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RESEARCH PAPER

Butterfly extinctions in European states: do socioeconomic conditions matter more than physical geography?

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ABSTRACT

Aim To distinguish the effects of physical geography and socioeconomic conditions on the extinction of butterflies in European states, and to compare patterns influencing extinctions with patterns influencing species richness.

Location Europe.

Method Per-state species richness and extinctions were taken from the *Red Data Book of European Butterflies*, and their relationships with physical geography and socioeconomic predictors were analysed using regression analysis. Two hypothesis were explored: (1) extinctions are related primarily to identical physical geography factors that influence species richness; and (2) extinctions are influenced primarily by human pressure on natural biotopes and follow correlates of modern land use.

Results Extinctions and richness are not correlated. Richness increased towards low latitudes and with biotope and topographic heterogeneity, and decreased in states affected by Quaternary glaciation and on islands. The only socioeconomic correlate was human density, exhibiting a weak negative effect. Extinctions were negatively correlated with area and with biotope and topographic heterogeneity. They peaked in regions with mild climate in central latitudes. The strongest socioeconomic correlate was high density of railways, interpreted as a proxy of early industrialization. Further correlates were human density and urban employment.

Main conclusion Topographic and biotope heterogeneity predicts both high species richness and low extinction rates. Losses of butterflies result from a complex interplay of geography and relatively recent economic history, as low topographic heterogeneity and flat relief favoured the early advent of industrialization and intensive land use.

Keywords
Butterflies, distribution, Europe, economic history, extinction rates, geography.

INTRODUCTION

The understanding of patterns and processes behind the recent extinction crisis is impeded by a paucity of data on actual species losses (Diamond, 1987; Smith *et al*., 1993; Purvis *et al*., 2000). Comprehensive knowledge of both historical and recent distributions is limited to just a few groups, such as molluscs and vertebrates. This forces researchers to extrapolate extinction risks from rarity, threat levels, or such general patterns as species-area curves (Pimm *et al*., 1988; May *et al*., 1995; Jones *et al*., 2003; Thomas C.D. *et al*., 2004). However, causes of threat differ among taxa (Sullivan *et al*., 2000) and rarity may be a poor prediction of actual risk (Purvis *et al*., 2000a,b). Also, predictions of losses from species–area curves may not be valid, as patterns of losses may deviate from reversals of species–area relationships (Ulrich & Buszko, 2004). Hence, it is desirable to explore *actually documented* losses across a wide range of taxa.

Here we analyse the socioeconomic and physical geography correlates of 20th-century butterfly losses from European states, focusing on two broad groups of potential predictors: socioeconomic conditions and physical geography.

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Whereas no general theory relates extinctions to geographical factors, the relationships between geography and species richness are intensively studied. As species losses are predicted routinely by reversing such richness-related patterns as the species–area relationships, we used the assumption that extinctions are related to species richness as a working hypothesis. Generally accepted correlates of terrestrial species richness include (1) area, (2) biotope heterogeneity, and (3) energy. Their hypothetical relationships with extinctions are as follows. (1) Larger areas contain more resources, including more types of biotopes, and hence allow more species to form viable populations (Gaston & Blackburn, 2000). Hence, loss of biotopes, changing land use, etc. should affect more species in small states than in large ones. (2) Heterogeneous areas also harbour more types of biotopes (e.g. Kerr *et al*., 2001; Triantis *et al*., 2003), and provide more refuges that may buffer against species losses. Finally, (3) regions receiving more solar energy support more species (Turner *et al*., 1987; Currie, 1991; Hawkins *et al*., 2003), which has been corroborated for European butterflies (Hawkins & Porter, 2003b). This seems to be due to higher chances that species will form viable populations in a region with more resources (Bonn *et al*., 2004; Gaston & Evans, 2004). Accordingly, any deterioration of conditions should cause more losses in energy-poor regions than in energy-rich ones.

Regarding socioeconomic conditions, declines of European butterflies have been attributed to such human-generated factors as habitat loss, agricultural intensification or a decline in traditional land use (e.g. Van Swaay & Warren, 1999; Asher *et al*., 2001; Thomas J.A. *et al*., 2004). It follows that extinctions should correlate with such proxies for intensive human pressure on natural biotopes as human density (Kerr & Currie, 1995; McKinney, 2002; Parks & Harcourt, 2002), and with indices of modern economy such as employment patterns, per-capita gross domestic product and density of railway and highway networks. Regarding employment patterns, we assume that a high share of agriculture indicates traditional farming and few extinctions (e.g. Robinson & Sutherland, 2002), whereas a high share of industry and services, or high GDP, indicate affluent economy and many extinctions (cf. Abbitt *et al*., 2000).

The evidence available to date does not allow socioeconomic and physical causes of butterfly losses to be distinguished. Northwestern Europe has suffered particularly high losses (Maes & Van Dyck, 2001; Dennis & Shreeve, 2003), which may be a consequence of high human activity and/or small and species-poor states. On the other hand, simulated species removal predicted faster losses in the Mediterranean region than elsewhere (Ulrich & Buszko, 2003). However, the relative contributions of socioeconomic and physical conditions were never addressed explicitly. We did so by performing regression analysis of available data on extinctions and, in parallel, on species richness, and comparing the two patterns.

