Which intrinsic traits predict vulnerability to extinction depends on the actual threatening processes

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Which intrinsic traits predict vulnerability to extinction depends on the actual threatening processes

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Abstract. Understanding what makes some species more vulnerable to extinction than others is an important challenge for conservation. Many comparative analyses have addressed this issue exploring how intrinsic and extrinsic traits associate with general estimates of vulnerability. However, these general estimates do not consider the actual threats that drive species to extinction and hence, are more difficult to translate into effective management. We provide an updated description of the types and spatial distribution of threats that affect mammals globally using data from the IUCN for 5941 species of mammals. Using these data we explore the links between intrinsic species traits and specific threats in order to identify key intrinsic features associated with particular drivers of extinction. We find that families formed by small-size habitat specialists are more likely to be threatened by habitat-modifying processes; whereas, families formed by larger mammals with small litter sizes are more likely to be threatened by processes that directly affect survival. These results highlight the importance of considering the actual threatening process in comparative studies. We also discuss the need to standardize and rank threat importance in global assessments such as the IUCN Red List to improve our ability to understand what makes some species more vulnerable to extinction than others.

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Introduction

Anthropogenic degradation of the world's ecosystems is widespread (Sanderson et al. 2002, Halpern et al. 2008, Barnosky et al. 2011), yet not all species are equally susceptible to perturbation. A wealth of comparative studies has provided insights into why some species are more vulnerable than others, linking vulnerability to extinction with intrinsic species' traits and extrinsic factors (Purvis et al. 2000, Cardillo et al. 2008, Davidson et al. 2009, Fritz et al. 2009, Lee and Jetz 2010, Murray et al. 2011, González-Suárez and Revilla 2013). However, apparently these studies have not contributed significantly

to conservation practice partly because results are ambiguous (varying across taxa and regions) but also because conservation practice is generally not proactive (Cardillo and Meijaard 2012). In addition, we think comparative analyses may have limited management applications because these studies often define vulnerability to extinction using general categories such as IUCN Red List status which do not provide information on the actual drivers that make species vulnerable (but see Isaac and Cowlishaw 2004, Price and Gittleman 2007). Two species listed under the same Red List status may be vulnerable due to very different drivers such as invasive species or climate change. A better understanding of the

threatening processes that make species more vulnerable could improve the usefulness of comparative analyses in conservation practice, for instance by revealing if particular traits make species more vulnerable to certain threats but not others.

In a general evaluation of the status of the world's mammals, Schipper et al. (2008) identified habitat loss/degradation and harvesting as the most common threats to mammals. These two drivers affect species differently as harvesting directly increases mortality, whereas habitat loss/degradation acts indirectly by reducing the carrying capacity of the environment. As a result, we can theoretically expect that threatening processes that reduce habitat availability, via fragmentation and loss, would be generally more damaging to ecologically specialized species than generalists. On the other hand, threats that directly affect survival, such as hunting or introduced predators, should present a greater problem for species with slow reproduction and long life cycles. In agreement with these predictions studies of fish, birds and mammals show that larger species, which generally have long life cycles, are at greater risk of suffering from exploitation (Jennings et al. 1999, Owens and Bennett 2000, Isaac and Cowlishaw 2004, Keane et al. 2005) and among hunted artiodactyls older weaning ages (slow reproduction) are associated with a higher risk of extinction (Price and Gittleman 2007). Meanwhile more specialized species of beetles, butterflies, birds and primates are particularly affected by habitat fragmentation and degradation (Davies et al. 2000, Owens and Bennett 2000, Isaac and Cowlishaw 2004, Ockinger et al. 2010, Newbold et al. 2013). However, not all previous results support the theoretical predictions. For example, a narrow ecological niche (restricted distribution range and living at high elevations) makes amphibians more prone to suffer declines associated with the fungal pathogen *Batrachochytrium dendrobatidis* (Bielby et al. 2008) although diseases presumably affect survival directly. Similarly, increased risk from habitat loss is associated with small body size in birds (Owens and Bennett 2000) and slow reproduction in butterflies (Ockinger et al. 2010).

Here, we use a large dataset representing global mammalian diversity to gain a better understanding of the threatening processes that

make mammals more vulnerable. First, we used the latest IUCN threat classification (version 3.0, IUCN 2010) to describe the prevalence and global spatial patterns of threatening processes affecting extant mammals. Our description builds on Schipper et al. (2008) account, updating their description of mammalian threats, which was based on a previous threat classification scheme. This previous scheme mixed stresses (consequence of a threat, e.g., habitat loss) and actual direct threats (e.g., harvesting) making it difficult to compare the different types of listed threats (Salafsky et al. 2008). Second, we explore if particular intrinsic species' traits explain the risk of extinction associated with different threatening processes, thus evaluating theoretical predictions for a large taxonomic group of conservation interest. We expect that habitat loss and fragmentation will represent a greater risk for more specialized mammals, while exploitation (and other threats directly affecting survival and reproduction) will be more damaging to species with slow reproduction and low reproductive output. Ultimately, we aim to provide a link between species' traits and the actual threatening processes that increase vulnerability to extinction. We hope this knowledge would be useful for conservation practitioners as management actions are often devised to protect species against particular threats.

METHODS

To define the specific threats and vulnerability status for each mammalian species we used the IUCN Red List version 2010.4 (IUCN 2010). The Red List describes the vulnerability status of 5491 mammals using a ranking system that classifies species as: LC (Least Concern), NT (Near Threatened), VU (Vulnerable), EN (Endangered), CR (Critically Endangered), EW (Extinct in the Wild), EX (Extinct) or DD (Data Deficient). The risk of extinction increases from LC to EW with species listed as VU or above considered threatened. In addition, the IUCN has generated a hierarchical threats classification scheme. We used the scheme version 3.0 which identifies 11 general types of threats (Table 1) divided into several subtypes (Salafsky et al. 2008). An update to this version (v. 3.1, IUCN 2012) was released after concluding this study. The updated version

Table 1. IUCN main threat categories and our reclassification.

Category	IUCN main threat
Direct effect	5.1 Biological resource use: Hunting & collecting of terrestrial animals
Direct effect	5.4 Biological resource use: Fishing and harvesting aquatic resources
Direct effect	8. Invasive & other problematic species & genes
Habitat effect	1. Residential and commercial development
Habitat effect	2. Agriculture and aquaculture
Habitat effect	3. Energy production and mining
Habitat effect	4. Transportation and service corridors
Habitat effect	5.2 Gathering terrestrial plants
Habitat effect	5.3 Logging and wood harvesting
Habitat effect	6. Human intrusions and disturbance
Habitat effect	7. Natural system modifications
Habitat effect	9. Pollution
Other	10. Geological events
Other	11. Climate change and severe weather

Note: IUCN categories defined by the classification scheme version 3.0. The category "Biological resource use" was separated into sublevels as sublevels represent distinct types of effects for our analyses.

follows the one used in the present study except for the inclusion of a new threat group defined as "Other options" and additional sublevels within category 8, "Invasive & other problematic species & genes." As of April 2013, these new categories have not been applied to any mammalian species.

