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LETTER

Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics

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Abstract

Whereas previous studies have investigated correlates of extinction risk either at global or regional scales, our study explicitly models regional effects of anthropogenic threats and biological traits across the globe. Using phylogenetic comparative methods with a newly-updated supertree of 5020 extant mammals, we investigate the impact of species traits on extinction risk within each WWF ecoregion. Our analyses reveal strong geographical variation in the influence of traits on risk: notably, larger species are at higher risk only in tropical regions. We then relate these patterns to current and recent-historical human impacts across ecoregions using spatial modelling. The body–mass results apparently reflect historical declines of large species outside the tropics due to large-scale land conversion. Narrow-ranged and rare species tend to be at high risk in areas of high current human impacts. The interactions we describe between biological traits and anthropogenic threats increase understanding of the processes determining extinction risk.

Keywords

Anthropogenic impact, body mass, conservation, geographical range size, life history, phylogenetic generalized linear model, population density, spatial autoregressive model, supertree.

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INTRODUCTION

The most comprehensive global assessment of species extinction risk, the IUCN Red List, currently lists 12% of bird species, 21% of mammals and 30% of amphibians as threatened by extinction (IUCN 2008). To counter the impending mass extinction with sparse conservation funds, it is necessary to understand the nature of threat factors to which species are exposed, and why species differ in their susceptibility to a given threat. Mammals are an appropriate study group for analyses of extinction risk because a fifth of their species are threatened, risk status for all mammalian species has been evaluated by the Red List (IUCN 2008), and their populations are declining rapidly (Collen *et al.* 2009). They are also of particular conservation concern because they are charismatic and fulfil important ecosystem functions. Additionally, mammals are currently the only species-rich taxon for which a species-level phylogeny, global distribution maps and extensive biological trait data are available (Bininda-Emonds *et al.* 2007; Jones *et al.* 2009).

Previous studies have shown that extinction risk is phylogenetically non-random even at small spatial scales, which implies that some biological traits shared by close relatives shape species' fates in the face of human impacts (Russell *et al.* 1998; Davies *et al.* 2008). The distribution of threatened species varies in space, as do anthropogenic threats such as habitat loss, overexploitation and invasive species (Baillie *et al.* 2004). Successful prediction of future risk will rely on knowledge of threats in a particular place, of traits that make species susceptible to those threats and of the phylogenetic relationships of the clade in question. Our study therefore aims to disentangle some of the complex interactions between threats and traits that shape extinction risk patterns both phylogenetically and spatially.

Due to the complexity of extinction risk processes, the global focus of many previous studies may obscure regional variation in both threats and species traits (Fisher & Owens 2004). Correlates of mammalian risk differ substantially among taxonomic groups and biogeographical regions, indicating that clade- or region-specific processes may drive the divergent patterns (Cardillo *et al.* 2008). The influence of certain traits on population decline or extinction risk in mammals and birds are specific to particular threat processes (Owens & Bennett 2000; Isaac & Cowlishaw 2004; Price & Gittleman 2007). Taxonomically focused analyses can describe taxon-specific threat processes more accurately (Fisher & Owens 2004), but global analyses of wider taxonomic focus can show more general patterns and are less affected by low sample sizes (Purvis 2008). We try to combine advantages of both approaches in our regionally focused study by building separate models for each WWF terrestrial ecoregion (Olson *et al.* 2001). Our aim is to map effects of species traits on mammalian extinction risk across taxonomic groups while accounting for both phylogenetic relationships and regional differences in threat processes.

We focus on the main biological traits that global studies have found to be related to high extinction risk: small geographical range size, low abundance or species population density, low fecundity or slow life history and large body size (see Fisher & Owens 2004; Purvis 2008 for recent reviews). Narrow distributions and/or low abundances make species susceptible, an effect believed to be intensified by habitat loss (Scharlemann *et al.* 2005). Low fecundities and slow life histories reduce the ability of populations to compensate for increased mortality and have been connected to overexploitation in particular (Owens & Bennett 2000; Isaac & Cowlishaw 2004; Price & Gittleman 2007). According to a recent global study, body size interacts with ecological and life-history variables: low reproductive rates and low abundance are associated with high risk, but only among larger mammals (Cardillo *et al.* 2005). Some taxonomically and regionally focused studies also find direct body size effects (Isaac & Cowlishaw 2004; Collen *et al.* 2006; but see Price & Gittleman 2007). Additionally, human impacts often interact with species traits to shape risk patterns. For example, large species are thought to be threatened disproportionately by overexploitation but not by habitat loss, as shown in birds (Owens & Bennett 2000) and primates (Isaac & Cowlishaw 2004) but not in artiodactyls (Price & Gittleman 2007).

Here, we use a novel two-stage combination of phylogenetic and spatial analyses to describe how anthropogenic threats interact with species traits to shape extinction risk. In contrast to other studies that have tended to focus on current human population density, we additionally use measures for human appropriation of ecosystem services, economic development and current and historical habitat loss via land conversion, all of which have been connected to extinction risk (Scharlemann *et al.* 2005; Luck 2007). In the first stage, we map regional patterns of the influence that selected species traits have on extinction risk when controlling appropriately for phylogenetic effects. Using spatially explicit analyses, the second stage then models these trait effects as functions of recent-historical and current human impacts across the globe.