METHODS

The data

The knowledge of both the historical and present distribution of European butterflies is unrivalled by any other invertebrate group (Kudrna, 2002). Only recently was the scattered information consistently summarized in the *Red Data Book of European Butterflies* (RDB) by Van Swaay & Warren (1999), which reports distribution trends, including records of extinct species, for individual states. Assembly of the data was consistent across all states. It relied on national experts, often coordinators of national butterfly surveys, who reflected consensual views of wide circles of lepidopterists in their countries. We used the extinction data provided in Appendix 5 of RDB and did not, for the sake of consistency, attempt to update them using more recent sources. We excluded only RDB-reported extinctions of eight alpine butterflies from the Ukraine that refer to species never found in the state (cf. Hruby, 1964).

Because RDB reports situations in individual states, we were restricted by political boundaries in our analyses. We did not consider Vatican, Monaco and San Marino (not in the RDB), Russia (disproportionately large and sparsely researched), the Canary Islands and Madeira (not in Europe geographically) and Turkey (RDB treats it separately as to European and Asian parts). In total, we considered 410 species in 39 states.

The restriction to national boundaries limited our selection of predictors (Table 1). Specifically, we had to use climatic data averaged across entire countries, as provided by the Tyndall Centre for Climate Change Research (http://www.cru.uea.ac.uk/~timm/cty/obs/). We also checked the effect of (centroid) altitude and latitude. For biotope heterogeneity, we used numbers of potential biomes per state (©The University of Wisconsin, http://www.sage.wisc.edu/atlas/index.php) (details in Ramankutty & Foley, 1999), per-state altitude range and length of coastline. We also considered insular position (states that are islands, i.e. Britain, Ireland, Malta and Cyprus), as islands have fewer species than comparable landmasses (Whittaker, 1998), and past glaciation, as these areas had to be repeatedly re-colonized (Schmitt & Hewitt, 2003) and hence may harbour fewer species than others.

All socioeconomic predictors were taken from the CIA *World Factbook* (CIA, 2002).

Statistical analyses

We constructed single-term and multiple regression models of per-state species richness (= extant plus extinct species) and extinctions (= numbers of extinct species controlled for species richness by forcing richness into regressions) against (i) physical geography and (ii) socioeconomic variables. We used the generalized linear modelling in S-PLUS 2000 (Math Soft, 1999), assuming the Gaussian distribution (link identity) for species richness and the Poisson distribution (link log) for extinctions.

The high number of potential predictors complicates interpretation of regression results. Nominal significance values become unreliable due to high numbers of tests, and the regressions should not be viewed as *predictive* models. We therefore follow information theory approach (Burnham & Anderson, 2002) and base our inference on the quasi-Akaike information criterion (*qAIC*; as computed by S-PLUS 2000) for selecting the most parsimonious models, i.e. regressions that fit the data well without becoming prohibitively complex. *F* and *P*-values are reported only

Table 1 Overview of variables used in regression analyses of butterfly species richness and extinctions in European countries. The means, medians and ranges refer to the 36 states used in the regression analyses, i.e. without Andorra, Malta and Liechtenstein

Variable	Details	Type*	Mean	Median	Range
Species richness		N	146	152	29–257
Extinct species		N	3.3	2	0–16
Physical geography					
Area		N	157,000	80,000	2586–604,000
Altitude range	Highest minus lowest altitude	N	2038.0	2231	180–4809
Coastline	(km)	N	2699	471	0–22,000
Glaciation	> 50% at peak of the last Ice Age	C			
Island	State is insular (1) or not (0)	C			
Latitude	Centroid latitude (km from equator)	N	2930	2830	2100–3840
Longitude	Centroid longitude (from null meridian)	N	926	1005	−480–1980
Maximum temperature	Daily maximum temperatures, 1961–2000 (°C)	N	13.2	13.3	5–23.8
Mean temperature	Daily mean temperature, 1961–2000 (°C)	N	8.8	8.8	1.5–18.4
Minimum temperature	Daily minimum temperatures, 1961–2000 (°C)	N	4.4	4.5	−2.4–13.1
Number of biomes	According to *Atlas of the Biosphere*	N	4.6	4	2–9
Precipitation	Mean precipitation, 1961–2000 (mm)	N	806.5	701.5	198–1537
Temperature range	Mean annual temperature range, 1961–2000 (°C)	N	8.6	8.5	6.5–10.8
Socioeconomics					
Agriculture	Percentage employed in agriculture	N	5.0	9	1–54
GDP	Expressed per capita in US dollars	N	13,420	11,850	1650–34,200
Industry	Percentage employed in industry	N	30	31	22–51
Highway density	Highway length divided by area	N	1.21	0.94	0.26–5.51
Human density	Persons per square kilometre	N	105.4	97.8	14.6–468.9
Services	Percentage employment in services	N	60	63	21–76
Railway density	Railway length divided by area	N	0.05	0.04	0–0.12
Urban employment	= Services + Industry	N	95	91	46–99

*Type of variable: N, numeric; C, categorical.

for comparison. The *qAIC* values do not depend on the order in which models are computed, or on numbers of competing predictors. Hence, the approach allows comparison of the effects of multiple predictors without violating the assumptions of regression analysis.