We first described the prevalence and spatial distribution of threats in mammalian species and families. Unfortunately, because threat data are not spatially explicit, we had to assume that listed threats affect a species throughout its distribution range to describe spatial patterns. We used the IUCN global distribution range maps for all mammals selecting areas where presence was described as "Extant" or "Probably Extant" only (IUCN 2010). We used a cylindrical equal area projection and defined a grid equivalent to $2° \times 2°$ near the equator (Hurlbert and Jetz 2007). For each grid cell we report the mean number of threats per species, the coefficient of variation as a measure of heterogeneity among coexisting species in the number of threats, and the proportion of species threatened by the two main threats (see *Results*) for each cell with at least three species present. In contrast with previous descriptions (Schipper et al. 2008) we control for differences in species richness across different regions by using the mean and proportion instead of total species numbers.

After the initial description we reclassified the IUCN threats into three general categories: threats that directly affect survival and fecundity (direct effect), threats that modify or destroy habitat (habitat effect), and other minor threats

(Table 1). Species were then classified as only suffering direct effects (*only-direct*), only suffering habitat effects (*only-habitat*), and *others* (this group includes species that suffer more than one type of effect, as no species are only affected by minor threats). Using this information we calculated the number of *only-direct* and *only-habitat* species in each mammalian family and evaluated their Red List status as threatened (listed as VU or higher) or non-threatened. Species listed as Data Deficient (DD) have an undefined Red List status but several have listed threats and available trait data. Therefore, we included DD species in our analyses using two options: a precautionary approach that classifies all DD species as threatened and a relaxed approach that considers all DD species as non-threatened.

Intrinsic species' trait data were obtained from the PanTHERIA database (Jones et al. 2009). PanTHERIA provides median estimates for 30 variables describing morphology, development, reproduction, ecology and spatial data for 5415 mammals, but data are not available for all species and some traits are particularly data-poor with a pattern of data not missing at random (González-Suárez et al. 2012). To address some of these limitations we only considered traits with data for >1000 species, among which we selected five variables that describe the reproductive and life-cycle speed and one describing diet breadth (Table 2). Unfortunately, we could not directly use diet breadth (the number of diet categories consumed by a species; Table 2) because it did not clearly separate specialists from generalists.

Table 2. Description of intrinsic species' traits considered in the analyses.

Variable	N (%)	Symbol	Description
Traits associated with specialization			
Habitat breadth	5236 (95.3)	*hab*	Number of distinct terrestrial ecoregions occupied regularly by a species standardized by its range area (no./$\log_{10}(km^2)$).
Diet specialist	2119 (38.6)	*diet*	Category indicating that a species consumes a single diet category as defined by PanTHERIA. Categories: vertebrate, invertebrate, fruit, flowers/nectar/pollen, leaves/branches/bark, seeds, grass and roots/tubers.
Traits associated with reproductive speed			
Adult body mass	3476 (63.3)	*mass*	Mass of live adult, in grams.
Litter size	2456 (44.7)	*litter*	Number of offspring born per litter per female.
Gestation length	1329 (24.2)	*gest*	Length of time of active fetal growth, in days.
Weaning age	1142 (20.8)	*wean*	Age when nutritional dependency on the mother ends and independent foraging begins, in days.
Sexual maturity age	1025 (18.7)	*matur*	Age when individuals are first physically capable of reproducing, in days.

Note: All traits except habitat breadth were obtained from PanTHERIA (Jones et al. 2009). Habitat breadth was calculated overlapping distribution range maps with the ecoregions defined by Olson et al. (2001), see *Methods*. N is the number of mammalian species with available data for a given trait, with the percentage that it represents out of the total 5491 mammals.

For example, a species that eats vertebrates and fruits has a diet breadth of two, but a species that eats fruits and seeds also has a breadth of two, even though the second species is more of a diet specialist than the first. Instead, we defined a new variable that separates species with a diet breadth of one (eating a single food category) from the rest. In addition, we estimated habitat breadth using the IUCN global distribution range maps for all mammals (IUCN 2010) and the world terrestrial ecoregion map available from the WWF (Olson et al. 2001). From the species' distribution maps we selected areas where presence was described as "Extant" or "Probably Extant", origin as "Native", and seasonality as "Resident" to ensure only regularly occupied ecoregions were considered. Both maps were projected onto the cylindrical equal area projection and overlapped to define the number of distinct ecoregions occupied by each species. The total number of regions occupied by a given species was then divided by its ($\log_{10}$-transformed) distribution range area calculated from the same distribution map to generate a standardized measure of habitat breadth, *hab*, that controls for the size of the distribution area, which is directly associated with extinction risk.

For each mammalian family we then calculat-ed the mean trait value (data were previously $\log_{10}$-transformed except for *hab*), the proportion of species in each family that consume a single diet category (*diet*), the number of threatened *only-habitat* species, the number of threatened *only-direct* species, and the total number of species. Because the number of species, and hence the number of families, with available data varies among traits (Table 2), we fitted both univariate models which use all available data and multivariate models which are more data limited but consider how combined multiple traits influence vulnerability. In both cases, we fitted two groups of models: one to determine how intrinsic traits influence vulnerability via habitat effects (with the number of threatened *only-habitat* species per family as dependent variable), and the other via direct effects (with the number of threatened *only-direct* species per family as dependent variable). The total number of species per family was the binomial denom-inator in both groups of models. We fitted generalized linear models (GLM) with a binomial distribution (probit link) using the glm proce-dure in R (R Development Core Team 2011). To avoid collinearity issues in multivariate analyses, we eliminated highly correlated variables (Pear-son $r > 0.7$; Appendix: Table A1). We also

calculated Variance Inflation Factors (VIF) to confirm collinearity was not a problem in the fitted models. Finally, because data from related species or families may are not truly independent samples (due to evolutionary relationships) we tested for evidence of phylogenetic signal in the residuals of fitted regression models as recommended by Revell (2010). We used the phylosig procedure from the package Phytools in R (testing both λ and K) with the recent family-level mammalian phylogeny of Meredith et al. (2011).