MATERIAL AND METHODS

Geographical range and life-history data for mammals excluding marine and strictly freshwater species were obtained from the PanTHERIA data set (Jones *et al.* 2009). Following global studies (Cardillo *et al.* 2005, 2008), we chose geographical range size, body mass, species population density and two life-history traits as explanatory variables in our models. To describe life-history variation independently of body size, gestation length and weaning age were chosen to represent reproductive output and timing (Bielby *et al.* 2007). Following Purvis *et al.* (2000), we converted the IUCN Red List 2007 ratings (IUCN 2007) into a numerical index from 0 to 5 as a measure of extinction risk and excluded species classified as Data Deficient and threatened species not listed under criterion A (recent or ongoing population decline) to avoid the circularity of including species listed due to small population sizes or geographical ranges. Risk status for species in both our phylogeny and distribution data set was: 2447 species in Least Concern, 563 Near Threatened, 444 threatened under criterion A, and one Extinct in the Wild. Data availability for each predictor variable ranged between all 3455 species (geographical range size) and 801 species (23%; species population density) (see Table S1).

To investigate regional impacts of different biological traits on global mammalian extinction risk, we modelled the relationship of traits with risk for each WWF terrestrial ecoregion in a phylogenetic framework. We chose ecoregions rather than grid cells as spatial units because they are at a relatively small scale for a study of global extent, but yield sufficiently large sample sizes for modelling. Ecoregions also represent more natural units than a grid as they delimit biogeographical units with distinct natural communities (Olson *et al.* 2001). Finally, the coarser scale of ecoregions may avoid some of the errors arising from converting imprecise species ranges to e.g. grid cell occurrence (Jetz *et al.* 2008). We overlaid ecoregion shapefiles (http://worldwildlife.org/science/data/terreco.cfm, accessed on August 2006) with mammal species ranges from Jones *et al.* (2009) and extracted the occurrence of species per ecoregion. Of the 825 terrestrial ecoregions, 791 contained mammals.

For our phylogenetic analyses, we updated the species-level supertree of Bininda-Emonds *et al.* (2007) to account for the more recent mammalian taxonomy of Wilson & Reeder (2005). Species identities were associated between the respective taxonomies (Wilson & Reeder 1993/2005) using information on taxonomic synonymy therein. Of the 4510 species in the original phylogeny, 3609 were unchanged between the taxonomies and 368 were simply renamed. Taxonomic lumping resulted in the loss of 111 species, whereas 422 species were split to 1043 tips to incorporate 675 new species names (retaining the original species name when applicable). All of these taxonomic changes to the original topology were performed using the Perl script SYNONOTREE v2.2b (Bininda-Emonds *et al.* 2004). The new topology of 5020 species was then redated using exactly the procedures and data sets detailed in Bininda-Emonds *et al.* (2007, corrigendum 2008). We also updated the sequence data for this procedure to account for the new taxonomy using the Perl script SEQCLEANER v1.0.3. To avoid potential ambiguity, only one-to-one renamings were applied here; sequence data affected by taxonomic lumping or splitting were deleted from the data set. The new phylogeny is available in Appendix S1 (nexus file format, containing three phylogenies which are the best, upper and lower date estimates).

Phylogenetic analyses

We used Pagel's λ (Pagel 1999) to test for phylogenetic signal in our variables. If there is no phylogenetic signal in the variable in question, λ is zero, and it approaches one with increasing phylogenetic pattern. Estimates for λ were significantly non-zero for all our traits, including IUCN extinction risk rating (see Table S1). Therefore, we accounted for phylogenetic effects by using phylogenetic generalized linear models (PGLM) for within-ecoregion models of extinction risk (Freckleton *et al.* 2002). In a PGLM, Pagel's λ is used to account appropriately for the phylogenetic covariance between response and explanatory variables. This method avoids the errors associated with assuming complete phylogenetic independence ($\lambda = 0$, equivalent to non-phylogenetic analyses) or the over-correcting caused by assuming complete phylogenetic covariance ($\lambda = 1$, equivalent to phylogenetically independent contrasts, Purvis 2008). We ran all models in R version 2.6.0 (R Development Core Team 2007), using code provided by Robert Freckleton for the PGLM (version 3.2; updated version available as part of the CAIC package from http://r-forge.r-project.org/projects/caic).

We log-transformed all explanatory variables for the analyses. To avoid overfitting, we discarded models where the number of fitted parameters was higher than one-third of the number of nodes in the ecoregion phylogeny, a strict measure of sample size for phylogenetic models (Crawley 2007). As models including all five explanatory variables could be fitted in only 379 ecoregions, we instead built separate models focusing on each of our selected traits in turn, while controlling for independent effects of the most confounding covariates. The only single-predictor model fitted geographical range size as the focal variable; all other models controlled for range size because it was the single most important predictor of species risk. Models for species population density, weaning age and gestation length as focal traits additionally controlled for body mass, which correlates strongly with all three. We did not fit interaction terms because of sample size restrictions within the ecoregions. Each of our five models was fitted to each ecoregion and also to the whole mammalian data set to compare global and regional results. To facilitate subsequent comparisons of coefficient estimates across the globe, we did not simplify models.