We first constructed single-term regressions of the response variables against all potential predictors. Proportions were arcsine-transformed, numeric predictors were tested as $\log_{10}(X+1)$, square-roots and 2nd-degree polynomials; transformations with the lowest qAIC relative to the null model ($Y\sim +1$) were used in subsequent analyses.

We then controlled for two potentially confounding aspects of the data, varying quality and spatial autocorrelation. RDB assesses the quality of data from individual states separately for distributions (herein overall quality, Qo) and trends (trend quality, Qt). We transferred both measures into four-grade ordinal scales ('very good', 'good', 'moderate' and 'poor and/or unknown'), used subsequently as covariables.

Spatial autocorrelation is a common phenomenon in geographical data. There are several methods to handle it (Lennon, 2000; Storch *et al.*, 2003), but their use becomes increasingly complex in such complex frames as political maps. One alternative is spatially autologistic models that include responses of dependent variables in neighbourhood areas (Augustin *et al.*, 1996). Following Dennis *et al.* (2002), we considered: the number of neighbouring states (D_N); mean species richness in neighbouring states (S_N); its coefficient of variation (S_{NV}); the mean number of extinctions in neighbouring states (S_{EX}); and its coefficient of variation (S_{EXV}). For islands, we used means from noninsular states.

Based on the two controls, we constructed 'controlled' single-term models, which tested the single effects of individual predictors after inclusion of significant quality and/or autocorrelation terms.

Next, we built multiple-regression models separately for physical geography and socioeconomic predictors. We proceeded iteratively, starting with nominally significant predictors and combining forward selection and backward elimination procedures until we obtained models with the lowest *qAIC*. We then checked systematically for the effects of nominally non-significant predictors, and proceeded with including and excluding predictors until we obtained a model that could not be improved further. We did so both without control for quality/autocorrelation and with inclusion of nominally significant covariables.

Finally, we checked whether the fits of the physical geography and socioeconomic models could be improved further by adding socioeconomic and physical geographical variables into them. If backward elimination following such addition suggested deleting some term(s) previously in the model, we did so, repeating this procedure until a best-fitting combined model was found. We thus obtained two combined models, 'Best1', based on adding socioeconomics into the geography model, and 'Best2', based on adding geography into the socioeconomic model.

RESULTS

Extinction rates vs. species richness

Overall, 89 butterfly species were lost in at least one state. Two species were lost from four states, and 63 from one state only. The distribution of extinctions was right-skewed: eight states did not lose any butterfly species, while three states, Belgium, Luxembourg and the Netherlands, lost > 10 species (Fig. 1). Neither absolute numbers of extinctions nor extinction rates correlated with species richness (Spearman's $s = -0.03$ and -0.21, both $P > 0.1$). Richness increased with area (log–log regression, $b = 0.12$, $F_{1,37} = 6.5$, $P < 0.05$, $r^2 = 0.17$). The relationship of extinctions to area was negative (log–log regression, $b = -0.01$) but not significant.