RESULTS

Describing mammalian threats

Under version 3.0 the Red List identifies ongoing threats for 2551 species from 131 families listed under diverse status (including Data Deficient). Although the remaining 2940 species included in the Red List have no ongoing threats listed under the classification scheme, some of these species have a verbal description of current threatening processes. Therefore, lack of listed threats under the scheme does not necessarily imply they are completely free of threats (Hayward 2009). A few species also have past ($N = 242$) and future ($N = 219$) threats listed. The most common ongoing threats are Biological resource use and Agriculture (Fig. 1) which affect >63% of mammalian species and >80% of families with described threats. Within the category Biological resource use, the subcategories logging and exploitation affect similar numbers of species, but logging affects fewer families than exploitation. Most other threats affect relatively few species (Fig. 1), but these species often belong to distinct taxonomic families thus, the risk is broadly distributed among different taxonomic groups for most threats. For example, the 20 species that suffer from Geological events represent 13 different families. Therefore, while in general the frequency ranking of the drivers is similar for species and families (Fig. 1), drivers that affect very few species often still affect a significant number of mammalian families (i.e., threats are not family specific).

Most mammals have relatively few listed threats (mean $\pm$ SD = 1.2 $\pm$ 1.59 for all species, 2.5 $\pm$ 1.42 for the 2551 species with $\geq$1 ongoing threat). However, the number of threats differs significantly among taxonomic orders (Kruskal-Wallis test, $\chi^2 = 976.2$, df = 26, $P < 0.001$; Appendix: Fig. A1), families ($\chi^2 = 1401.9$, df = 155, $P < 0.001$), and genera ($\chi^2 = 2714.8$, df = 1241, $P < 0.001$). Large mammals such as the carnivores, primates, and ungulates have more listed threats than the smaller, but species-rich, rodents or bats (Appendix: Fig. A1). There are also spatial differences in threat prevalence with terrestrial mammals in the northern hemisphere, particularly Europe, the Palearctic, and south Asia, having on average a greater number of described threats compared to species in most of South America, sub-Saharan Africa and Australia (Fig. 2). Interestingly, the coefficient of variation (CV) values are low in most threat hotspots indicating a consistently high number of threats for the species in these areas (mean number of threats per grid = 3.2). On the other hand, heterogeneity (high CV) is greater in areas with low means, such as Australia or tropical Africa, where species with both high and low number of threats coexist. Marine areas in the northern hemisphere and coastal Asia are occupied by the mammals with the higher number of threats, while species living near Antarctica exhibit fewer threats. Considering only species affected by the most common threats, Resource biological use and Agriculture, we find that Resource biological use is a much more widespread risk than Agriculture (Fig. 2c, d). Within Resource biological use the threat direct exploitation is widespread, possibly because widely-distributed species are more often hunted, while the risk of logging is associated with the main remaining forested areas in the world (Appendix: Fig. A2). It is also noteworthy that Resource biological use, specifically direct exploitation, which includes both harvesting and incidental take (Appendix: Fig. A2), is widespread and prevalent among marine mammals. In fact, there is no area of the oceans without affected mammals (Fig. 2c).

After reclassifying drivers we find 207 *only-direct* species (only affected by direct exploitation and invasive or native problematic species) and 1162 *only-habitat* (agriculture, logging, fragmentation, etc.; Table 1) which show distinct spatial patterns (Appendix: Fig. A3). The remaining species are affected by the combination of direct and habitat effects ($N = 998$), habitat and minor effects ($N = 70$), and all three effects together ($N =$
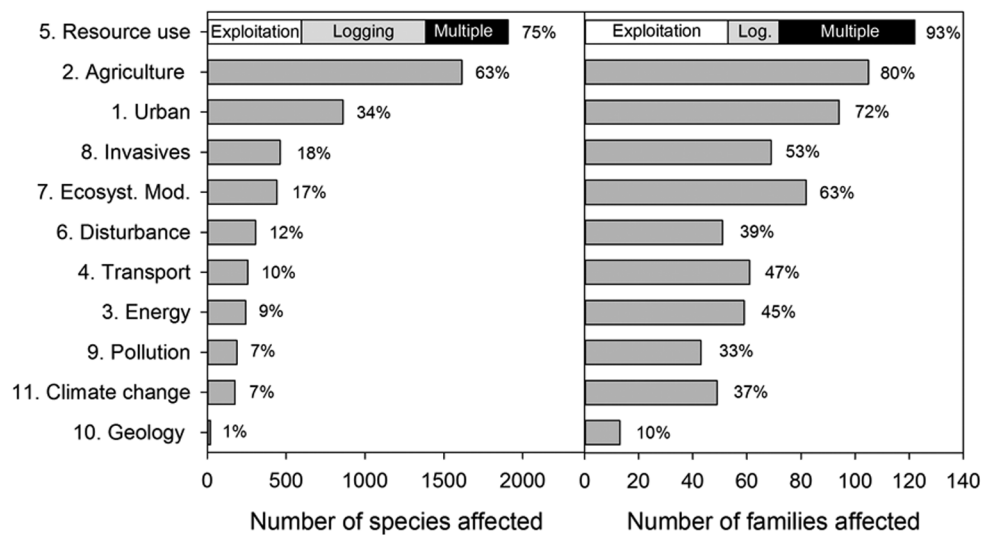
Fig. 1. Prevalence among mammals of the 11 IUCN threat categories. The bars represent the number of species (left panel) or families (right panel) for which each threat is listed. The percentages are from the total of 2551 species (131 families) with at least one listed threat. For Biological resource use (5. Resource use) we present the data separated into the main sublevels as they reflect very different types of threats (see Table 1).

114). No species are affected only by minor effects or by the combination of direct and minor effects. Evaluated at the family level we find that among the 156 extant mammalian families, 29 have no species listed as threatened (or 38 families if Data Deficient species are considered as non-threatened, i.e., relaxed approach). From the 127 families with listed threatened species, 32 have threatened *only-direct* species (mean = 2.4 species, range: 1–13, representing 0.003–50% of the species in the family), and 61 have threatened *only-habitat* species (mean = 10.1 species, range: 1–105, representing 0.01–100% of the species in the family). An additional 12 families have non-threatened *only-habitat* species.

Threats and intrinsic species' traits

Univariate analyses show that different types of mammals are at risk from habitat and direct effects (Table 3, Fig. 3). As expected, specialization traits (*hab* and *diet*) are associated with greater risk via habitat effects but not via direct effects, whereas traits that indicate slow reproduction (large body mass, smaller litter sizes, longer gestation periods, later weaning and sexual maturity ages) are associated with direct effect threats. In addition, we find that reproductive speed traits are also associated with risk via

habitat effects but in this case, fast reproductive strategies predict higher risk (Table 3).