Spatial analyses

In comparative studies, not only phylogenetic but also spatial non-independence can inflate degrees of freedom in statistical testing and violate the assumption of independently distributed errors in ordinary least-squares (OLS) regression (Dormann *et al.* 2007). As each of our phylogenetic models was on the comparatively small scale of a single ecoregion, spatial autocorrelation of species values within these models should be negligible. We therefore only account for the spatial non-independence in our models across ecoregions, effectively using a two-step process to incorporate both phylogenetic and spatial effects. Approaches that combine phylogeny and space in a single-step analysis are being developed (Freckleton & Jetz 2009) but do not yet support multiple regression models.

We used non-spatial and spatially-explicit multiple regression to relate the differences in susceptibility caused by intrinsic traits (i.e. the coefficients from the phylogenetic models) to environmental variables across ecoregions. Using an ARCINFO macro, we calculated ecoregion values for several variables describing available environmental energy, topology, anthropogenic and biological factors. Definitions of variables and data sources are listed in Table 1. Prior to analysis, we transformed environmental variables based on best approximation of a normal distribution: ecoregion area and the number of threatened species were log-transformed, and proportional variables were square-rooted (proportions of small-ranged and large species).

To avoid collinearity and reduce the data set dimensions, we ran a principal components analysis (PC) on seven proxy measures of anthropogenic impact (see Table S2). We used the first three PCs as explanatory variables, because they cumulatively explained over 90% of the total variance. PC1 mostly represented measures of current human impact (human population density, human appropriation of net primary productivity, human influence index and gross domestic product; Table S2). PC2 had a high negative loading of historical agriculture, reflecting land-use intensity throughout the past 300 years, and PC3 represented current urban land cover (Table S2).

Table 1 Description and sources for variables used in the non-spatial and spatial models across ecoregions

Variable group	Acronym	Variable description	Source
Energy	AET	Mean annual actual evapotranspiration (mm)	UNEP (1994)
Topology	ELEV	Mean elevation (m)	USGS EROS (1996)
	HABH	Habitat heterogeneity	Olson (1994)
	Area	Ecoregion area (km^2)	Olson *et al.* (2001) (available at: http://worldwildlife.org/science/data/terreco.cfm, accessed on August 2006)
Human influence	PC1	Principal component 1, reflecting current human pressures	See Table S2
	PC2	Principal component 2, reflecting historical agriculture	See Table S2
	PC3	Principal component 3, reflecting current urban land cover	See Table S2
Biology	THRSP	Number of threatened species	Jones *et al.* (2009); IUCN (2007/2008)
	SmallGR	Proportion of small-ranged species	Jones *et al.* (2009)
	LargeBM	Proportion of large species	Jones *et al.* (2009)

We measured habitat heterogeneity as the number of ecosystems. The number of threatened species was the number of species listed above Least Concern (excluding Data Deficient species and species in the three threat categories not listed under criterion A, IUCN 2007). We defined species as small-ranged if their range was in the lowest quartile of all ranges in the data set, i.e. < 33 180 km^2 (Jetz & Rahbek 2002). Large species were those with a body mass > 3 kg (Cardillo *et al.* 2005).

We initially fitted all environmental variables in Table 1 to each of our five response variables (the coefficient estimates from the phylogenetic models). These starting models were then simplified to minimum adequate models (MAMs) by sequentially removing the most non-significant variable until only significant ones remained in the MAM (Crawley 2007). Between two and six data points were removed from the MAMs because they were overly influential (absolute studentized residuals > 4). We report results without these, but indicate where results including them differed qualitatively.

Following Lichstein *et al.* (2002), we tested for the presence of spatial non-independence in the regression residuals of our MAMs using Moran's *I* correlograms, and accounted for it using spatial autoregression (SAR, simultaneous autoregressive model). This method assumes that the response is a function of both the explanatory variables and the values of the response at neighbouring locations (Kissling & Carl 2008). The SAR$_{\text{error}}$ approach we used models the autoregressive process in the error term, and has been recommended as the most reliable spatial autoregressive method (Kissling & Carl 2008). We report results of both OLS and SAR models for three reasons. First, SAR models have only recently been adopted in spatial ecology and there is no standard approach to model selection yet (Dormann *et al.* 2007). Second, it is unclear whether OLS coefficient estimation is biased by residual spatial autocorrelation (Hawkins *et al.* 2007). Third, OLS models potentially show broad-scale trends, whereas SAR models preferentially select for variables influencing the response at finer spatial scales (Diniz-Filho *et al.* 2003); both are of interest here.

We generated Moran's *I* correlograms and spatial models using the R packages spdep (Bivand 2007) and ncf (Bjørnstad 2006). Standardized *I* values were tested for significance using a one-tailed randomization test for positive autocorrelation (999 permutations, Lichstein *et al.* 2002). In the SAR models, we defined neighbours as data points closer than a model-specific maximum distance and used a row-standardized coding scheme for the spatial weights matrix (Kissling & Carl 2008). The maximum neighbour distance chosen for each model optimized its Akaike's information criterion value (AIC, Crawley 2007). Following Lichstein *et al.* (2002), we calculated R^2 values for the SAR models using Nagelkerke's formula, and assessed the contribution of each variable to OLS and SAR model fits using likelihood ratio tests for nested models.

