by contrast, time-lags between different human pressures and subsequent species responses occur, the number of threatened species should better reflect historic rather than contemporary values of these drivers. We measure the values of these drivers by three indicators of human socioeconomic activities that are known proxies of environmental pressures on biodiversity (2, 7, 8, 20): human population density (PD), per capita GDP, and human appropriation of net primary production (HANPP) (21). We estimated HANPP as the ratio of the net

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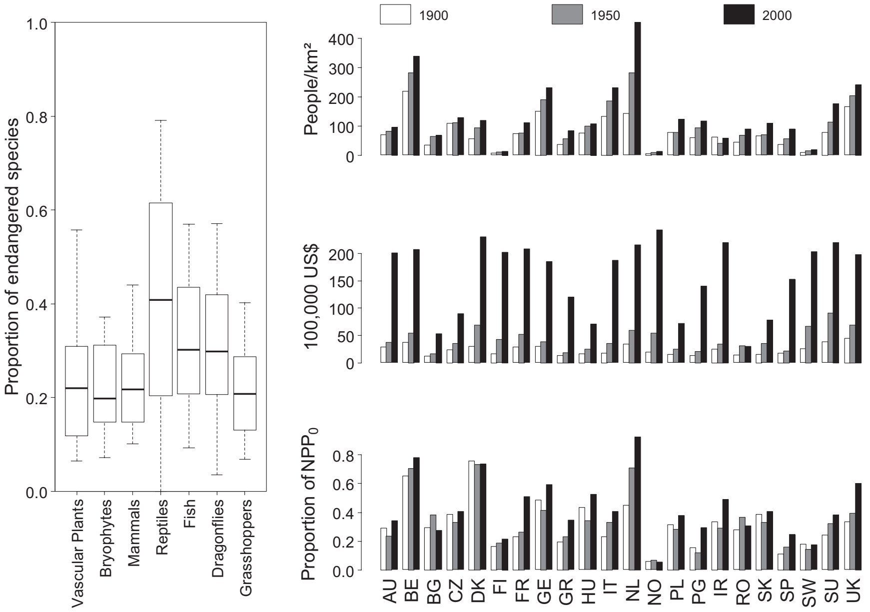

Fig. 1. Proportions of species facing medium-to-high extinction risks in NRLs and trends in socioeconomic indicators in Europe over the 20th century. (*Left*) Proportions of threatened species (IUCN categories EN, VU, CR) per taxonomic group across 22 European countries. (*Right*) Levels of three socioeconomic variables [human population density in people square kilometer; per capita GDP in 100,000 International Geary–Khamis dollars; and human appropriation of net primary productivity, which is defined here as the proportion of the total net primary productivity harvested by humans to the net primary productivity of the potential vegetation (NPP_0)] for the years 1900, 1950, and 2000. See Table S1 for country codes.

primary productivity harvested by humans (NPP_h) to the NPP of potential vegetation (NPP_0). HANPP is therefore the hypothetical undisturbed vegetation cover of the harvested area and is a useful proxy for land use intensity.

We use generalized linear and mixed-effects models with a logistic link function (*Materials and Methods*) to relate these three indicators evaluated for both the early (1900–1910) and the mid-20th century (1950) as well as for the recent past (year 2000) to the proportions of national floras and faunas listed as threatened [International Union for Conservation of Nature (IUCN) categories endangered (EN), vulnerable (VU), and critically endangered (CR)] on NRLs and compare how the data support these three alternative models. We have chosen socioeconomic data from the early 20th century to represent pre-World War I conditions, whereas the situation in 1950 precedes the phase of rapid growth of the European economies after World War II.

Results

Averaged across the 22 countries, between ∼20% and 40% of the species examined are currently considered as facing medium-to-high extinction risks with reptiles, fish, and dragonflies figuring most prominently on NRLs (Fig. 1). The indicators of human socioeconomic activities have increased considerably during the 20th century, but at different rates in individual countries (Fig. 1). Consequently, the cross-national variation in the magnitude of these indicators is correlated across time, but with some scatter (Fig. S1).

Joint analysis across all seven taxonomic groups demonstrates that values of socioeconomic activity explain current red-listed species numbers better the longer they date back into the past (Tables 1 and 2). The difference is particularly pronounced between models using socioeconomic data from 1900 and those using data from the subsequent time points; this is true for multivariate models of the combined effect of all three indicators and for any single variable model comprising only one individual indicator.

The multivariate models of each individual taxonomic group demonstrate that the 1900 data best explain current proportions of threatened species of bryophytes, vascular plants, dragonflies, and grasshoppers (Fig. 2; Table 3). With respect to vertebrates, the results are less clear, with threatened fish being most closely correlated to contemporary indicator levels, whereas for mammals and reptiles, the models of 1900 and 1950 have similar support (Fig. 2).

The environmental Kuznets curve hypothesis proposes that wealthier economies tend to reduce their impact on the environment by increasing expenditure toward environmental management and protection (20, 22). Because investment in such measures has played a much more important role toward the end of the 20th century than in the previous 100 y, its potential mitigating effects might bias correlations between indicators of socioeconomic activity and numbers of threatened species toward a historical explanation. To test for such a bias we repeated all analyses after adding country-specific values of recent environmental

Table 1. Proportions of threatened species from seven taxonomic groups and 22 European countries as explained by multivariate models of historical or current socioeconomic indicators

	1900	1950	2000
PC1	−0.31	−0.23	−0.15
PC2	0.13	0.04	0.06
PC3	−0.20	−0.10	−0.06
R^2_{MF}	0.22	0.09	0.04
AIC	4,830	5,637	5,943
AW	>99.9	<0.01	<0.01

Fixed-effect estimates, McFadden's R^2, Akaike information criterion (AIC), and Akaike weights (AW) for generalized linear mixed-effects models relating the variation in the proportion of red-listed species to either historical (1900 and 1950) or contemporary (2000) values of impact indicators. The three impact indicators—human population density (PD), per capita GDP (GDP), and human appropriation of net primary productivity (HANPP)—were subjected to a principal component analysis before fitting the regression models to remove multicollinearity among independent variables (PC1–PC3). All fixed-effect estimates are different from 0 with a probability >0.99.

Table 2. Proportions of threatened species from seven taxonomic groups and 22 European countries as explained by single variable models of historical or current socioeconomic indicators

	1900	1950	2000	1900	1950	2000	1900	1950	2000
PD	0.18	0.15	0.13						
GDP				0.23	0.14	0.01			
HANPP							0.35	0.23	0.16
R^2_{MF}	0.06	0.04	0.03	0.10	0.04	0.00	0.18	0.08	0.04
AIC	5,837	5,972	6,043	5,599	5,986	6,213	5,085	5,730	5,950
AW	>99.9	<0.01	<0.01	>99.9	<0.01	<0.01	>99.9	<0.01	<0.01

Fixed-effect estimates, McFadden's R_2, Akaike information criterion (AIC), and Akaike weights (AW) for generalized linear mixed-effects models relating the variation in the proportion of red-listed species to either historical (1900 and 1950) or contemporary (2000) values of impact indicators. All fixed-effect estimates are different from 0 with a probability >0.99.

expenditures as an additional independent variable. This extension indeed improved model fit (compare Tables 1 and 2 and Table S3; Akaike weights >99.9 in favor of the models with the expenditures included); however, it did not change the relative ranks of the models from 1900, 1950, and 2000, except for fish, which appear most closely correlated to socioeconomic activity from 1950 rather than 2000, when expenditures are taken into account (Fig. S2).