From the initial variables, *matur* was not considered in multivariate analyses because of its high correlation with both *mass* and *wean* (Appendix: Table A1). VIF estimates indicate collinearity among the remaining variables was not a serious problem in any of the fitted models (Table 4). We also found no evidence of phylogenetic signal in the residuals of the tested models ($\lambda < 0.001$, $K < 0.19$, in all cases $P > 0.62$) indicating phylogenetic correction was not necessary (Revell 2010). Multivariate models confirm univariate results showing that habitat and direct effects affect different types of mammals (Table 4, Fig. 3). In particular, the proportion of threatened *only-habitat* species in a family increases with habitat specialization (fewer used biomes per area occupied) but unexpectedly, it may also decrease with the number of diet specialists (the relationship is only significant with the precautionary approach of considering all DD species as threatened). Habitat effects also threatened small body mammals, and likely those with shorter weaning ages (Table 4). On the other hand, no specialization variables are associated with risk from direct effects only, but families with large mean body mass, smaller
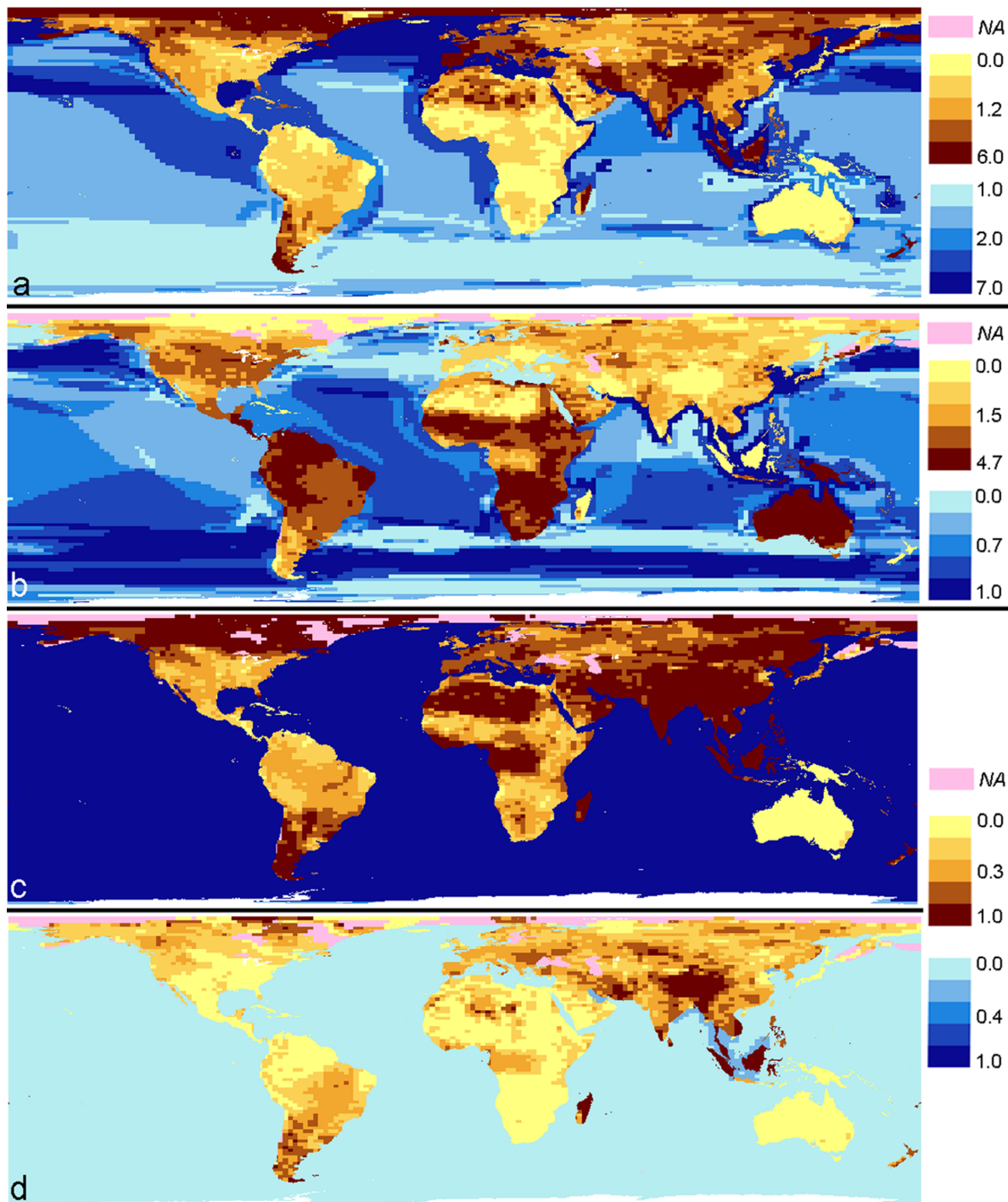
Fig. 2. Global distribution of the threats affecting terrestrial and marine mammals as described by the IUCN. (a) Mean number of threats. (b) Coefficient of variation (CV) in the number of threats, *NA* indicates areas with a single species present for which CV could not be estimated. (c, d) The proportion of mammals affected by the most common threats: Biological resource use and Agriculture, respectively. *NA* indicates areas with <3 species for which proportions were not estimated. For direct comparison panels c and d are plotted in the same scale.

Table 3. Coefficient estimates for univariate models.

		Only-habitat effects		Only-direct effects	
Variable	N	Precautionary	Relaxed	Precautionary	Relaxed
Specialization					
hab	135	−0.76 (0.142)**	−0.90 (0.164)**	−0.13 (0.291)	−0.14 (0.316)
diet	147	−0.47 (0.158)*	−0.40 (0.177)*	−0.26 (0.313)	−0.35 (0.374)
Reproductive speed					
mass	151	−0.24 (0.025)**	−0.23 (0.028)**	0.22 (0.032)**	0.13 (0.038)**
litter	149	0.52 (0.093)**	0.50 (0.105)**	−0.75 (0.186)**	−0.56 (0.212)*
gest	132	−0.43 (0.065)**	−0.40 (0.074)**	0.56 (0.122)**	0.24 (0.140)†
wean	130	−0.63 (0.075)**	−0.56 (0.084)**	0.49 (0.111)**	0.23 (0.135)†
matur	124	−0.47 (0.057)**	−0.41 (0.064)**	0.48 (0.103)**	0.22 (0.119)†

Note: Models explore how intrinsic species' traits influence the proportion of threatened species per family affected by each threat effect exclusively. N is the sample size in each model. Data Deficient (DD) species are classified as threatened under the precautionary approach and as non-threatened under the relaxed approach.
  *$P < 0.05$, ** $P < 0.001$, †$P < 0.10$.