RESULTS

Figure 1a shows the total species number and number of threatened species within each ecoregion, illustrating the spatial coverage of our data. Globally, each species trait was significantly associated with risk when analysed separately, although gestation length and body mass were non-significant in the global model that included all species traits (Table 2). Models for each focal trait were fitted in 602–729 ecoregions (Table 3). No models could be fitted in Antarctica or Oceania because of low species numbers there, but every other biogeographical realm was

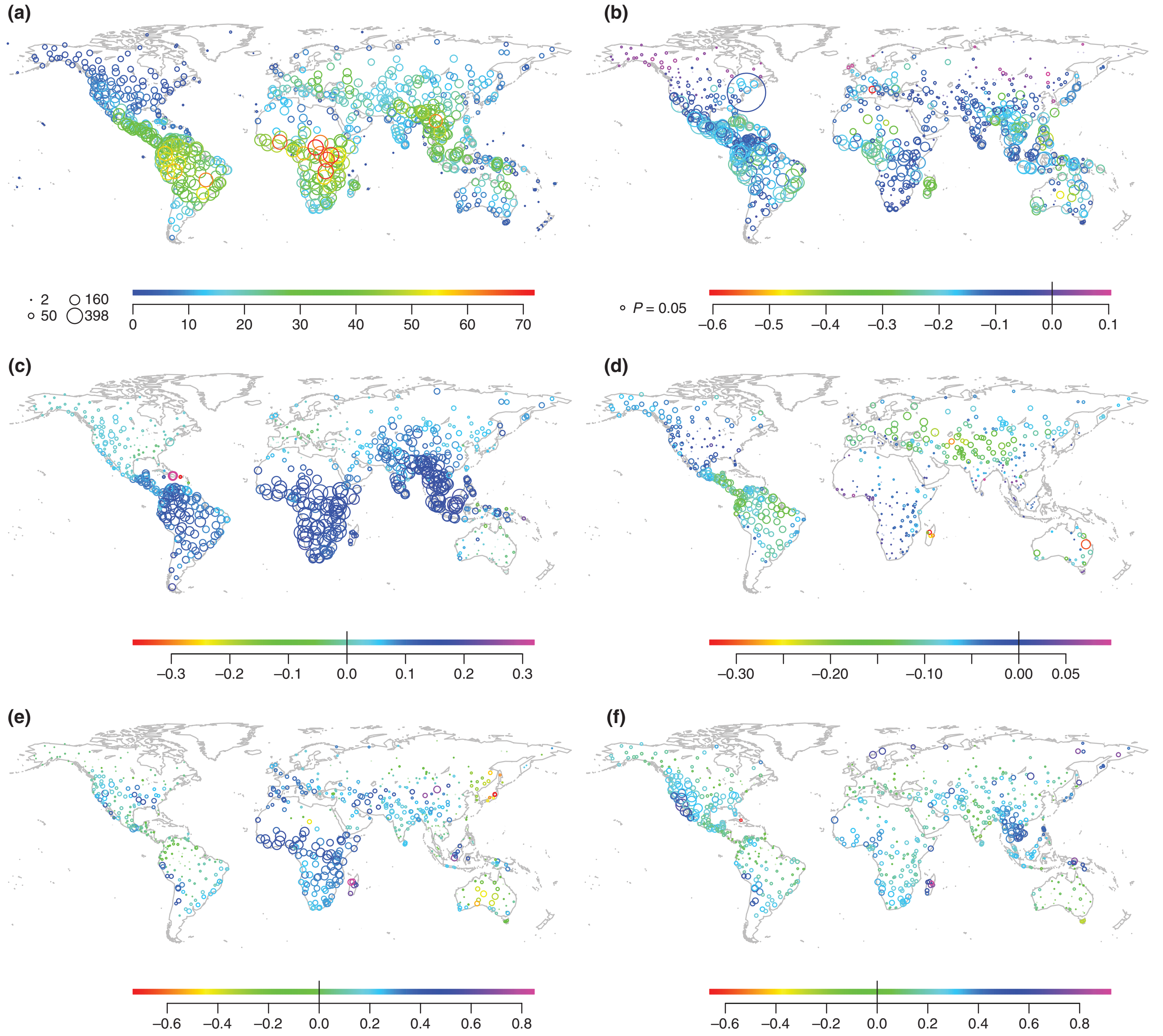

Figure 1 Species numbers per ecoregion (a) and results of within-ecoregion models for mammalian species extinction risk (b–f). In (a), a circle is plotted on the centroid of each ecoregion with > 1 mammal species. Circle size is proportional to total species number, and the size legend indicates the minimum, 1st and 3rd quartile and maximum circle size (species numbers were square-root transformed for plotting). Circles are coloured to indicate the number of species ranked above Least Concern, as shown in the colour key (excluding Data Deficient species and species in the three threat categories not listed under criterion A, IUCN 2007). In (b–f), a circle is plotted on the centroid of each ecoregion where a model could be fitted. Circle colour indicates the coefficient estimate for the focal explanatory variable in a PGLM against extinction risk, as given by the colour key, where a coefficient of zero is highlighted by a horizontal line. Circle size shows the significance of this coefficient, illustrated by the size legend in (b) for plots (b–f). The size legend indicates the size of a circle if the coefficient estimate is just not significantly different from zero (*t*-test, $P = 0.05$), i.e. smaller circles designate non-significant coefficients. Focal explanatory variables were: (b) geographical range size, (c) body mass, (d) species population density, (e) weaning age and (f) gestation length. All models controlled for geographical range size, and models (d), (e) and (f) also controlled for body mass.

represented. We found high regional heterogeneity in influences of some biological traits on extinction risk (Table 3, Fig. 1b–f).