Discussion

Even though human impacts on the environment greatly intensified following World War II (3, 6, 23, 24), our results suggest that the current threat status of many species reflects a legacy of several decades, and for four taxa even as much as a century. Such extended time-lags have indeed been observed in habitat-scale studies on vascular plants (12, 18) or cryptogams (25) for which historic indicators most markedly outperformed current indicators in explaining the proportion of threatened species in our country-scale study as well (Table 3). Contrary to common expectations (10, 26), however, the risks faced by taxonomic groups represented by short-lived species such as dragonflies and grasshoppers seem to reflect human impacts on the environment with a delay similar to that for plants. For a similar taxonomic group, butterflies, the available empirical evidence for delayed population response to habitat loss is mixed with some studies reporting rather fast (several years) (12, 27) and others relatively long (several decades or more) relaxation times (17). In addition, theoretical simulations have suggested that the delay in insect metapopulation extinctions can extend well beyond 100 y (28), and that their lag times are particularly long if available habitat networks are reduced to levels close to the extinction threshold (29), as might be the case in many landscapes of Europe where an intensively used agricultural matrix is interspersed by remnants of near-natural and nonintensively used habitats (30).

For the vertebrate taxa, time-lags between socioeconomic indicators and population decline appear to be less pronounced. In particular, fish were the only taxonomic group for which extinction risks appear more closely correlated to contemporary indicators. We do not know why fish behave differently, but it might be that anthropogenic impacts on freshwater ecosystems, such as water pollution, channelization, construction of dams, and water abstraction (31), have a more immediate effect because they not only reduce the quality and quantity of habitats, but directly and uniformly modify the medium in which species live. Additionally, historic legacies might be masked by the particularly intense but more recent modification of the aquatic environments (23). Mammals, however, might be particularly sensitive to habitat loss and fragmentation because they often need large contiguous habitats for survival (32) and can hence reach their extinction thresholds (29) during an earlier stage of habitat degradation and loss.

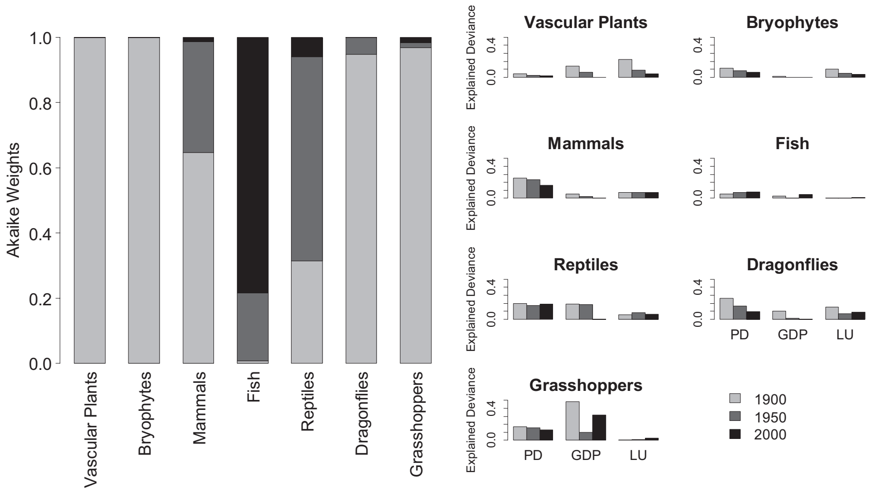

Fig. 2. Proportions of species facing medium-to-high extinction risks from seven taxonomic groups in 22 European countries (for data sources, see Table S2) as explained by current and historic socioeconomic models. (*Left*) Relative support (Akaike weights) for multiple logistic regressions models explaining the proportions of red-listed species by historical (1900, light gray; 1950, dark gray) or contemporary (2000, black) levels of socioeconomic impact indicators. The three indicators (human population density, per capita GDP, human appropriation of net primary productivity) were subjected to a principal component analysis before fitting the regression models to remove multicollinearity among explanatory variables. (*Right*) The deviance explained by simple logistic regression models relating the proportion of threatened species separately to either historical or contemporary levels of the three individual indicators: GDP, per capita GDP; LU, land use, i.e., human appropriation of net primary productivity; and PD, human population density.

Table 3. Goodness of fit of models relating the proportion of threatened species from seven different taxonomic groups across 22 European countries to either historical or contemporary socioeconomic impact indicators

	AIC$_{1900}$	AIC$_{1950}$	AIC$_{2000}$	D^2_{1900}	D^2_{1950}	D^2_{2000}
Vascular plants	3,589	4,458	4,824	0.30	0.13	0.05
Bryophytes	828	861	873	0.14	0.10	0.09
Mammals	177	179	185	0.27	0.25	0.19
Fish	212	206	203	0.01	0.15	0.17
Reptiles	139	138	143	0.26	0.27	0.22
Dragonflies	171	177	193	0.26	0.22	0.10
Grasshoppers	103	111	111	0.51	0.39	0.40

Akaike Information Criterion (AIC), and Explained Deviance (D^2) of multiple logistic regression models. The three indicators (human population density, per capita GDP, and human appropriation of net primary productivity) were subjected to a principal component analysis before fitting the regression models to remove multicollinearity among explanatory variables.

In conclusion, our results suggest that our perception of extinction risks at large geographical scales lags considerably behind increases in socioeconomic pressures on biodiversity across different taxonomic groups. With respect to the future, this long lag time implies that contemporary human pressures have already influenced the threat that biodiversity will face in the next decades, and this is underestimated by current NRLs. Indeed, the rapid recent increase in socioeconomic activity has triggered new, or at least greatly intensified, pressures on biodiversity arising from processes such as atmospheric nitrogen or acidic deposition (33), biological invasions (5, 34, 35), and climate change (2), which now reinforce and synergistically interact with habitat loss and fragmentation, the main drivers of population decline and extinction in the past. Although these novel pressures have rarely been studied in an extinction debt context (10), their effects on biodiversity might be characterized by similarly long lag times (5, 18). For example, both recent observations (36) and modeling studies (37) suggest that range adaptations of native species to changing climates considerably lag behind the velocity of climate change (38) and that remnant populations (39) currently occupy sites that are no longer climatically suitable for them in the long run (18).

Given this accumulating extinction debt from different sources, reducing further pressures on ecosystems might not be sufficient to reduce future biodiversity loss. In addition, long lag times might also blur cause–effect relationships, and if delayed responses by species to historic drivers (e.g., land use change) are confused with responses to more recent phenomena (e.g., climate change), mitigation measures might target the wrong drivers. Our results, combined with the evidence of both global (4) and European (40) failure to reach the 2010 biodiversity target, suggest current commitments to stop biodiversity loss in the region are even more inadequate than currently appreciated. From a global perspective, the extended time lags in extinction risk in Europe might also be a feature of other industrialized regions that have followed a similar development path—e.g., North America and Australia (6). Future measures to counter extinctions in these areas will probably require the mobilization of efforts well beyond current investment in conservation policies and importantly account for both new drivers of population declines as well as for those that have acted for over a century. Minimizing the magnitude of the "sixth extinction crisis" (41) might be an even greater challenge when temporal delays are taken into account.