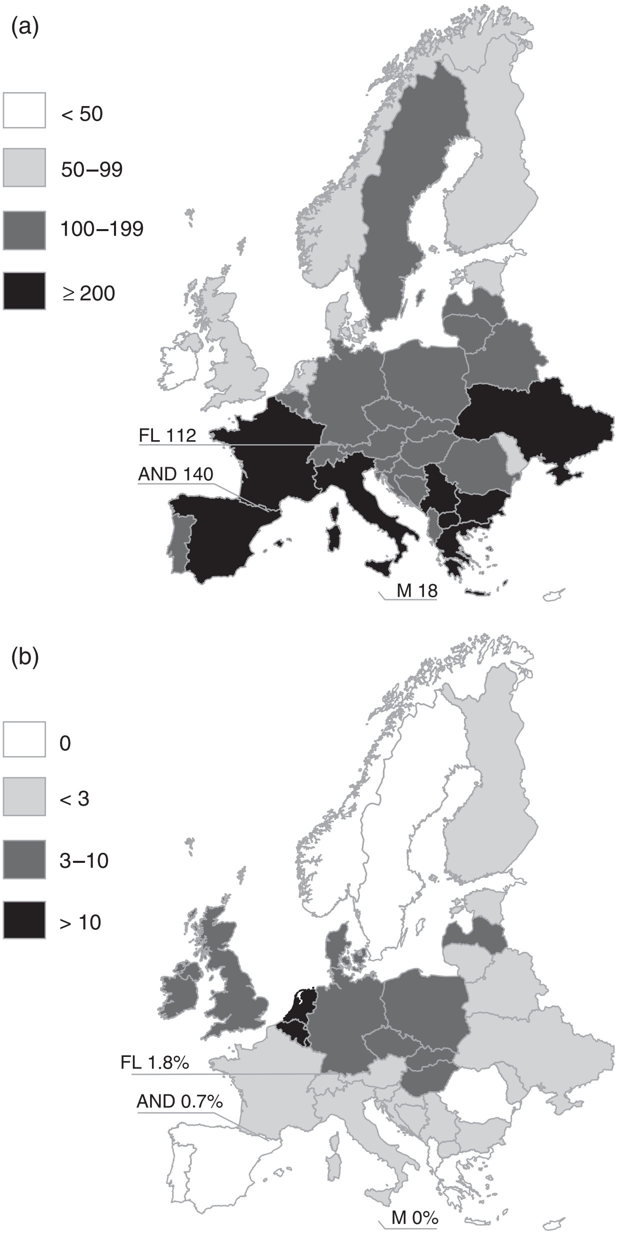

Figure 1 Charts of European states showing (a) species richness of butterflies and (b) butterfly extinction rates (percentages), as reported in the *Red Data Book* by Van Swaay & Warren (1999).

Three small states, Andorra, Liechtenstein and Malta, lost disproportionately few species (2, 1 and 0) for their small size. Excluding them gave a negative area–extinctions relationship (log–log, $b = -0.35$, $F_{1,34} = 4.9$, $P < 0.05$, $r^2 = 0.10$) (Fig. 2), while the richness–area relationship became insignificant (log–log regression, $b = 0.12$, $F_{1,34} = 3.9$, $P = 0.07$, $r^2 = 0.10$). Further analyses are without the three states.

Data quality and autologistic models

Species richness was unrelated to overall quality (both Qo and Qt: $P > 0.1$), but trend quality was related to extinctions (Qt: $b = 0.48$, $F_{1,34} = 10.0$, $P < 0.01$, $r^2 = 0.23$; Qo: $P > 0.1$; regressions on residuals after entering species richness). Species richness increased with mean richness in surrounding states ($b = 0.68$, $F_{1,34} = 30.0$, $P < 0.001$, $r^2 = 0.47$) and with the number of surrounding states ($b = 0.44$, $F_{1,34} = 8.1$, $P < 0.01$, $r^2 = 0.19$); the two variables had an additive effect (Table 2). Extinctions increased with mean extinctions in surrounding states ($b = 0.73$, $F_{1,34} = 39.6$, $P < 0.001$, $r^2 = 0.54$). Therefore, we included the terms $D_N + S_N$ into controlled models for species richness, and the terms $Qt + S_{EX}$ into controlled models for extinctions (Tables 2 and 3).

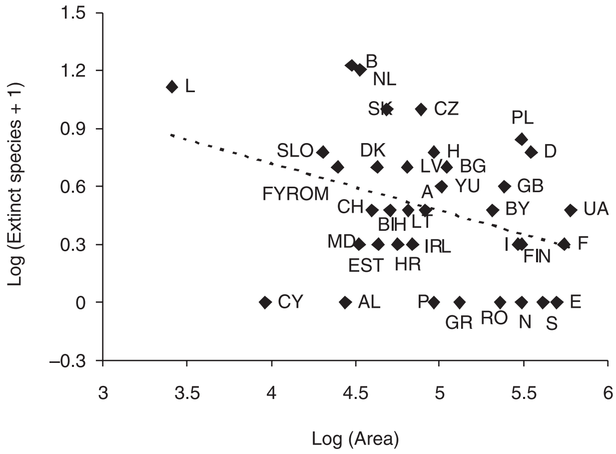

Figure 2 Numbers of extinct species in European states related to state areas. The dotted line, fitted after exclusion of small states AND, FL, and M, shows a significantly negative linear relationship ($b = -0.35$, $F_{1,34} = 4.9$, $P < 0.05$, $r^2 = 0.10$). Key: A: Austria, AL: Albania, AND: Andorra, B: Belgium, BG: Bulgaria, BIH: Bosnia and Herzegovina, BY: Belarus, CH: Switzerland, CY: Cyprus, CZ: Czech Republic, D: Germany, DK: Denmark, E: Spain, EST: Estonia, F: France, FIN: Finland, FL: Liechtenstein, FYROM: Former Yugoslav Republic of Macedonia, GB: Britain, GR: Greece, H: Hungary, HR: Croatia, I: Italy, IRL: Ireland, L: Luxembourg, LV: Latvia, LT: Lithuania, M: Malta, MD: Moldavia, N: Norway, NL: the Netherlands, P: Portugal, PL: Poland, RO: Romania, S: Sweden, SK: Slovakia, SLO: Slovenia, YU: Yugoslavia, UA: Ukraine.