litter sizes and unexpectedly shorter weaning ages have more threatened *only-direct* species. Overall, how DD species were classified (following either a precautionary or a relaxed approach) did not qualitatively influence our results, suggesting identified patterns are robust to the uncertainty associated with the threat status of DD species. Univariate and multivariate results
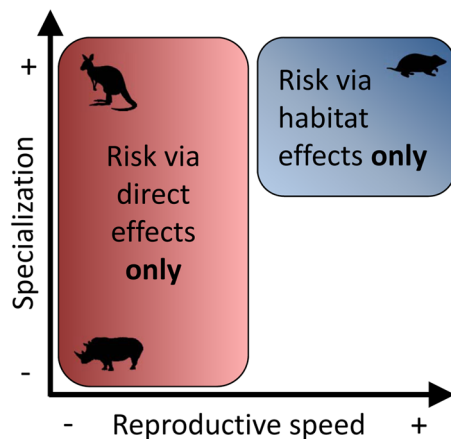

Fig. 3. General patterns of risk via distinct types of threats as a function of life-history and ecological species traits in mammals affected exclusively by one of those types of threats (reflecting results from Tables 3 and 4). Direct effects include threats that directly affect survival and fecundity (e.g., hunting), while habitat effects describe threats that modify or destroy habitat (e.g., agriculture and urbanization. See Table 1 for more details). Silhouettes represent examples of affected mammals along the spectrum of specialization and reproductive speed features.

were also qualitatively similar when species listed as threatened under Red List criterion B (small range area) were excluded from the analyses (Appendix: Tables A2 and A3).

As expected univariate analyses show that families with more species at risk from direct effects have late weaning ages, however multivariate results suggest the opposite pattern (Tables 3, 4). This is partly a consequence of the change in sample size and composition between analyses as model coefficients for *wean* in univariate models that use only data for the 111 families included in the multivariate model are not significant (precautionary approach b = 0.20, SE = 0.137, $P = 0.14$, relaxed approach b = 0.24, SE = 0.146, $P = 0.10$). In addition, *mass* and *wean* have a relatively high correlation ($r = 0.63$, Appendix: Table A1) and we find that after excluding *mass* from the multivariable model, *wean* is no longer significant (precautionary approach b = 0.06, SE = 0.194, $P = 0.76$, relaxed approach b = 0.02, SE = 0.213, $P = 0.92$). On the other hand, excluding *wean*, *mass* remains significant (precautionary approach b = 0.18, SE = 0.052, $P < 0.001$, relaxed approach b = 0.16, SE = 0.055, $P = 0.004$). In addition, longer gestation periods are associated with greater risk via direct effects in univariate analyses but under the relaxed approach there is a marginally significant negative relationship (shorter gestation associated with greater risk). Model coefficients for *gest* in univariate models that use only data for the 111 families included in the multivariate model are not significant (precautionary approach b = 0.23, SE = 0.140, $P = 0.10$, relaxed approach b = 0.25, SE = 0.151, $P = 0.10$). *Mass* and *gest* also have

Table 4. Coefficient estimates for multivariate models.

Variable	Only-habitat effects		Only-direct effects	
	Precautionary	Relaxed	Precautionary	Relaxed
Specialization				
hab	−1.03 (0.197)**	−1.28 (0.222)**	−0.34 (0.387)	−0.30 (0.423)
diet	−0.54 (0.254)*	−0.28 (0.279)	0.26 (0.432)	0.06 (0.489)
Reproductive speed				
mass	−0.29 (0.042)**	−0.26 (0.048)**	0.28 (0.068)**	0.25 (0.073)**
litter	0.10 (0.223)	0.15 (0.247)	−0.88 (0.403)*	−1.20 (0.447)*
gest	0.26 (0.167)	0.28 (0.184)	−0.40 (0.245)	−0.46 (0.258)†
wean	−0.28 (0.130)*	−0.27 (0.146)†	−0.52 (0.245)*	−0.51 (0.266)†
VIF	<5.2	<5.0	<3.6	<3.8

Note: Models describe how intrinsic species' traits associated with specialization and reproductive speed influence the proportion of threatened species per family affected by each threat effect exclusively. Models are all based on 111 families with available trait data. Data Deficient (DD) species are classified as threatened under the precautionary approach and as non-threatened under the relaxed approach.

$*P < 0.05$, $** P < 0.001$, $†P < 0.10$.

a relatively high correlation ($r = 0.60$, Appendix: Table A1) and after excluding *mass* from the multivariable model under the relaxed approach, *gest* is no longer significant (b = −0.24, SE = 0.277, $P = 0.39$). On the other hand, after excluding *gest*, *mass* remains significant (b = 0.22, SE = 0.070, $P = 0.002$).

DISCUSSION

Describing threats

Biological resource use and Agriculture are the most common threats to all mammals. Compared to a previous description that identified as the most common threat the general category of habitat loss/degradation (Schipper et al. 2008), the new classification allows us to show that the main source of habitat loss/degradation is Agriculture, followed by Urban and Logging (included in Biological resource use), which are also the key steps in the temporal land-use change transition described by Foley et al. (2005). Interestingly, while direct exploitation is only the fourth driver in importance among all mammals, it is the most common threat among mammals with deteriorating status, those that increased in vulnerability between the 1996 IUCN assessment and the 2008 assessment (Hoffmann et al. 2011). Direct exploitation may also be particularly relevant in impoverished regions where wildlife meat is often required for subsistence (Milner-Gulland et al. 2003). Worryingly, we detect an increase in the prevalence of invasive species as mammalian threats, which

affected 309 mammals in a previous assessment (Schipper et al. 2008) but now affects 461 species. Invasive species are a common threat among species with deteriorating status (Hoffmann et al. 2011) and may be a difficult to prevent or treat driver of extinction (Hayward 2011), raising concerns over the detected increase in prevalence. This change is not simply due to an increase in the number of assessed species (from 5487 to 5491) but whether it indicates greater awareness regarding invasive species or a true increase in risk remains to be determined. Invasive species may be the final driver of extinction for species reduced to small population sizes (Wyatt et al. 2008), and thus, may be a more relevant threat, or be perceived as such, for extinct or near extinct species. In addition, invasive or problematic native species are a particularly important problem for island endemics (Clavero et al. 2009) and indeed we find that among the 32 extinct mammals that were affected by invasives, 72% were island endemics. Finally, it is worth remarking that most threats have broad taxonomic impacts even if they affect few species. We find that while most threats affect <20% of mammalian species with listed threats, all threats except geology affect >37% of families with listed threats.