Mammalian species extinction risk was negatively correlated with geographical range size in 62% of ecoregions throughout the world (Table 3, Fig. 1b). Controlling for range size, large body mass was correlated with high extinction risk in approximately half of the ecoregions (Table 3); significant correlations were mostly restricted to the Neotropical, Afrotropical and Indo-Malayan realms

Table 2 Results of global extinction risk models for the complete mammal data set using PGLM

	n	R^2	λ	Slope	Error	d.f.	t
Geographical range size	3455	0.17	0.72	−0.149	0.006	3453	26.80***
Body mass	2944	0.20	0.64	0.116	0.014	2941	8.56***
Population density	797	0.24	0.59	−0.051	0.016	793	3.11**
Weaning age	943	0.21	0.50	0.171	0.054	939	3.15**
Gestation length	1097	0.23	0.48	0.170	0.074	1093	2.30*
Full model	468	0.24	0.64				
Geographical range size				−0.213	0.022	462	9.80***
Body mass				0.060	0.034	462	1.77$^{(*)}$
Population density				−0.070	0.022	462	3.25**
Weaning age				0.203	0.082	462	2.49*
Gestation length				0.036	0.116	462	0.32

All models for focal traits controlled for geographic range size, and the models for species population density, weaning age and gestation length also controlled for body mass. The number of species for the model (n), adjusted R^2, optimized λ and the coefficient estimate (slope) with its standard error, degrees of freedom (d.f.) and absolute t-value are given. All λ values were significantly different both from zero and one (χ^2 tests, all $P < 0.001$). Significance levels for t: $^{(*)}P = 0.077$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Table 3 Results of within-ecoregion models of extinction risk for each biogeographic realm

		Geographical range		Body mass		Population density		Weaning age		Gestation length	
	T	M	S	M	S	M	S	M	S	M	S
Australasia	83	65	43	64	8	22	4	48	4	49	1
Antarctic	4	0	0	0	0	0	0	0	0	0	0
Afrotropic	114	102	74	102	96	96	0	101	87	102	25
Indo-Malaysia	106	101	91	100	91	80	0	97	5	98	25
Nearctic	118	107	27	107	8	96	13	107	9	106	47
Neotropic	179	166	153	166	125	142	105	145	12	146	26
Oceania	24	0	0	0	0	0	0	0	0	0	0
Palearctic	197	188	62	188	79	166	51	181	11	185	26
Total	825	729	450	727	407	602	173	679	128	686	150

T, total number of ecoregions; M, number of ecoregions with fitted models; S, number of ecoregions for which the slope of the focal trait was significantly different from zero in a PGLM ($P < 0.05$).

All models for focal traits controlled for geographic range size, and the models for species population density, weaning age and gestation length also controlled for body mass.

(Fig. 1c). Species population density and life-history variables displayed more heterogeneous spatial patterns of influence on extinction risk after controlling for range size and body mass, and were independently significant in only 19–29% of ecoregions (Table 3, Fig. 1d–f).

Spatial (SAR) models always had lower AIC values and explained a higher amount of variance than non-spatial (OLS) models (Table 4). They also successfully removed nearly all significant residual spatial autocorrelation (see Fig. S1). At least one anthropogenic variable was significant in each non-spatial model (Table 4). In both spatial and non-spatial models, current human impacts were strongly correlated with impacts of geographical range size on risk (Fig. 2a), whereas the effects of large body mass were greatest where there had been least historical land conversion (Fig. 2b). Effects of species population density and life-history traits on risk correlated with different anthropogenic measures, although associations were non-significant in spatial models for gestation length and species population density (Table 4, Fig. 2c–e).

At least one biological variable was significant in each model across ecoregions, and biology explained most of the variance especially in the spatially-explicit models (Table 4, Fig. 2). Available energy predicted the effects of body mass and life-history traits only (Fig. 2b,d,e). Topological variables (especially habitat heterogeneity) were significant in

Table 4 Results of non-spatial OLS and spatially-explicit SAR models across ecoregions