Materials and Methods

Total and Red List Species Numbers. We extracted total species numbers from national checklists, standard faunas, and floras, with some updates by national experts. Numbers of threatened species included on red lists were taken from the most recent NRLs, >90% of which have been published between 1995 and 2010 (Table S2). We have included only species that face medium-to-high extinction risks (IUCN categories EN, VU, and CR) (19), which are generally referred to as threatened species. We excluded species that had already gone extinct [extinct (EX) and extinct in the wild (EW)] to avoid bias in favor of an historical explanation. We used the recent NRLs in Europe that were developed following standardized criteria established for national to global red listing led by the IUCN since the 1990s (19). The five IUCN criteria for assessing extinction risks are based on current status and trends in population size, geographic range, and area of occupancy, and include quantitative analyses of extinction risks (e.g., population viability analysis).

Socioeconomic Indicators. The scarcity of historical socioeconomic data limited our sample size to 22 countries (Table S1), but these are representative of the variation in European socioeconomic trajectories and include nations from both sides of the former Iron Curtain. Data on current and historical population densities and per capita GDP were taken from the Total Economy Database (www.ggdc.net/databases/ted.htm). We standardized current and historical per capita GDP to 1990 International (Geary–Khamis) dollars, a hypothetical currency unit with the same purchasing power that the US dollar had in the United States in 1990. In calculating net primary productivity harvested by humans NPP$_h$, we used a broad definition of harvested NPP (21), which encompasses biomass extracted for further economic use and biomass destroyed during harvest.

Calculation of HANPP. As a proxy for land use intensity we used an indicator that measures the human impact on trophic energy availability in ecosystems, thereby quantifying the human influence on certain important ecosystem processes (42, 43). We divided the total amount of harvested NPP$_h$ by the NPP of the potential vegetation, i.e., the vegetation assumed to exist in the absence of human land use (NPP$_0$) to take biogeographic variation in natural productivity into account. The ratio NPP$_h$/NPP$_0$ is an indicator of land use intensity, and it is one variant of HANPP for which several empirical studies (44–46) support the hypothesis that it is a valid indicator of pressures on biodiversity (47). Different authors have used different definitions of HANPP. Vitousek et al. (42) proposed three definitions; the definition used here is similar, but somewhat less inclusive than Vitousek's intermediate definition also adopted by Rojstaczer et al. (48) and Imhoff et al. (49). Vitousek's intermediate definition includes the entire NPP of intensively managed ecosystems, whereas NPP$_h$ includes only plants actually harvested or destroyed during harvest.

We use an encompassing concept of biomass harvest that also includes biomass grazed by livestock and biomass destroyed during harvest, such as belowground biomass on cropland (21, 43). Data on the harvest of crops and timber are derived from statistical sources (50–54). Grazed biomass is estimated on the basis of feed balances using livestock and market feed data from the Food and Agriculture Organization and demand factors that considered species, region, and time (21, 55). Extraction of crop residues, harvest losses in forestry, and belowground biomass on cropland and harvested forest areas are estimated using region and time-dependent coefficients based on Krausmann et al. (56). NPP$_0$ was calculated for 1910 and 2000 (Table S4) with the LPJmL model (57). Both NPP$_h$ and NPP$_0$ are measured in terms of carbon content.

For a few countries, historic land-use data were only available for 1910. However, because land-use changes in Europe primarily occurred in the post-World War II period (6), we consider this approach to be justified.

Data Analysis. National floras and faunas of European countries vary considerable in species richness due to differences in country area, climatic conditions, biogeographic setting, and other factors. We accounted for this uneven distribution of regional biodiversity by considering the numbers of species on NRLs as proportions of the countries' total native floras and faunas (Table S2): our response variable was hence the average probability of a species from a country-specific species pool to be on a particular country's red list in the early 21st century. For analyzing the data across all seven taxonomic groups, we related the proportions of threatened species with the three socioeconomic variables by means of generalized linear mixed-effects models (GLMMs) with a logit link function for binomial error distributions (function *glmer* of the R package *lme4*) (58). We used each of the seven taxonomic groups as a grouping variable and estimated random effects for the intercept. More complex model structures with random effects for each predictor variable did not converge with the available fitting algorithms, especially in the case of multivariate regression models (see below).

For contemporary and historical economic conditions, we fitted such models separately for each of the three socioeconomic variables and for all three of them together. In the latter case, we first subjected the three variables of contemporary and historic socioeconomic pressures to principal component analyses (PCA) separately for each of the time points and then used the scores of the 22 countries on the three axes of these PCAs as explanatory variables in the GLMMs to avoid problems possibly arising from multicollinearity. The PCAs were done by means of a singular value decomposition of the centered and scaled data matrices as implemented in the R function *prcomp* (59).

For each fitted GLMM, we calculated the corrected Akaike information criterion (AIC_c), which includes a second-order bias correction appropriate for small sample sizes (60). We then compared the AIC_c of each model pair [with the same independent variable(s) from 1900, 1950, or 2000] by means of Akaike weights. Akaike weights are derived from AIC_cs and quantify the relative support for individual candidate models as the probability that each of them delivers the best explanation for a given dataset (60). In addition, we assessed goodness-of-model fit by calculating McFadden's R^2 values (61), defining the respective null models as GLMMs with an intercept term as the only fixed effect (and the same random effects).

Regression models that include each of the socioeconomic variables separately or in combination were also fit for each taxon separately using logistic regression [generalized linear models (GLMs) with a logit link function] instead of GLMMs. Goodness-of-GLM fit was evaluated by calculating the explained deviance (62) (D^2), and multivariable single-taxon models were compared by means of Akaike weights in the same way as described for GLMMs. Using the geographical coordinates of the country's capitals, we checked the residuals of all GLMs for spatial autocorrelation by calculating Moran's I for a neighborhood radius of 1,000 km (to guarantee that each country has at least one neighbor in the neighborhood matrix). The probability of getting an I value higher than the empirical one purely at random was assessed by means of 999 permutations of the vector of model residuals using the function *moran.mc* implemented in the R package *spdep* (63). To safeguard against possible bias from spatial autocorrelation, we refitted GLMs with a low such probability (<0.1) as autologistic models, i.e., by additionally introducing an autocovariate calculated by means of the function *autocov_dist* in the R library *spdep* (63). Residual autocorrelation was reduced in these autologistic models (with the exception of the grasshopper model for the year 2000, Table S5), and the probability of randomly generating an higher residual autocorrelation hence increased, but in no case was the ranking of goodness-of-fit reversed between historic and contemporary models compared with the respective ordinary GLMs. We hence consider our results robust and qualitatively unaffected by spatial autocorrelation.

To test for an eventual bias due to recent investments into environmental protection, we collected data on recent levels of public environmental expenditures of the 22 countries (in percent of GDP) extracted from the European Commission's Eurostat Web site (http://epp.eurostat.ec.europa.eu/tgm/table.do?tab=table&init=1&language=en&pcode=ten00049&plugin=0, accessed May 10, 2011; Table S4). We calculated the mean of the available data from the years 1998–2009, and repeated all multivariable GLMMs and GLMs using these expenditures as an additional covariate. All statistical analyses were done in R 2.13.1 (60).