Table 2 Single-term regressions of butterfly species richness in European states against physical geography and socioeconomic variables. Regressions without control for covariables (= ordinary), and with control for significant covariables $D_N + S_N$, number of neighbouring states and species richness in neighbouring states (controlled). Only variables that gave a significant result in at least one the two tests are shown. The darts indicate orientation of the relationships, '↑↓' stand for convex polynomials, and '(–)' for negative effect of categorical variables. *F*-tests compare fitted models with null model for ordinary regressions, and with model containing the covariates $D_N + S_N$ for controlled regressions

	Ordinary				*Controlled*			
		d.f.	*qAIC*	*P*		d.f.	*qAIC*	*P*
Null		35	123,876.6			35	123,876.6	
$D_N + S_a$						2, 33	59,689.6	****
Physical geography								
Altitude range	↑	1, 34	56,277.5	****	↑	3, 32	41,307.5	***
Area	^{L}	1, 34	117,575.1		↑^{L}	3, 32	39,532.4	***
Coastline	^{L}	1, 34	130,840.9		↑^{L}	3, 32	52,702.6	*
Glaciation	(–)	1, 34	71,002.7	****		3, 32	58,984.0	
Island	(–)	1, 34	92,453.9	***	(–)	3, 32	51,990.8	*
Latitude	↓	1, 34	98,790.7	**		3, 32	62,291.2	
Max. temperature	↑↓	2, 33	115,950.8	*		4, 31	65,729.3	
Number of biomes	↑	1, 34	84,884.0	****		3, 32	49,891.5	**
Temperature range	↑	1, 34	111,012.5	*		3, 32	66,830.0	
Socioeconomics								
Human density		1, 34	129,179.5		↓^{L}	3, 32	54,676.2	*

^{L}Predictor variable log-transformed.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$.

Table 3 Single-term regressions of butterfly extinctions in European states against physical geography and socioeconomic variables. Regressions are fitted after forcing species richness to the models. Ordinary models do not contain any further covariables, controlled models contain covariables $Qt + S_{EX}$, trend quality and mean number of extinctions in neighbouring states. Only variables significant in at least one the two tests are shown. The darts indicate orientation of the relationships, '↑↓' stand for convex polynomials, and '–' for negative effect of categorical variables. *F*-tests are against null model for ordinary regressions, and with model containing $Qt + S_{EX}$ for controlled regressions

	Ordinary				*Controlled*			
		d.f.	*qAIC*	*P*		d.f.	*qAIC*	*P*
Null		35	159.2			35	159.2	
Species richness		1, 34	161.7			1, 34	161.7	
$Qt + S_{EX}$						3, 32	86.1	****
Physical geography								
Altitude range		2, 33	149.2		↓	4, 31	77.0	*
Area	↓^{L}	2, 33	144.8	*	↑^{L}	4, 31	76.8	*
Coastline	↓^{R}	2, 33	127.6	**	↑^{R}	4, 31	66.5	**
Island	(–)	2, 33	147.9	*		4, 31	83.5	
Latitude	↑↓	3, 32	98.5	***	↑↓	5, 30	78.6	*
Longitude	↑↓	3, 32	126.1	**		5, 30	82.2	
Annual temperature	↑↓	3, 32	99.7	***	↑↓	5, 30	67.0	**
Min. temperature	↑↓	3, 32	113.4	***	↑↓	5, 30	68.5	**
Max. temperature	↑↓	3, 32	97.9	***	↑↓	5, 30	63.8	**
Number of biotopes	↓	2, 33	125.6	**	↓	4, 31	53.5	***
Temperature range	↑↓	3, 32	139.1	*		4, 31	91.2	
Socioeconomics								
Human density	↑^{L}	2, 33	99.8	****		4, 31	89.3	
Agriculture	↓	2, 33	150.5	*		4, 31	90.2	
Urban employment	↑	2, 33	149.9	*		4, 31	90.1	
Railway density	↑^{R}	2, 33	71.7	****	↑^{R}	4, 31	65.4	**
Highway density	↑	2, 33	109.9	***		4, 31	89.1	

^{L}Independent variable log-transformed; ^{R}Independent variable transformed as square root.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$.

Physical geography

Species richness was high in southern and mountainous states containing high numbers of potential biomes, and low on islands and in countries affected by Quaternary glaciation (Table 2). It increased with mean temperature range, while maximum temperatures showed a polynomial response. Control for autocorrelation masked the effects of such spatially autocorrelated variables as latitude and glaciation, pointing to the positive effects of area and long coastlines.

Extinctions decreased with state area, number of potential biomes and coastline length (Table 3). They peaked in states with middle values of maximum, minimum and mean temperature, and a similar hump-shaped response applied to latitude, implying that states with average (in terms of Europe) climatic conditions lost most butterfly species. A weaker convex trend applied to longitude, and few species disappeared from islands. Controlled models retained the convex response to temperatures/latitude, strengthened the negative correlation with number of potential biomes and unmasked a negative correlation with heterogeneous relief.

Socioeconomic geography

Whereas none of the socioeconomic predictors showed a relationship with species richness in ordinary regressions, controlled models revealed a negative correlation between richness and human density (Table 2).

Extinctions (Table 3) were correlated positively with human density, percentage of urban employment and dense railway and highway networks. They decreased with employment in agriculture. The strongest correlate was the density of railways, which — as the only socioeconomic variable — sustained control for quality of data and spatial autocorrelation.