Europe and South Asia are threat hotspots, regions consistently occupied by mammals with high number of threats (Fig. 2). These are also among the most humanized environments with high prevalence of croplands and human settlements (Foley et al. 2005, Ellis and Ramankutty

2007). Unfortunately, South Asia is also a biodiversity hotspot for mammals (Schipper et al. 2008) and birds (Lee and Jetz 2010), but rapid development and environmental degradation are already placing many mammalian species at risk which may lead to multiple extinctions in the near future. Additional more localized threat hotspots are found in regions of high endemism (Madagascar) or extreme environments such as the Artic that are occupied by few species with many described threats (e.g., Polar bear, *Ursus maritimus*). In the marine realm, threat hotspots appear in the northern oceans and coastal Asia, but worryingly no marine areas are totally threat-free. Halpern et al. (2008) also found that no ocean areas are free of human impacts. Because marine mammals generally have broad distribution, their ranges often overlap with areas of high human use leading to widespread threats (Pompa et al. 2011). Mapping the most common threats only, we find that Biological resource use is a more widespread threat than Agriculture, possibly because species threatened by the former are on average more widely distributed (median range area 136,082.3 km^2) than species threatened by Agriculture (79,438.24 km^2). Both common threats are prevalent in South Asia but not in other tropical areas. This contrasts with results by Schipper et al. (2008) who found high prevalence of both common threats (habitat loss and hunting) in all tropical areas. However, Schipper et al. mapped the absolute number of species and thus, the highest number of threats was found where most mammals live (the tropics). Correcting for species richness we find that Agriculture does not affect a very high proportion of mammals in tropical South America or Africa, yet South Asia remains a clear threat hotspot.

While describing the threat patterns we noticed that the number of subcategories and details used to define a threat level by the IUCN do not correspond well with the prevalence of that threat among mammals. For example Pollution is one of the threat types described in more detail (six sublevels) yet Pollution is a threat for only 187 species (Fig. 1). On the other hand, some of the most common threats are not described in much detail. For example, Urban is the third most common threat affecting 34% of all mammals but only has three sublevels. Well-

described threats may be very important for other taxa assessed by the IUCN justifying the level of details. However, it is also possible that details are included based on our perception of diversity in potential sources (of pollution for example) rather than how relevant these sources are currently. This potential bias and how it may affect policy-building should be further studied.

Threats and life-history traits

Our results show that ecologically specialized species are most affected by threatening processes related to habitat loss and fragmentation. Mammalian families with more habitat specialists are likely to suffer negatively from habitat effects but not from direct effects (see also Isaac and Cowlishaw 2004). However, unexpectedly, the number of diet specialists may reduce the risk from habitat effects. It is possible that our estimate of diet breadth does not reflect specialization adequately. Because more detailed data were not available, we used the proportion of species in a family that consumes a single diet type. However, this means that a family with 10 species consuming only fruits and seeds (two distinct diet types) would have a *diet* = 0.0, whereas a family with 10 species, one consuming only fruits and nine consuming fruit, seeds and invertebrates would have a diet = 0.1, suggesting greater specialization in the second family when in reality the first group has more dietary specialists. Alternatively, or additionally, diet specialization may provide some unanticipated protection against habitat threats, but this possibility should be explored with more detailed diet information.

Species with slow reproduction and long life cycles are expected to suffer most from threats that directly affect survival and fecundity. Multivariate results provide partial support for this hypothesis. As expected, in multivariate models large mammals with small litter sizes are more threatened by direct effects. However, controlling for mass and litter size, mammals with shorter weaning ages are also at higher risk, suggesting that larger mammals with small litter size but relatively shorter weaning ages may be those most affected by direct threats. This surprising result is not confirmed by the univariate models, which show families with longer weaning ages are more affected. Multivariate models were

based on a reduced (and possibly biased) sample size because trait data were not available for all groups, which could have affected the results (González-Suárez et al. 2012). In addition, there are relatively few, but quite distinct threatened *only-direct* species. For example, the two families with most threatened *only-direct* mammals are the Cricetidae (Rodentia) and the Delphinidae (Cetacea) which represent very different species.

Interestingly, we also find that generally fast reproductive and life cycles (particularly small body mass and short weaning ages) are associated with higher risk from habitat effects. Large body mass in mammals has been often associated with greater risk of extinction (Purvis et al. 2000); however, we find that depending on the type of threatening process larger or smaller mammals are more prone to be at risk. Put simply, bigger is worse if you are hunted while being small is worse if your habitat is being converted to agriculture. This pattern has also been observed in other taxa: habitat loss is associated with small body size in birds while larger birds are more at risk from exploitation (Owens and Bennett 2000). Our finding provide a potential mechanism to explain a previously reported pattern: that larger mammals are only at greater risk in the tropics (Fritz et al. 2009). Higher risk for large mammals in the tropics may be due to higher unregulated hunting pressure in these areas (Robinson and Bodmer 1999).

Overall, our results provide support for theoretical predictions regarding how threats affect different types of species, but also reveal some unexpected patterns (see also Bielby et al. 2008, Ockinger et al. 2010). These departures likely reflect the fact that intrinsic traits can interact in complex ways with extrinsic factors (Fréville et al. 2007) so that the same human activity may represent a risk for a given species only under certain conditions. For example, a potential game species may be at risk of exploitation if it lives in an area where alternative food resources are limited (Keane et al. 2005), whereas if it lived in a different region it may not be exploited. Departures from the expected may also result from data limitations. The IUCN listing of threats is partly subjective and not consistently rated (Hayward 2009) and thus, not all relevant threats are included while some actual threatening processes are not listed. It is possible that some

species are perceived as having greater risks from some threats based on their intrinsic characteristics and thus, the threat is included in the listing even if the actual risk is not very high. We also have more biological information on some species of mammals (González-Suárez et al. 2012), and likely the threatening processes are better understood in better known species so that the description of threats may be biased in itself. In addition, some threats may be more important than others but the current IUCN list does not reliably rank threats. We agree with Hayward (2009) on the need to standardize and consistently rate the threat assignment (see Cassini 2011 for a suggestion on how to rank threats in a more quantitative manner) because understanding the actual causes of decline is essential for effective conservation.

In conclusion, mammals are affected by threats across the globe, with threat hotspots in South Asia and Europe. The most common threats are Biological resource use and Agriculture highlighting the importance of both habitat loss and direct exploitation for mammals. However, at the extremes, species affected only by habitat loss or only by direct effects are distinct types of mammals, with small-size habitat specialists being particularly at risk from habitat loss and fragmentation, whereas larger mammals producing fewer young are at higher risk from direct exploitation or invasive species (Fig. 3). Comparative analyses aimed to understanding what makes some species more vulnerable should consider the diversity of extinction drivers as distinct species respond differently to the same threats. In addition, it is clear that local conditions will influence how a given threat affects a species thus, local scale analyses that explicitly account for such conditions are ultimately essential for effective management.