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Supporting Information

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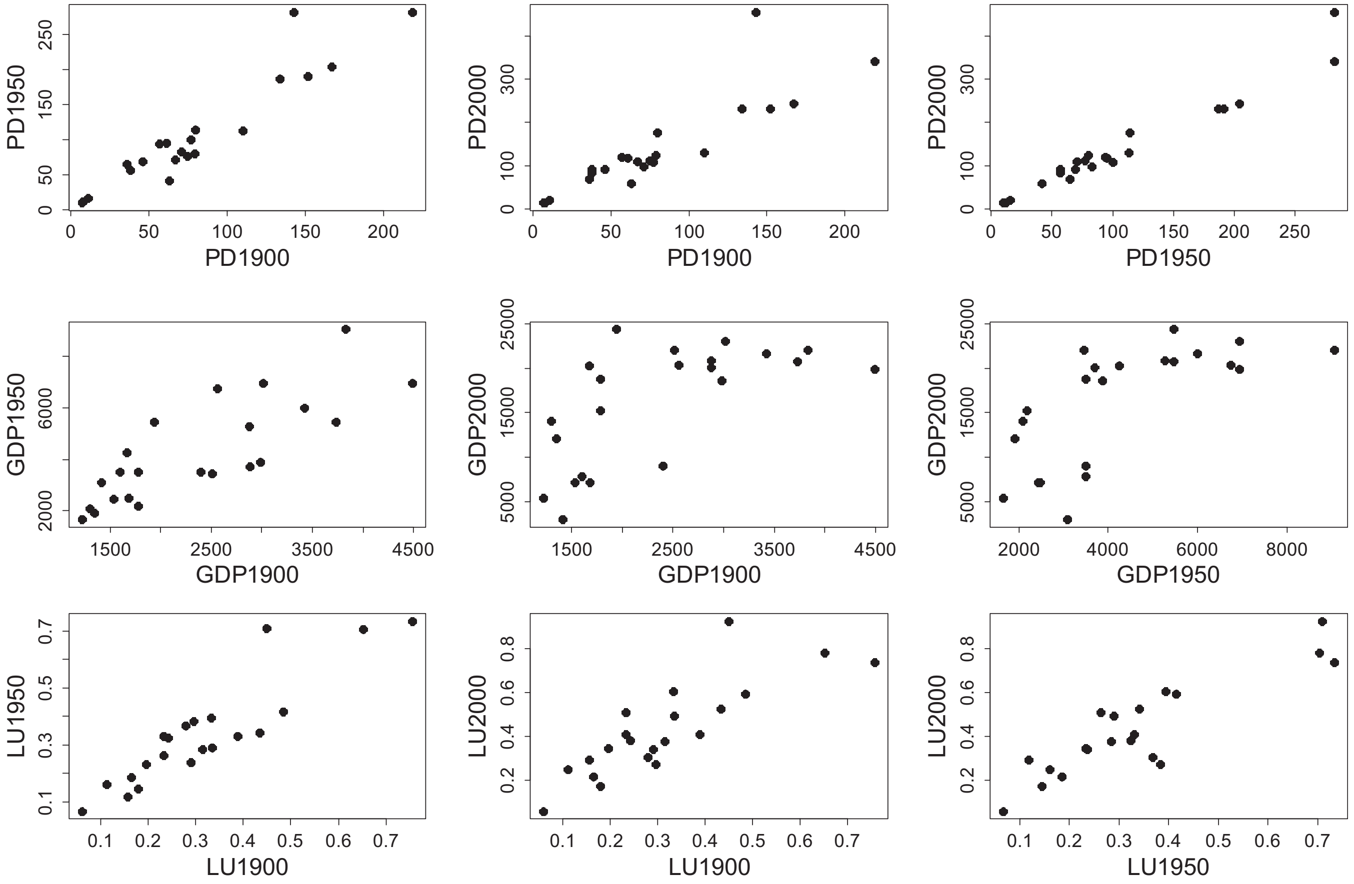

Fig. S1. Temporal correlations among socioeconomic variable levels in 22 European countries. GDP, per capita domestic product in 1,000 International Geary–Khamis follars; LU, land use, i.e., human appropriation of net primary productivity (NPP) as a proportion of the net productivity of the potential vegetation (NPP_0); PD, human population density in people per square kilometer.

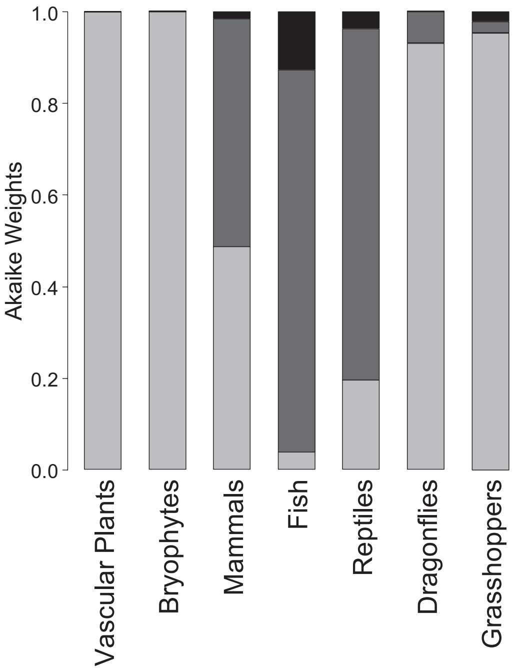

Fig. S2. Relative support (Akaike weights) for logistic multivariate regressions models explaining the variation in the proportion of threatened species in seven taxonomic groups among 22 European countries by historical (1900, light gray; 1950, dark gray) or contemporary (2000, black) levels of socioeconomic variables plus levels of recent public expenditures on environmental protection. The four independent variables were subjected to a principal component analysis before fitting the regression models to remove multicollinearity.

Table S1. Numbers of threatened and total number of native species from seven taxonomic groups in the 22 European countries covered by this study

	Vascular plants		Bryophytes		Mammals		Fish		Reptiles		Dragonflies		Grasshoppers	
	Total	Threatened	Total	Threatened	Total	Threatened	Total	Threatened	Total	Threatened	Total	Threatened	Total	Threatened
Austria (AU)	3,000	985	918	238	100	27	84	39	15	9	77	44	126	48
Belgium (BE)	1,700	380	729	182	79	25	54	20	8	4	69	30	50	13
Bulgaria (BG)	2,957	728	752	228	101	10	99	29	33	2	67	n.d.	201	n.d.
Czech Republic (CZ)	2,256	1,148	849	278	82	17	57	26	11	8	71	37	97	14
Denmark (DK)	1,050	405	n.d.	n.d.	50	11	48	12	8	0	50	11	33	5
Finland (FI)	1,500	180	856	123	69	7	55	8	5	2	55	4	30	4
France (FR)	4,650	384	n.d.	n.d.	109	11	69	15	37	10	93	n.d.	202	n.d.
Germany (GE)	2,700	772	1,121	333	96	21	89	22	13	8	81	42	76	29
Greece (GR)	4,992	538	n.d.	n.d.	106	29	79	45	55	11	77	n.d.	317	n.d.
Hungary (HU)	2,183	718	629	116	82	31	64	14	16	6	66	n.d.	122	15
Italy (IT)	4,674	553	800	277	110	48	48	27	49	21	90	n.d.	338	n.d.
Netherlands (NL)	1,490	335	832	151	55	8	46	17	7	5	71	20	45	10
Norway (NO)	1,360	217	1,062	142	73	9	48	10	6	0	48	13	29	2
Poland (PL)	2,350	224	925	164	92	13	66	11	8	3	73	7	79	15
Portugal (Pg)	3,800	327	n.d.	n.d.	104	17	52	n.d.	26	4	65	n.d.	126	n.d.
Republic of Ireland (IR)	950	128	828	156	26	3	35	6	1	0	29	8	14	3
Romania (RO)	3,297	210	900	65	101	29	97	9	24	19	67	n.d.	170	n.d.
Slovakia (SK)	3,000	903	935	301	87	20	67	20	12	5	73	25	119	14
Spain (SP)	5,050	1,128	n.d.	n.d.	118	23	68	24	56	14	82	18	371	n.d.
Sweden (SW)	1,556	266	1,037	107	63	13	65	21	6	2	56	2	35	3
Switzerland (SU)	2,600	939	1,093	401	83	27	55	24	19	15	72	24	105	37
United Kingdom (UK)	1,625	345	1,034	132	42	15	42	8	6	3	44	8	27	6

Threatened species from International Union for Conservation of Nature (IUCN) categories endangered (EN), vulnerable (VU), and critically endangered (CR). Taxonomic groups include vascular plants, n.d., not determined.