Multiple regressions

For species richness, the models based on physical geography achieved a very good fit, accounting for > 80% of variation in the ordinary model and about 30% of the variation in the controlled model (Table 3). Both models pointed to high species richness in mountainous states and low richness on islands; the controlled model included increase of species richness with area. The only socioeconomic variable that entered a richness model was human density, which had a weak effect (< 5%) after control for spatial autocorrelation.

For extinctions, physical geography and socioeconomic models fitted approximately equal amounts of variation, both approaching 70%. Both ordinary and controlled models for geography included a convex variation of extinctions with latitude and a decrease of extinctions with increasing number of potential biomes. In socioeconomic models, the strongest correlate was the density of railways, alone explaining nearly 70% of variation in the ordinary model and > 10% of variation in the controlled model.

Adding geography predictors to the (controlled) socioeconomic model for species richness (Best1 in Table 4) dramatically increased explained variance. For extinctions, both adding geography to socioeconomic models (Best1) and adding socioeconomic variables to geographical models (Best2) caused similar increases in variance explained. The geographical variables that entered the socioeconomic model were number of biomes and quadratic polynomial of maximum temperature, whereas the variable that entered the geography model was human density (Fig. 3).

Table 4 Multiple regressions for physical geography and socioeconomic correlates of butterfly species richness, and numbers of butterfly extinctions in European states. Extinctions are fitted to residuals of models that include original species richness. Model 'Best1' and 'Best2' combine physical geography and socioeconomic predictors, and were fitted by adding socioeconomic predictors to final physical geography models (Best1), and by adding physical geography predictors to the final socieconomic models (Best2)

	Species richness	d.f.	*AIC*	D^2	*Extinctions*	*d.f.*	*AIC*	D^2
	Null model	35	123,876.6		*Species richness model*	1, 34	161.7	4.2
	Ordinary models				*Ordinary models*			
Geography	+ Altitude range (–) Island (–) Glaciation	3, 32	26,335.4	82.2	± Latitude –Number of biomes	4, 31	65.8	67.7
Socioeconomic	n.a.	–	–	–	+ R(Railway density)	2, 33	71.7	69.3
Best1	= Geography model				± Latitude –Number of biomes +L (Human density)	5, 30	57.2	80.2
Best2	n.a.				+R (Railway density) –Number of biomes ± Max. temp.	5, 30	51.6	75.2
	Controlled models ($\sim D_N + S_N$)	2, 33	59,689.6	56.9	*Controlled models* ($\sim Qt + S_{EX}$)	3, 32	85.8	53.5
Geography	+L (Area) (–) Island + Altitude range	5, 30	26,129.0	84.1	–Number of biomes ± Latitude	6, 29	41.9	80.5
Socioeconomic	–L (Human density)	3, 32	54,691.3	62.7	+R (Railway density)	4, 31	64.8	67.5
Best1	–L (Human density) + Altitude range (–) Island	5, 30	28,564.5	82.6	= Geography model			
Best2	–L (Human density) + Altitude range (–) Island	5, 30	28,564.5	82.6	+R (Railway density) –Number of biomes ± Max. temp.	7, 28	38.6	83.4

D^2: percentage of deviation fitted by a model, i.e. explained variation; ±: convex polynomial relationship of dependent variable; (–): negative response to a categorical predictor. L: log-transformed predictor; R: square-root transformed predictor; Qt: quality of trend for individual states; D_N: number of neighbouring states; S_N: mean number of species in neighbouring states; S_{EX}: mean number of extinctions in neighbouring states.