		Geographical range		Body mass		Population density		Weaning age		Gestation length	
		OLS	SAR	OLS	SAR	OLS	SAR	OLS	SAR	OLS	SAR
AIC		−1835.5	−2090.3	−2556.7	−2996.8	−1780.6	−2261.8	−464.1	−916.2	−682.3	−1043.1
Res. d.f.		698	696	694	692	589	587	657	655	665	663
R^2		40.2	58.5	56.6	76.9	14.1	61.8	18.2	58.7	12.3	48.8
Distance			870.8		1068.2		929.6		1120.7		939.7
Autoregressive error		0.711		0.871		0.859		0.862		0.798	
Energy	AET	n.s.		< 0.001***	< 0.001	n.s.		> −0.001***	> −0.001*	> −0.001**	> −0.001***
Topology	ELEV	n.s.		n.s.		n.s.		< 0.001***	< 0.001	n.s.	
	HABH	0.002***	0.002***	−0.002***	−0.001***	−0.002***	> −0.001	−0.004***	−0.001	n.s.	
	Area	n.s.		n.s.		n.s.		n.s.		−0.010*	−0.012***
Human	PC1	−0.007***	−0.005***	n.s.		0.008***	0.001	0.022***	0.010**	−0.008**	−0.005
	PC2	n.s.		0.012***	0.005***	0.006*	−0.001	n.s.		0.027***	−0.007
	PC3	n.s.		n.s.		0.012***	> −0.001	0.018*	−0.010	0.017*	0.005
Biology	THRSP	−0.039***	−0.040***	0.035***	0.023***	−0.007*	−0.018***	0.056***	0.043***	0.029***	0.057***
	SmallGR	n.s.		n.s.		n.s.		0.172*	0.075	0.341***	0.190***
	LargeBM	0.221***	0.059	0.228***	0.105***	0.103***	−0.177***	0.465***	0.109	0.260***	0.227*

OLS, ordinary least-squares; SAR, simultaneous autoregressive.

The response variables were the coefficient estimates for focal traits derived from phylogenetic extinction-risk models within ecoregions. Coefficient estimates and their significance are given for each environmental variable used as an explanatory term (see Table 1 for acronyms). For OLS models, variables fitted but not retained in the minimum adequate model are listed as non-significant (n.s.); these variables were not fitted in the corresponding SAR models. We also give AIC, residual degrees of freedom and R^2 (or pseudo-R^2) for all models, and the maximum neighbourhood distance and estimated autoregressive error coefficient for SAR models. Significance levels for the coefficient estimates: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

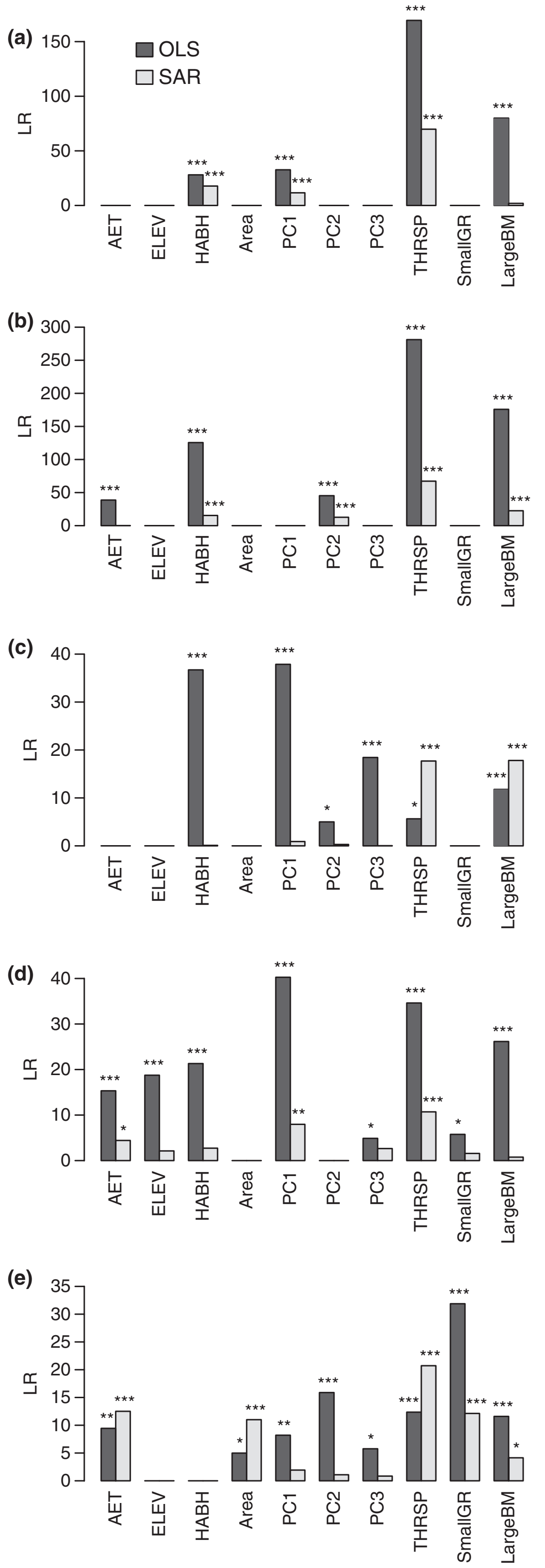

Figure 2 Results of likelihood ratio (LR) tests for non-spatial (OLS) and spatial (SAR) models across ecoregions. LR illustrates the contribution to model fit for explanatory variables that were significant in the non-spatial minimum adequate model (see Table 1 for variable acronyms). Stars above the bars indicate significance levels for the variables as in Table 4. Responses were the coefficient estimates from phylogenetic models of extinction risk within ecoregions for the following explanatory variables: (a) geographical range size, (b) body mass, (c) species population density, (d) weaning age, (e) gestation length.

each of the non-spatial models, although they were nearly all non-significant in spatial models for population density and life-history traits (Table 4, Fig. 2).