Table S2. Sources for numbers of threatened and total number of native species from seven taxonomic groups and for the 22 European countries covered by this study

References	Country	Taxon	Data type
Niklfeld H, Schratt-Ehrendorfer L (1999) Rote Liste gefährdeter Farn- und Blütenpflanzen Österreichs, ed Niklfeld H. Rote Listen gefährdeter Pflanzen Österreichs. (Austria Medien Service, Vienna), pp. 33–152.	Austria	Vascular plants	RL, CL
Grims F, Köckinger H (1999) Rote Liste gefährdeter Laubmoose (Musci) in Österreich, ed Niklfeld H. Rote Listen gefährdeter Pflanzen Österreichs. (Austria Medien Service, Vienna), pp. 157–171.	Austria	Bryophytes (mosses)	RL, CL
Saukel J, Köckinger H (1999) Rote Liste gefährdeter Lebermoose (Hepaticae) und Hornmoose (Anthoercatae) in Österreich, ed, Niklfeld H. Rote Listen gefährdeter Pflanzen Österreichs. (Austria Medien Service, Vienna), pp. 172–186.	Austria	Bryophytes (*Hepaticae, Anthoceratae*)	RL, CL
OASIS (2010) Österreichisches Artenschutz-Informationssystem. Available at www.umweltbundesamt.at/oasis.	Austria	Various	RL, CL
Zulka P, ed (2005) Rote Listen gefährdeter Tiere Österreichs, Grüne Reihe Band 14/1. (Böhlau, Vienna).	Austria	Various	RL, CL
Zulka P, ed (2005) Rote Listen gefährdeter Tiere Österreichs, Grüne Reihe Band 14/2. (Böhlau, Vienna).	Austria	Various	RL, CL
INBO (2010) Red list of breeding birds in Flanders. Available at www.inbo.be/content/page.asp?pid=EN_FAU_BIR_BRE_redlist.	Belgium - Flanders	Birds	RL, CL
Portail Wallonie (2010) La biodiversité en Wallonie: Bryophytes. Available at http://biodiversite.wallonie.be/fr/especes.html?IDC=3025.	Belgium - Wallonie	Various	RL, CL
Decleer K, Devriese H, Hofmans K, Lock K, Barenbrug B, Maes D (2000) Atlas et "liste rouge" provisoire des sauterelles, grillons et criquets de Belgique (Insecta, Orthoptera). Available at www.inbo.be/docupload/1961.pdf.	Belgium	Grasshoppers	RL, CL
INBO (2010) Red list of fish in Flanders. Available at www.inbo.be/content/page.asp?pid=EN_FAU_FIS_redlist.	Belgium - Flanders	Fish	RL, CL
INBO (2010) Red list of reptiles in Flanders. Available at http://www.inbo.be/content/page.asp?pid=EN_FAU_AMP_redlist.	Belgium - Flanders	Reptiles	RL, CL
Van Landuyt W, Vanhecke L, Hoste I (2006) Rode Lijst van de vaatplanten van Vlaanderen en het Brussels Hoofdstedelijk Gewest [Red list of vascular plants of Flanders and region of Brussel], eds Van Landuyt W et al. Atlas van de Flora van Vlaanderen en het Brussels Gewest. (INBO en Nationale Plantentuin van België, Brussel).	Belgium - Flanders	Vascular plants	RL, CL
Natcheva R, Ganeva A, Spiridonov G (2006) Red List of the bryophytes in Bulgaria. *Phytol Balcan* 12:55–62.	Bulgaria	Bryophytes	RL, CL
Velchev V (ed) (1984) Red Data Book of the People's Republic of Bulgaria. Vol 1: Plants. (Publication House of the BAS, Sofia), 443 pp.	Bulgaria	Vascular plants, bryophytes	RL, CL
Pesev C, ed (1985) Červena Kniga na NR Bălgarija v dva toma. Tom 2 [Red Data Book of the People's Republic of Bulgaria. Vol 1: Animals]. (Publication House of the BAS, Sofia), 185 pp.	Bulgaria	Various animals	RL, CL
Bulgarian National Rarities Committee (sine dato) List of the Birds Recorded in Bulgaria.	Bulgaria	Birds	CL
Plesnik J, Hanzal V, Brejskova L (2003) Cerveny seznam ohrozenych druhu Ceske republiky Obratlovci [Red List of threatened species in the Czech Republic: Vertebrates]. (Priroda 22, Praha), 184 pp.	Czech Republic	Vertebrates	RL, CL
Holub J, Prochazka F (2000): Red list of vascular plants of the Czech Republic. *Preslia* 72:187–230.	Czech Republic	Vascular plants	RL, CL
Farkac J, Kral D, Škorpik M, eds. (2005) Červený seznam ohrožených druhů České republiky. Bezobratlí. List of threatened species in the Czech Republic. Invertebrates. (Agentura ochrany přírody a krajiny ČR, Praha), 760 pp.	Czech Republic	Invertebrates	RL, CL
Stasny K, Bejcek V, Hudec K (2006) Atlas hnizdnilo Rozsirem Ptaku v Ceske Republice. (Aventum).	Czech Republic	Birds	RL, CL
Lusk S (1996) The status of the fish fauna in the Czech Republic. In Conservation of Endangered Freshwater Fish in Europe, eds Kirchhofer A, Hefti D. Advances in Life Sciences. (Birkhäuser, Basel), pp. 85–98.	Czech Republic	Fish	RL, CL
Kučera J, Váňa J (2005) Check and Red List of bryophytes of the Czech Republic. *Příroda* 23:1–104.	Czech Republic	Bryophytes	RL, CL
DMU (2007) The Danish Red Data Book. Available at www2.dmu.dk/1_Om_DMU/2_Tvaer-funk/3_fdc_bio/projekter/redlist/artsgrupper_en.asp.	Denmark	Various	RL, CL
Estonian eBiodiversity (2010) Estonian Red List of threatened species. Available at http://elurikkus.ut.ee/prmt.php?lang=eng.	Estonia	Various	RL, CL
Kalkman VJ, Boudot JP, Bernard R, Conze KJ, De Knijf G, et al. (2010) European Red List of Dragonflies. (Publications Office of the European Union, Luxembourg).	Europe	Dragonflies	CL

Table S2. Cont.