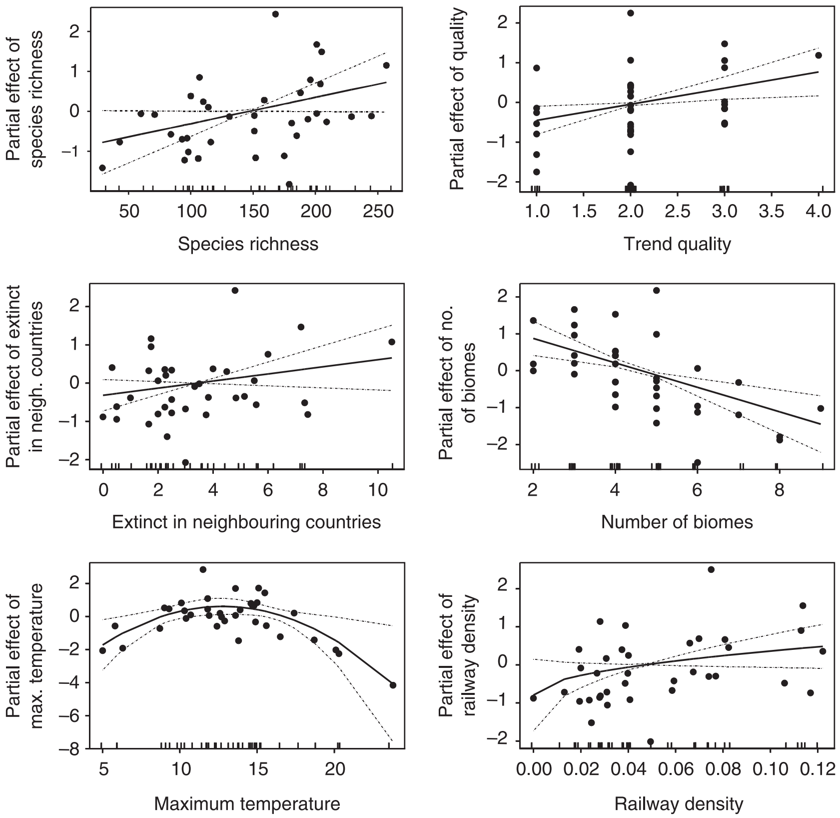

Figure 3 Scatterplots of the effects of individual predictors from a multiple-regression model of correlates of butterfly extinctions in European states. Controlled model Best2, was created by adding physical geography variables to the model already containing species richness, trend quality and spatial autocorrelation terms and the socioeconomic variable Railway density. The thick lines are partial effects of individual predictors on residuals (dots) fitted after including all other predictors to the model, the broken lines are standard errors.

DISCUSSION

Data quality and reliability of results

Three smallest states, Andorra, Liechtenstein and Malta, deviated from a negative extinctions–area relationship. For all the larger states, including the fourth smallest, Luxembourg, there is historical butterfly literature that allows tracking faunal changes back to the 19th century. This is not the case with the smallest states. This necessarily underestimates extinctions, which justified excluding the smallest states from the analyses.

The quality of distribution data (Qo) did not affect regression results for species richness, implying that even 'poor quality' data were sufficiently good. Surveying of butterflies has such a rich tradition in Europe that even in poorly studied countries, there is little chance of discovering hitherto unreported species, and hence changing the richness patterns. Trend quality (Qt), on the other hand, explained some 20% of variation in extinctions, implying that there might be some unreported losses in less surveyed states. However, fitting Qt as covariable did not change the general relationships with predictors, implying that the information on losses is relatively good even in poorly surveyed countries.

Controls for autocorrelation changed responses to some predictors, particularly with respect to extinctions. This was clearly due to masking the effects of spatially correlated predictors, such as latitude and climate (Diniz *et al*., 2003). On the other hand, the controls unmasked relationships with spatially uncorrelated variables, such as state area and altitude range.

Physical geography

The interrelations between extinctions and species richness were complex. Richness increased and extinctions decreased with area and biotope heterogeneity, the latter expressed as length of coastline, altitude range and the number of potential biomes. The latter two variables, which are closely correlated (Spearman's $s = 0.70$, $t_{34} = 5.79$, $P < 0.001$), entered multiple-regression models for richness and extinctions, respectively. Extinctions were also negatively correlated with temperature range, a variable that again expresses diversity of abiotic conditions. The positive association between heterogeneity of physical conditions and species richness has been reported for a variety of taxa (Kerr & Packer, 1997; Kerr *et al*., 2001; Rahbek & Graves, 2001; Hawkins & Porter, 2003a; Choi, 2004). The negative effect on extinction risks is considerably less known and its existence suggests that one of the mechanisms behind high richness of heterogeneous regions might be lower extinction risk associated with heterogeneity.

Effects of climatic variables were quite unexpected. First, richness was better fitted by latitude than by temperature, and the effect of (maximum) temperature was polynomial rather than increasing linearly. Strong positive association between richness and temperature is a rule in studies using more precise resolution, such as regular grids (e.g. Hawkins & Porter, 2003a,b). Using average climatic values per states led to the paradox that species rich countries of southern Europe, such as Greece, Italy and Spain, ended up with relatively low temperatures: all of them contain climatically harsh mountains. The hottest states then became Cyprus and Portugal, both with relatively poor fauna. Although the underlying cause behind the latitudinal pattern is most probably climatic/energetic (Hawkins & Porter, 2003b; Hawkins & Diniz, 2004), centroid latitude described species richness of individual states better than the average climatic values.

Another unexpected result was the hump-shaped relationships between extinctions and both thermal conditions and latitude. Ordinary models with latitude, annual temperature and maximum temperature attained nearly identical *qAIC* values, thus becoming indistinguishable in terms of parsimony (models differing in *AIC* by < 2.0 are considered equivalent, cf. Burnham & Anderson, 2002). However, latitude rather than a climatic variable tended to enter multiple-regression models. In any case, butterfly losses peak in climatically mild states of middle latitudes of Europe and the belt of high losses stretches from Belgium, Denmark, the Netherlands and northern France (Dennis *et al*., 2002) across Germany to East-Central Europe.

Schmitt & Hewitt (2003) proposed a biological interpretation of the pattern. Due to the Holocene faunal development, the fauna of central latitudes of Europe consists of a mixture of northern relics and southern arrivals. As far as southern species are considered, their declines in central Europe correlate with genetic impoverishment attributable to post-glacial colonization bottlenecks. In addition, many species persist in suboptimal conditions of range margins there (Shreeve *et al*., 1996; Wilson *et al*., 2002). Hence, a hump-shaped pattern in extinctions is fully expectable. The argument is consistent with the paucity of extinctions on islands (colonized by the most resistant species) and in mountainous states (species may respond to a changing environment by uphill and downhill movements).