There were no qualitative differences in non-spatial models when excluding overly influential points, but three spatial models changed. In the geographical range model, proportion of large species was significant when including all data points ($z = 2.98$, d.f. = 702, $P < 0.01$). When including all data points in the body mass model, the proportion of large species was non-significant ($z = 1.45$, d.f. = 698, $P > 0.05$). In the gestation length model with all data points, proportion of small-ranged species was non-significant ($z = 1.71$, d.f. = 665, $P > 0.05$) and contributed much less to model fit than proportion of large species [likelihood ratio (LR) = 2.9 for small-ranged, LR = 20.3 for large species].

DISCUSSION

Globally, small geographical range, large body mass, low population density, high weaning age and high gestation length were associated with high extinction risk, but ecoregion models showed that the influence of each of these species traits varied substantially across the world. The strong spatial variation at the ecoregion scale demonstrates that to understand extinction-risk processes, small-scale analyses are needed. Our results also successfully relate current and recent-past human impacts to the influence of biological traits on species extinction risk, emphasizing the role of species traits in increasing susceptibility to different anthropogenic threats.

Similarly to previous studies, geographical range size was the single most important predictor of mammalian extinction risk both in our global and ecoregion models (Fisher & Owens 2004; Cardillo *et al.* 2008). Large size mattered in the global model when controlling for range size, but became non-significant when life-history traits and population density were added. Also, global models focusing on life-history traits and species population density did not explain much additional variance compared with the global model for body mass. These findings could be attributed to body–

mass interactions with life-history traits (Cardillo *et al.* 2005), but our ecoregion results reveal that the signal of body mass itself varies in space. Global models mask these regional differences, whereas our combination of phylogenetic and spatial analyses adds further understanding of the processes underlying extinction risk.

Body mass

The striking spatial pattern for body mass impacts, with large species at higher risk only in the tropics, does not stem from a latitudinal gradient in body mass because mammals do not show such a simple pattern (Rodríguez *et al.* 2008). Statistical power of our methods may play a role, because the observed relationship between large body mass and high extinction risk is stronger in ecoregions with more threatened species and a higher proportion of large species. However, when controlling for these variables, body mass additionally influences risk more strongly in areas with lower overall impact of historical agriculture. This suggests the presence of an extinction filter (Balmford 1996), whereby regions with a high agricultural impact throughout the past 300 years have lost their large species already. The implication is that proportion of species threatened due to large body mass should be highest at intermediate levels of land conversion (Davies *et al.* 2008). Accordingly, current human impacts did not correlate with body mass effects on risk in our study; presumably, most species susceptible due to large size have already been removed in many areas with highest current anthropogenic threat.

Data on historical extinctions and geographical distributions are patchy before the 19th century, but since then medium- and large-sized species in Europe, North America and Australia have definitely suffered range contractions and local extinctions (Ceballos & Ehrlich 2002). Many large species still exist in these areas, but have experienced declines in recent history that are not reflected by current Red List status, as these take only the last 10 years or three generations into account. For example, the brown bear (*Ursus arctos*) and the wolf (*Canis lupus*) are rated Least Concern (IUCN 2008). According to the threshold model of Barnosky (2008), both human and livestock biomass levels have skyrocketed above normally supportable levels since the industrial revolution, sustained by the mining of fossil fuels. If these increases throughout the past 300 years and the related large-scale land conversion have caused declines and local extinctions of large mammals in developed countries, they would have left large species only in the tropics. There, agricultural land conversion and human population have sharply increased only during the last few decades, so the recent and ongoing declines of tropical large species are reflected in the current Red List.

Our results provide evidence for a post-industrial extinction filter that has already affected large mammals in temperate regions and is now affecting those in the tropics. These body–mass effects might derive from underlying life-history variation, with large size increasing extinction risk only in areas where species have predominantly slow life histories and low reproductive output (Cardillo *et al.* 2005). On the other hand, body mass remained a significant variable in nearly all tropical ecoregions in our models fitting weaning age or gestation length, which may suggest a life-history-independent effect of body mass in the tropics. As we were not able to control for trait interactions on risk, our results cannot distinguish whether the high tropical impact of body mass on risk is truly independent of life-history traits or whether it reflects an interaction between body mass and life-history traits in the tropics.

Leaving life-history aside, there are two mechanisms by which large body mass could directly affect risk, which we could not account for due to a shortage of globally consistent data. Firstly, large mammals tend to have large home ranges, so they are more likely to encounter threats (Woodroffe & Ginsberg 1998). Home range size is positively correlated with extinction risk in global models, but not in taxonomically or regionally restricted ones (Cardillo *et al.* 2008). Secondly, human exploitation preferentially targets large mammals, and hunting has been shown previously to cause body mass selectivity in extinction risk (Owens & Bennett 2000; Isaac & Cowlishaw 2004; Collen *et al.* 2006). Subsistence hunting is largely confined to tropical regions and extracts more biomass in the Afrotropics than in the Neotropics (Fa *et al.* 2002), which coincides well with areas of strong body–mass effects on risk identified in our study. Our results are therefore consistent with the speculation that, in addition to habitat loss via land conversion, subsistence hunting in the tropics contributes to the higher risk faced by large species in the tropics than elsewhere.