References	Country	Taxon	Data type
Rassi P, Alanen A, Kanerva T, Mannerkoski I, eds. (2001) The Red List of Finnish Species. (Ministry of the Environment and Finnish Environment Institute, Helsinki), 432 pp.	Finland	Various	RL, CL
UICN France, MNHN (2009) La Liste rouge des espèces menacées en France. Available at www.uicn.fr/Liste-rouge-France.html.	France	Various	RL, CL
Voisin JF (2003) Atlas des Orthoptères et des Mantides de France. (Patrimoines Naturels, 60 Paris, MNHN).	France	Grasshoppers	CL
Olivier L, Galland JP, Maurin H, eds (1995) Livre Rouge de la flore menacée de France. Tome I: Espèces prioritaires. Collection Patrimoines Naturels (Série Patrimoine Génétique). No. 20. (SPN-IEGB/MNHN, DNP/Ministère Environnement, CBN Porquerolles, Paris), 486 pp.	France	Vascular plants	RL, CL
MNHN, UICN France, ONEMA, SFI (2009) La Liste rouge des espèces menacées en France, selon les catégories et critères de l'UICN. Chapitre Poissons d'eau douce de France métropolitaine. (Dossier de presse, Paris).	France	Fish	RL, CL
UICN France, MNHN, ONCFS, SEOF (2008) La Liste rouge des espèces menacées en France, selon les catégories et critères de l'UICN. Chapitre Oiseaux nicheurs de France métropolitaine. (Dossier de presse, Paris).	France	Birds	RL, CL
UICN France, MNHN, SHF (2008) La Liste rouge des espèces menacées en France, selon les catégories et critères de l'UICN. Chapitre Reptiles et Amphibiens de France métropolitaine. (Dossier de presse. Paris).	France	Reptiles	RL, CL
MNHN, UICN France, ONCFS, SPEFM (2009) La Liste rouge des espèces menacées en France, selon les catégories et critères de l'UICN. Chapitre Mammifères de France métropolitaine. (Dossier de presse, Paris).	France	Mammals	RL, CL
Ott J, Piper W (1998) Rote Liste der Libellen (Odonata), eds Binot M, Bless R, Boye P, Gruttke H, Pretscher P. Rote Liste gefährdeter Tiere Deutschlands. *Schr-R Landschaftspfl u Natursch* 55:260–263.	Germany	Dragonflies	RL, CL
Ludwig G, Schnittler M (1996) Rote Listen der Pflanzen Deutschlands. Schriftenreihe für Vegetationskunde 28, 744 pp.	Germany	Vascular plants, bryophytes	RL, CL
Haupt H, Ludwig G, Gruttke H, Binot-Hafke M, Otto C, et al. (2009) Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band 1. (Naturschutz und Biologische Vielfalt 70), 386 pp.	Germany	Vertebrates	RL, CL
Maas S, Detzel P, Staudt A (2002) Gefährdungsanalyse der Heuschrecken Deutschlands. Verbreitungsatlas, Gefährdungseinstufung und Schutzkonzepte. (BfN-Schriftenvertrieb im Landwirtschaftsverlag, Münster), 401 pp.	Germany	Grasshoppers	RL, CL
Ludwig G, Düll R, Philippi G, Ahrens M, Caspari S, et al. (1996) Rote Liste der Moose (Anthocerophyta et Bryophyta) Deutschlands. *Schriftenreihe für Vegetationskunde* 28:189–306.	Germany	Bryophytes	RL, CL
Econimidis PS (1995) Endangered freshwater fishes of Greece. *Biol Cons* 72:201–211.	Greece	Fish	RL, CL
Legakis A, Maragou P, eds (2009) The Red Data Book of threatened animals of Greece. (Hellenic Zoological Society, Athens), 528 pp.	Greece	Various	RL, CL
Erzberger P, Papp B (2004) Annotated checklist of Hungarian bryophytes. *Studia Bot Hung* 35:91–149.	Hungary	Bryophytes	CL
Rajczy M (1990) Mohák-Bryophyta, ed Rakonczai Z. Vörös könyv. Budapest: Akademiai Kiadó, pp. 322–325.	Hungary	Bryophytes	RL, CL
Kiraly G, ed. (2007) Vörös Lista. A magyarországi edényes flóra veszélyeztetett fajai. [Red list of the vascular flora of Hungary]. (Saját kiadás, Sopron), 73 pp.	Hungary	Vascular plants	RL, CL
Keresztessy K (1996) Threatened freshwater fish in Hungary. In Conservation of Endangered Freshwater Fish in Europe, Kirchhofer A, Hefti D, eds). Advances in Life Sciences. (Birkhäuser, Basel) pp. 73–78.	Hungary	Fish	RL, CL
Rakonczay Z, ed. (1989) Red Data Book - extinct and endangered plant and animal species in Hungary (Akadémiai Kiadó, Budapest).	Hungary	Various	RL, CL
Marnell F, Kingston N, Looney D (2009) Ireland Red List No. 3: Terrestrial Mammals. (National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, Dublin, Ireland).	Ireland	Mammals	RL, CL
Birdwatch Ireland (2010) Birds of conservation concern in Ireland. Available at www.birdwatchireland.ie/Ourwork/SurveysProjects/BirdsofConservationConcern/tabid/178/Default.aspx	Ireland	Birds	RL, CL
Nelson B, Ronayne C, Thompson R (2011) Ireland Red List No. 6: Damselflies & Dragonflies (Odonata). (National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, Dublin, Ireland).	Ireland	Dragonflies	RL, CL
King JL, Marnell F, Kingston N, Rosell R, Boylan P, et al. (2011) Ireland Red List No. 5: Amphibians, Reptiles, and Freshwater Fish. (National Parks and Wildlife Service, Department of Arts, Heritage and the Gaeltacht, Dublin, Ireland).	Ireland	Fish, reptiles	RL, CL
Curtis TGF, McGough HN (1988) The Irish Red Data Book. Vol. 1: Vascular plants. (Wildlife Service Ireland, Dublin).	Ireland	Vascular plants	RL, CL

Table S2. Cont.