The central European peak might be even stronger than documented here. Whereas the RDB reflects the state of knowledge in mid-1990s, several recent surveys reveal even higher extinction rates in some countries. For instance, RDB lists nine extinctions for the Czech Republic, but the actual number is 18 (Benes *et al*., 2002). Indeed, the models from Table 3 predict extinctions of 12–15 species for the country, i.e. closer to the actual number.

Socioeconomic variables

The only socioeconomic correlate of species richness was human density. Hence, states with the densest populations are not the richest in butterflies. This contrasts, e.g. with the situation in birds (Gaston & Evans, 2004), but the birds were analysed at a finer scale. Possibly, the pattern in butterflies might be due to high species richness in mountainous states (cf. Dennis *et al*., 1991), which tend to be sparsely populated.

The strongest socioeconomic correlate of extinctions was high density of railways. To interpret this pattern, note that the correlation with railways was considerably more robust than the correlation with highways (Table 3). Railways were built earlier than highways and dense railway networks constitute a legacy of early industrialization, prior to the arrival of combustion engines (e.g. Stepan, 1958; Gourvish, 1980). Industrialization propelled migration of workforces to cities, urbanization of landscapes, abandonment of traditional farming in less productive regions and replacement of traditional farmland and forest use by intensive methods elsewhere. These processes, already noted by their contemporaries, are widely documented by historians of economy (Pollard, 1968; Berlanstein, 1992; Clark, 1993; Schwartz, 1999). They radically altered the traditional European landscapes to which butterflies had adapted since the Neolithic (Thomas, 1993; Van Swaay, 2002). Railway density thus constitutes a proxy for an early beginning, and long duration, of such alternations (Gourvish, 1980; Hobsbawm, 1994). Indeed, the earliest butterfly extinctions date back to the 19th century (e.g. Asher *et al*., 2001; Benes *et al*., 2002).

Incidentally, the states with densest railway networks are situated in the middle latitudes of Europe, and combined multiple-regressions selected either the latitudinal peak, or railway density. Nevertheless, railway densities provide a stronger correlate of butterfly extinctions than latitude, according to *qAIC* values.

Another correlate of extinctions was the density of human population. Such an association was repeatedly reported for vertebrates (e.g. Kerr & Currie, 1995; Parks & Harcourt, 2002) but, to our knowledge, we provide the first evidence for insects. However, the effect was much weaker than that of railways, did not withstand control for data quality and autocorrelation and the two predictors were intercorrelated ($s = 0.64$, $P < 0.001$).

Other socioeconomic predictors were much weaker. They included a negative correlation between extinctions and employment in agriculture and a positive correlation between extinctions and urban employment. Employment in industry and services, or per-capita GDP, were unrelated to extinctions. It was interesting that losses were relatively high in several states of east-central Europe that had experimented with 'collectivization of agriculture', or expropriation of small farmers followed by massive investment in the state-operated agricultural sector. This development brought about a deterioration in biodiversity comparable to that of north-western Europe (cf. Donald *et al*., 2001), but failed to yield intended economic outputs (cf. Repassy & Symes, 1993). These observations again suggest that butterfly losses are attributable to persistent patterns of economic history rather than to the recent situation.

Synthesis and implications for conservation

Two patterns emerging from our analyses are low butterfly losses in topographically diverse states and high losses in early industrialized states. Therefore, incidences of extinctions are explicable to both geographical conditions and history of human pressure on biotopes.

Does the importance of early industrialization contradict the hypothesis of Schmitt & Hewitt (2003) associating threat rates in mid-latitude Europe with the much older history of postglacial colonization? Not necessarily. Although their role in early industrialization is still debated (e.g. Rosenberg & Birdzell, 1986), some physical conditions of mid-latitude Europe that correlate with high extinction rates might have favoured early industrialization. These include mild climate, flat relief and an intermediate position between southern and northern latitudes facilitating trade. The coincidence may explain much of the difficulties encountered by conservationists in regions where many species reach distribution margins, and where *at the same time* human pressure on natural habitats has been most intensive.

The association between extinctions and early industrialization leads to a pessimistic prediction. The land use changes that had begun in north-western and central Europe during the Industrial Revolution have spread subsequently throughout the entire continent. Assuming time lags between the alternation of biotopes and species losses (Tilman *et al.*, 1994; Ehrlich, 1995) and considering that RDB reports butterfly declines even in countries without extinctions, we warn that increasing numbers of states will soon face losses comparable to those in Belgium, the Czech Republic or the Netherlands.

On the other hand, the finding that extinction rates are low in states with high topographic and biotope heterogeneity offers some hope. Topographically diverse areas host a majority of species with restricted distribution, including European endemics (cf. Dennis *et al.*, 1991). It is hence possible that species occupying small ranges in heterogeneous regions face more optimistic prospects than species that have relatively large ranges, but inhabit the risky regions of Central Europe.

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