Geographical range size

In accordance with global studies (e.g. Cardillo *et al.* 2008), we found a close relationship of high extinction risk and small geographical range size. Our ecoregion results additionally show that small range sizes are consistently linked to high risk across most of the world. This relationship appears not to be driven by narrow-ranged endemics, because the proportion of narrow-ranged species within ecoregions was not a significant predictor in our spatial analyses. At high northern latitudes, low species richness and predominantly large range sizes may explain the non-significant relationships (Davies *et al.* 2008).

Additionally, our composite measure of current human impact (PC1) was significantly correlated with the influence of range size on risk, indicating that high human population densities, high appropriation of net primary productivity and/or high economic development increase the effect of small geographical range size on extinction risk. The overwhelming impact of range size on risk is thought to stem from habitat loss, which affects species globally and narrow-ranged species in particular (Baillie *et al.* 2004; Scharlemann *et al.* 2005). Given that our human impact measure incorporated land transformation as part of the human influence index, our results may provide evidence for this link of habitat loss and high threat in narrow-ranged species. However, our results may also emphasize the role of more subtle habitat changes through extraction of ecosystem services, especially as historical agriculture (another indicator for habitat loss in our models) was non-significant here. We show that current human activities clearly play a role in increasing risk for narrow-ranged mammals virtually everywhere, but future studies should endeavour to separate the effects of different aspects of human influence on the relation between geographical range size and extinction risk (Luck 2007).

We are aware of two possible biases which could lead to consistently more threatened Red List status for narrow-ranged species. First, if the distributions of small-ranged species are mapped at a smaller grid resolution than larger-ranged ones, estimates of range size for risk assessments are exaggerated for all but the smallest ranges (Cowley *et al.* 1999), which could overestimate proportions of threatened narrow-ranged species. This bias is unlikely to affect our analyses because distribution maps usually overestimate range sizes for narrow-ranged species (Jetz *et al.* 2008), and because we excluded species ranked as threatened due to small range size only.

The second possible bias arises if most threatened mammals have already had their ranges reduced, because then small current geographical ranges would reflect susceptibility to human impacts. We found comparatively strong phylogenetic pattern in our geographical range size data ($\lambda = 0.63$). This may indicate that either geographical range size can be more phylogenetically conserved than previously thought (Webb & Gaston 2003) or that present range sizes include effects of phylogenetically selective susceptibility to human threats. Our result stresses a need to understand more about the factors that shape geographical range size, both spatially and phylogenetically (e.g. Cooper *et al.* 2008).

Abundance and life-history traits

Species population density, gestation length and weaning age showed much more spatially varied effects on extinction risk than body mass or geographical range size. Clearly, data availability plays a larger role in these three models, with data available for only about a quarter as many species as for body mass and range size. However, over 75% of our ecoregion models were still based on more than 40 species.

Our results show that low species population density is more strongly linked with high extinction risk where current human impacts are high, indicating that anthropogenic threats preferentially affect rare species, at least in some regions of the globe. We also provide some evidence that human activities influence the effects of reproductive timing and output on risk when controlling for body mass. High spatial heterogeneity of trait effects may indicate that the spatial scale of our study could be too large to separate mixed signals if extinction drivers vary within ecoregions, given that impacts of life-history variables on risk are likely to be linked to particular threats (Isaac & Cowlishaw 2004; Price & Gittleman 2007). The great importance of threatened species richness and proportion of large species in our species population density and life-history models may be due to the power of our method, but may also signify that low abundances and slow life histories affect the extinction risk of large species more strongly (Cardillo *et al.* 2005).

CONCLUSIONS

Our regional models of extinction risk revealed strong global heterogeneity in both the impact of biological traits and their interactions with the environment. Clearly, species extinction risk is determined by anthropogenic threats, environmental factors, species traits and interactions between these, but our analyses have highlighted some of the most important ones. We found that large size correlated strongly with high extinction risk only in tropical regions which are characterized by overall low historical agricultural impact, probably reflecting the effects of an extinction filter acting over the past 300 years, and possibly of current subsistence hunting. Our results also indicated that small geographical range sizes predispose species to extinction across much of the world, and that high current human impact increases the effects of low species population density and slow life history on risk.

Although our analyses are still on a larger scale than most protected areas, their spatial resolution makes them more useful for practical conservation science than global models. Our results also emphasize the importance of including several measures of both historical and current facets of anthropogenic threats, rather than oversimplifying human impact to just current human population density. The novel regional approach we used here illustrates and explains spatial heterogeneity in risk processes across the globe. Yet, to improve our knowledge of extinction risk further and to make predictions useful for conservation biologists on the ground, we need to better separate the effects of different aspects of human exploitation, and to better understand the reasons behind phylogenetic and spatial patterns of biological traits that shape susceptibility.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Moran's I correlograms of non-spatial and spatial model residuals.
Table S1 Data availability and phylogenetic signal for species traits in our mammal data set.
Table S2 Human influence measures and their loadings in the PCA.
Appendix S1 The phylogeny of 5020 extant mammal species.
Appendix S2 References for human influence measures in Table S2.

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