References	Country	Taxon	Data type
Smith AJE (2003) Chapter 4: Mosses, liverworts and hornworts. In Hawsksowrth DL (ed) The changing wildlife of Great Britain and Ireland. (CRC Press).	Ireland and United Kingdom	Bryophytes	RL, CL
Bulgarini F, Calvario E, Fraticelli F, Petretti F, Sarrocco S (2007) Libro Rosso degli animali d'Italia. Vertebrati. WWF Italia.	Italy	Vertebrates	RL, CL
Aleffi M, Schumacker R (1995) Check-list and red-list of the liverworts (Marchantiophyta) and hornworts (Anthoerceratophyta) of Italy. *Flora Mediterranea* 5:73–161.	Italy	Bryophytes	RL, CL
Conti F, Manzi A, Pedrotti F (1992) Libro rosso delle piante d'Italia. WWF Italia in collaborazione con la Società Botanica Italiana. (WWF, Camerino).	Italy	Vascular plants	RL, CL
Scientific Council of the Institute of Biology of Latvian Academy of Sciences (2000) Red Data Book of Latvia. http://enrin.grida.no/biodiv/biodiv/national/latvia/species/table_1.htm.	Latvia	Various	RL, CL
Pilats V (1999) A short description of the Latvian mammal fauna. *Hystrix* 8:61–66.	Latvia	Mammals	RL, CL
Andrusaitis G, ed (2003) Red Data Book of Latvia. Rare and Threatened Species of Plants and Animals. Volume 5. Riga.	Latvia	Reptiles	RL, CL
Environment Protection Department of the Republic of Lithuania, ed (1992) Red Data Book of Lithuania.	Lithuania	Various	RL, CL
Balevicius K, Ladyga A (1992) Lietuvos raudonoji knyga [The Red Data Book of Lithuania]. (Lithuanian Department of Environmental Conservancy, Vilnius), 364 pp.	Lithuania	Vascular plants	RL, CL
Jukonienė I (1996) Rare and threatened bryophyte species in Lithuania. *Bot Lithuanica* 2:327–342.	Lithuania	Bryophytes	RL, CL
Creemers RCM, van Delft JJCW (2009) Rode Lijsten Amfibieen en Reptielien [Red List of reptiles and amphibians in the Netherlands]. (Nederlandse Fauna 9, Nationaal Natuurhistorisch Museum Naturalis, European Invertebrate Survey, Leiden).	Netherlands	Reptiles	RL, CL
Siebel HN, Bijlsma RJ, Bal D (2006) Toelichting op de Rode Lijst Mossen. Rapport LNV Directie Kennis No. 2006/034.	Netherlands	Bryophytes	RL, CL
De Nie H (2003) Red listing of freshwater fishes and lampreys in the Netherlands. Available at http://home.planet.nl/~hwdenie/redlistfishes.pdf.	Netherlands	Fish	RL, CL
Dutch Dragonflies (2011) Red list of Dutch Odonata 2011. Available at http://www.dutchdragonflies.eu/redlist.html.	Netherlands	Dragonflies	RL, CL
Hustings F, Borgreve C, Van Turnhout C, Thissen J (2004) Basisrapport voor de Rode Lijst Vogels volgens Nederlandse en IUCN-criteria. SOVON onderzoeksrapport 2004/14. (SOVON Vogelonderzoek Nederland/Vogelbescherming Nederland, Beek-Ubbergen).	Netherlands	Birds	RL, CL
Kålås JA, Viken Å, Bakken T, eds (2006) Norsk Rødliste 2006 [2006 Norwegian Red List]. (Artsdatabanken, Norway).	Norway	Various	RL, CL
PAS (2004) Polish Red Data Book of Animals. Available at www.iop.krakow.pl/pckz/default.asp?nazwa=szukaj&je=en.	Poland	Animals	RL, CL
Zarzycki K, Wojewoda W, Heinrich Z (1992) Lista roślin zagrożonych w Polsce. 2nd ed. (Instytut Botaniki PAN, Kraków).	Poland	Bryophytes, vascular plants	RL, CL
Gowaqcinski Z, ed. (2002) Red list of threatened animals in Poland. (Polish Academy of Sciences, Institut of Nature Conservation).	Poland	Various	RL, CL
ICNB (2005) Red List of reptiles of Portugal. Available at www.icn.pt/destaques/destaques_anexos/anexos_L_Ver/répteis.pdf.	Portugal	Reptiles	RL, CL
ICNB (2005) Red List of mammals of Portugal. Available at www.icn.pt/destaques/destaques_anexos/anexos_L_Ver/mamíferos.pdf.	Portugal	Mammals	RL, CL
Almaça C (1995) Freshwater fish and their conservation in Portugal. Biological Conservation 72: 125–127.	Portugal	Fish	RL, CL
Oltean M, Negrean G, Popescu A, Roman N, Dihoru G, et al. (1994) Lista rosie a plantelor superioare din România [Red list of higher plants from Romania]. (Institutul de Biologie, Academia Româna), 52 pp.	Romania	Vascular plants	RL, CL
Botnariuc N, Tatole V, eds. (2005) Cartea Rosie a Vertebratelor din România [The Red Data Book of vertebrates of Romania]. (Academiei Române, Bucuresti).	Romania	Vertebrates	RL, CL
SOPSR (2010) Červený zoznam ohrozených rastlín Slovenska. Available at www.sopsr.sk/webs/redlist/.	Slovakia	Bryophytes, vascular plants	RL, CL
Balaz D, Marhold K, Urban P (2001) Cerveny Zoznam Rastlín a Zivocíchov Slovenska [Red Lists of Plants and animals of Slovakia]. Ochrana Prirody Suplement 20, 156 pp.	Slovakia	Various	RL, CL

Table S2. Cont.

References	Country	Taxon	Data type
Orthoptera SK (2010) Mapovanie Orthoptera Slovenska. Available at http://www.orthoptera.sk/sk/.	Slovakia	Grasshoppers	CL
Dantos, ed (2002) Birds distribution in Slovakia. (Slovenski Akademia Vied, Bratislava).	Slovakia	Birds	CL
Blanc JC, Gonzalez JL (1992) Libro Rojo de los vertebrados de Espana. (Ministerio de Medio Ambeinte, Madrid).	Spain	Vertebrates	RL, CL
Pleguezuelos JM, Márquez R, Lizana M (2002) Atlas y Libro Rojo de anfibios y reptiles de Espana. (Ministerio de Medio Ambeinte, Madrid).	Spain	Reptiles	RL, CL
Lozano LD (ed) (2000) Lista Roja de la Flora Vascular Española [Red List of Spanish vascular flora]. Conservación Vegetal. Boletín No. 6 (Comisión de Flora del Comité Español de la Unión Mundial para la Conservación Naturaleza, Madrid).	Spain	Vascular plants	RL, CL
Verdu JR, Numa C, Galante R (2011) Atlas y Libro Rojo de los invertebrados amanazados de España. Vol I: Artropodos. (Organismo Autónomo Parques Nacionales, Madrid).	Spain	Invertebrates	RL, CL
Elvira B (1996) Endangered freshwater fishes of Spain. In Conservation of Endangered Freshwater Fish in Europe, Kirchhofer A, Hefti D, eds. Advances in Life Sciences. (Birkhäuser, Basel), pp. 55–61.	Spain	Fish	RL, CL
Sérgio C, Casas C, Brugués M, Cros RM (1994) Lista Vermelha dos Briófitos da Península Ibérica [Red List of Bryophytes of the Iberian Peninsula]. [Instituto da Concervacao da Natureza e Museu, Laboratório e Jardim Botânico, Universidade de Lisboa (MLJB), Lisbon].	Spain, Portugal	Bryophytes	RL, CL
Gärdenfors U, ed (2010) Rödlistade arten i Sverige 2010 [The 2010 red list of Swedish species]. Artdata. Available at www.artdata.slu.se/rodlista/.	Sweden	Various	RL, CL
Cordillot F, Klaus G (2011) Gefährdete Arten in der Schweiz. Synthese Rote Listen. Stand 2010. (Bundesamt für Umwelt, Bern), Umwelt-Zustand No. 1120, 111 pp.	Switzerland	Various	RL, CL
Keller V, Gerber A, Scmid H, Volet B, Zbinden N (2010) Rote Liste der Brutvögel. Gefährdete Arten der Schweiz, Stand 2010. BAFU, Umwelt-Vollzug No. 1019, pp. 53 pp.	Switzerland	Birds	RL, CL
Vences M, Köhler J, Ziegler T, Böhme W, eds (2006) Reptiles in the Red Data Book of Ukraine: A new species list, status. *Proceedings of the 13th Congress of the Societas Europaea Herpetologica.* pp. 55–59.	Ukraine	Reptiles	RL, CL
Akimowa IA, ed (2009) Tschernowa Kniga Ukrainii. (Nationalna Akademija Nauk Ukrainii, Kiew), 624 pp.	Ukraine	Various	RL, CL
Eaton MA, Brown AF, Noble DG, Musgrove AJ, Hearn RD, et al. (2009) The population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Birds* 102:296–341.	United Kingdom	Birds	RL, CL
Orthoptera UK (2010) Orthopteroids of the British Isles Recording Scheme. Available at www.orthoptera.org.uk/.	United Kingdom	Grasshoppers	CL
Dines TD, Jones RA, Leach SJ, McKean DR, Pearman DA, et al. (2005) The Vascular Plant Red Data List for Great Britain. *Species Status* 7:1–116. (Joint Nature Conservation Committee, Peterborough).	United Kingdom	Vascular plants	RL, CL
Maitland PS, Lyle AA (1996) Threatened freshwater fishes of Great Britain. In Conservation of Endangered Freshwater Fish in Europe, Kirchhofer A, Hefti D, eds. Advances in Life Sciences. (Birkhäuser, Basel), pp. 9–21.	United Kingdom	Fish	RL, CL
Langton TES, Beckett CL (1996) Reptiles and amphibians in the U.K.: A review of their status and international significance. (JNCC, Peterborough).	United Kingdom	Reptiles	RL, CL
Church JM, Hodgetts NG, Preston CD, Stewart NF (2004) British red data books. Mosses and liverworts. (JNCC, Peterborough), 168 pp.	United Kingdom	Bryophytes	RL, CL
Cox NA, Terry A, eds (2007) European Red List of Mammals. Available at http://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European_mammals.pdf.	Various countries	Mammals	CL
Cox NA, Temple HJ, eds (2009): European Red List of Reptiles. Available at http://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European_reptiles.pdf.	Various countries	Reptiles	CL

Given are data sources; the country and the taxonomic groups for which they contain data; and the type of data (CL, species checklist; RL, red list). Threatened species are from International Union for Conservation of Nature (IUCN) categories endangered (EN), vulnerable (VU), and critically endangered (CR). Taxonomic groups include vascular plants, bryophytes, mammals, fish, reptiles, dragonflies, and grasshoppers.

Table S3. Proportions of threatened species from seven taxonomic groups and 22 European countries as explained by multivariate models of historical or current socioeconomic indicators

	1900	1950	2000
PCA 1	−0.29	0.19	−0.12
PCA 2	−0.15	−0.01	0.09
PCA 3	0.08	−0.17	−0.09
PCA 4	0.19	−0.06	−0.02
R^2_{MF}	0.22	0.11	0.05
AIC	4,807	5,539ss	5,915
AW	>99.99	<0.001	<0.001

Fixed-effect estimates, McFadden's R_2, Akaike information criterion (AIC), and Akaike weights (AW) for generalized linear mixed-effects models relating the variation in the proportion of red-listed species to either historical (1900 and 1950) or contemporary (2000) values of impact indicators plus levels or recent expenditures on environmental protection. The three impact indicators—human population density (PD), per capita GDP (GDP), and human appropriation of net primary productivity (HANPP)—plus the environmental expenditures were subjected to a principal component analysis before fitting the regression models to remove multicollinearity among independent variables. All fixed-effect estimates are different from 0 with a probability > 0.999. except for the one of PCA 4 for the year 2000 ($P = 0.95$).

Table S4. Contemporary (year 2000) and historic (years 1900 and 1950) socioeconomic variables for the 22 European countries included in this study

Country	PD$_{1900}$	GDP$_{1900}$	HANPP$_{1900}$	PD$_{1950}$	GDP$_{1950}$	HANPP$_{1950}$	PD$_{2000}$	GDP$_{2000}$	HANPP$_{2000}$	EnvExp
Austria (AU)	71	2,882	0.291	83	3,706	0.237	98	20,097	0.342	0.726
Belgium (BE)	219	3,731	0.652	282	5,462	0.705	340	20,742	0.78	0.56
Bulgaria (BG)	36	1,223	0.296	65	1,651	0.384	70	5,365	0.274	0.367
Czech Republic (CZ)	110	2,400	0.388	113	3,501	0.330	130	9,047	0.406	0.43
Denmark (DK)	57	3,017	0.757	94	6,943	0.734	120	23,010	0.735	0.744
Finland (FI)	8	1,668	0.165	12	4,253	0.186	16	20,235	0.217	0.59
France (FR)	75	2,876	0.233	77	5,271	0.264	112	20,808	0.508	0.553
Germany (GE)	152	2,985	0.485	191	3,881	0.415	231	18,596	0.593	0.409
Greece (GR)	38	1,351	0.196	57	1,915	0.233	84	12,044	0.345	0.565
Hungary (HU)	77	1,682	0.434	100	2,480	0.342	109	7,138	0.525	0.575
Italy (IT)	134	1,785	0.233	187	3,502	0.331	231	18,740	0.406	0.859
Netherlands (NL)	143	3,424	0.449	282	5,996	0.709	454	21,591	0.924	1.7
Norway (NO)	7	1,937	0.060	10	5,463	0.067	14	24,364	0.058	0.657
Poland (PL)	79	1,536	0.315	80	2,447	0.284	124	7,215	0.377	0.525
Portugal (Pg)	61	1,302	0.156	95	2,086	0.118	118	14,022	0.293	0.516
Republic of Ireland (IR)	63	2,510	0.335	42	3,453	0.290	59	22,015	0.49	0.53
Romania (RO)	46	1,415	0.297	69	3,093	0.368	91	3,002	0.305	0.309
Slovakia (SK)	67	1,600	0.388	71	3,501	0.330	110	7,837	0.406	0.256
Spain (SP)	38	1,786	0.112	57	2,189	0.161	91	15,269	0.249	0.262
Sweden (SW)	11	2,561	0.180	16	6,739	0.145	20	20,321	0.174	0.299
Switzerland (SU)	80	3,833	0.242	114	9,064	0.323	176	22,025	0.381	0.85
United Kingdom (U.K.)	167	4,492	0.333	204	6,939	0.394	242	19,817	0.602	0.513

EnvExp, public expenditures in percent of GDP, means of the available data from the years 1998–2009; GDP, standardized per capita GDP in 1990 International (Geary–Khamis) dollars; HANPP, ratio of the amount of net primary productivity harvested by humans (NPP$_h$) to the net primary productivity of a hypothetical undisturbed natural vegetation cover of the same area (NPP$_0$); PD, human population density (people square kilometer).

Table S5. Residuals of multivariable logistic regression models relating the proportion of threatened species in seven different taxonomic groups across 22 European countries to either historical (1900, 1950) or contemporary (2000) levels of socioeconomic variables plus levels of recent public expenditures on environmental protection

Taxonomic group	1900	1950	2000
Vascular plants	0.39	0.34	0.35
Bryophytes	0.08 (0.19)	0.06 (0.18)	0.07 (0.11)
Mammals	0.50	0.25	0.47
Fish	0.46	0.43	0.29
Reptiles	0.20	0.14	0.39
Dragonflies	0.12	0.12	0.08 (0.38)
Grasshoppers	0.46	0.95	0.05 (0.02)

Results of permutation tests (n = 999) for the spatial correlation (Moran's I) of model residuals. The socioeconomic variables were human population density, per capita GDP, and human appropriation of net primary productivity. Values represent the probability that a random permutation of the spatial structure would produce a Moran's I larger than the empirical data. Values in brackets represent the equivalent probabilities from autologistic models (see *Materials and Methods* for details).