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Literature Cited

Barnosky, A. D., et al. 2011. Has the Earth's sixth mass extinction already arrived? Nature 471:51–57.

Bielby, J., N. Cooper, A. A. Cunningham, T. W. J. Garner, and A. Purvis. 2008. Predicting susceptibility to future declines in the world's frogs. Conservation Letters 1:82–90.

Cardillo, M., G. M. Mace, J. L. Gittleman, K. E. Jones, J. Bielby, and A. Purvis. 2008. The predictability of extinction: biological and external correlates of decline in mammals. Proceedings of the Royal Society B 275:1441–1448.

Cardillo, M. and E. Meijaard. 2012. Are comparative studies of extinction risk useful for conservation? Trends in Ecology & Evolution 27:167–171.

Cassini, M. 2011. Ranking threats using species distribution models in the IUCN Red List assessment process. Biodiversity and Conservation 20:3689–3692.

Clavero, M., L. Brotons, P. Pons, and D. Sol. 2009. Prominent role of invasive species in avian biodiversity loss. Biological Conservation 142:2043–2049.

Davidson, A. D., M. J. Hamilton, A. G. Boyer, J. H. Brown, and G. Ceballos. 2009. Multiple ecological pathways to extinction in mammals. Proceedings of the National Academy of Sciences USA 106:10702–10705.

Davies, K. F., C. R. Margules, and J. F. Lawrence. 2000. Which traits of species predict population declines in experimental forest fragments? Ecology 81:1450–1461.

Ellis, E. C. and N. Ramankutty. 2007. Putting people in the map: anthropogenic biomes of the world. Frontiers in Ecology and the Environment 6:439–447.

Foley, J. A., et al. 2005. Global consequences of land use. Science 309:570–574.

Fréville, H., K. McConway, M. Dodd, and J. Silvertown. 2007. Prediction of extinction in plants: interaction of extrinsic threats and life history traits. Ecology 88:2662–2672.

Fritz, S. A., O. R. P. Bininda-Emonds, and A. Purvis. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. Ecology Letters 12:538–549.

González-Suárez, M., P. M. Lucas, and E. Revilla. 2012. Biases in comparative analyses of extinction risk: mind the gap. Journal of Animal Ecology 81:1211–1222.

González-Suárez, M. and E. Revilla. 2013. Variability in

life-history and ecological traits is a buffer against extinction in mammals. Ecology Letters 16:242–251.

Halpern, B. S., et al. 2008. A global map of human impact on marine ecosystems. Science 319:948–952.

Hayward, M. 2011. Using the IUCN Red List to determine effective conservation strategies. Biodiversity and Conservation 20:2563–2573.

Hayward, M. W. 2009. The need to rationalize and prioritize threatening processes used to determine threat status in the IUCN Red List. Conservation Biology 23:1568–1576.

Hoffmann, M., J. L. Belant, J. S. Chanson, N. A. Cox, J. Lamoreux, A. S. L. Rodrigues, J. Schipper, and S. N. Stuart. 2011. The changing fates of the world's mammals. Philosophical Transactions of the Royal Society B 366:2598–2610.

Hurlbert, A. H. and W. Jetz. 2007. Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. Proceedings of the National Academy of Sciences USA 104:13384–13389.

Isaac, N. J. B. and G. Cowlishaw. 2004. How species respond to multiple extinction threats. Proceedings of the Royal Society B 271:1135–1141.

IUCN. 2010. IUCN Red List of Threatened Species. Version 2010.4. http://www.iucnredlist.org/

IUCN. 2012. IUCN Threats classification scheme, version 3.1. http://www.iucnredlist.org/technical-documents/classification-schemes/threats-classification-scheme

Jennings, S., J. D. Reynolds, and N. V. C. Polunin. 1999. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. Conservation Biology 13:1466–1475.

Jones, K. E., et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:2648–2648.

Keane, A., M. D. Brooke, and P. J. K. McGowan. 2005. Correlates of extinction risk and hunting pressure in gamebirds (Galliformes). Biological Conservation 126:216–233.

Lee, T. M. and W. Jetz. 2010. Unravelling the structure of species extinction risk for predictive conservation science. Proceedings of the Royal Society B 278:1329–1338.

Meredith, R. W., et al. 2011. Impacts of the Cretaceous terrestrial Revolution and KPg extinction on mammal diversification. Science 334:521–524.

Milner-Gulland, E. J., Bennett, E. L. and SCB 2002 Annual Meeting Wild Meat Group. 2003. Wild meat: the bigger picture. Trends in Ecology & Evolution 18:351–357.

Murray, K. A., D. Rosauer, H. McCallum, and L. F. Skerratt. 2011. Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. Proceedings of

the Royal Society B 278:1515–1523.

Newbold, T., J. P. W. Scharlemann, S. H. M. Butchart, Ċ. H. Şekercioğlu, R. Alkemade, H. Booth, and D. W. Purves. 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. Proceedings of the Royal Society B 280:20122131.

Ockinger, E., O. Schweiger, T. O. Crist, D. M. Debinski, J. Krauss, M. Kuussaari, J. D. Petersen, J. Poyry, J. Settele, K. S. Summerville, and R. Bommarco. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters 13:969–979.

Olson, D. M., et al. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. BioScience 51:933–938.

Owens, I. P. F. and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences USA 97:12144–12148.

Pompa, S., P. R. Ehrlich, and G. Ceballos. 2011. Global distribution and conservation of marine mammals. Proceedings of the National Academy of Sciences USA 108:13600–13605.

Price, S. and J. Gittleman. 2007. Hunting to extinction: biology and regional economy influence extinction risk and the impact of hunting in artiodactyls. Proceedings of the Royal Society B 274:1845–1851.

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining

species. Proceedings of the Royal Society B 267:1947–1952.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Revell, L. J. 2010. Phylogenetic signal and linear regression on species data. Methods in Ecology and Evolution 1:319–329.

Robinson, J. G. and R. E. Bodmer. 1999. Towards wildlife management in tropical forests. Journal of Wildlife Management 63:1–13.

Salafsky, N., D. Salzer, A. J. Stattersfield, C. Hilton-Taylor, R. Neugarten, S. H. M. Butchart, B. E. N. Collen, N. Cox, L. L. Master, S. O'Connor, and D. Wilkie. 2008. A standard lexicon for biodiversity conservation: unified classifications of threats and actions. Conservation Biology 22:897–911.

Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. BioScience 52:891–904.

Schipper, J., et al. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322:225–230.

Wyatt, K. B., P. F. Campos, M. T. P. Gilbert, S.-O. Kolokotronis, W. H. Hynes, R. DeSalle, S. J. Ball, P. Daszak, R. D. E. MacPhee, and A. D. Greenwood. 2008. Historical mammal extinction on Christmas Island (Indian Ocean) correlates with introduced infectious disease. PLoS ONE 3:e3602.

SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Correlations among family mean values of intrinsic species' traits.

Trait	hab	diet	mass	litter	gest	wean
diet	0.23					
mass	0.26	−0.19				
litter	−0.04	−0.05	−0.32			
gesta	0.29	−0.06	0.60	−0.59		
wean	−0.15	−0.10	0.63	−0.51	0.46	
matur	0.18	0.03	**0.75**	−0.59	0.69	**0.78**

Note: All variables, except *hab* and *diet*, were $\log_{10}$-transformed. High correlations (Pearson $r > 0.7$) are indicated in boldface.
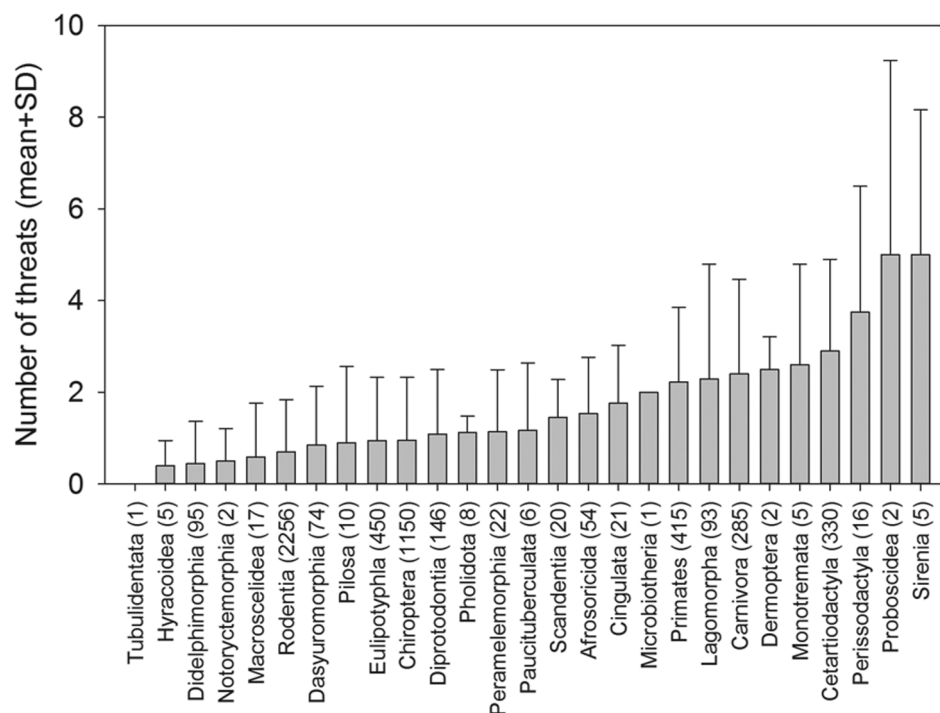
Fig. A1. Mean and standard deviation (SD) of the number of threats per species for each taxonomic order (including species with no threats). Numbers in parenthesis indicate the number of species in each order. Note that the single Tubulidentata species has no recorded threats.
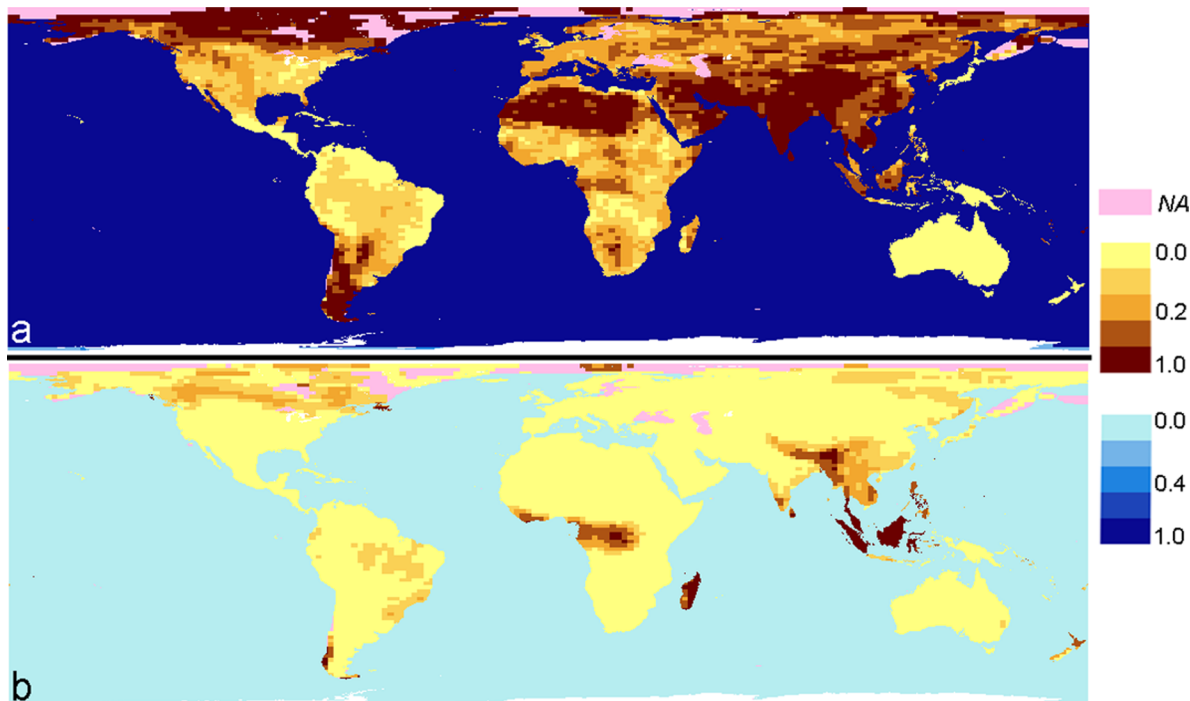

Fig. A2. Global distribution of the proportion of terrestrial and marine mammals at each site affected by direct exploitation/bycatch (a) and by logging (b). *NA* indicates areas with <3 species for which proportions were not estimated. For direct comparison both panels are plotted in the same scale.
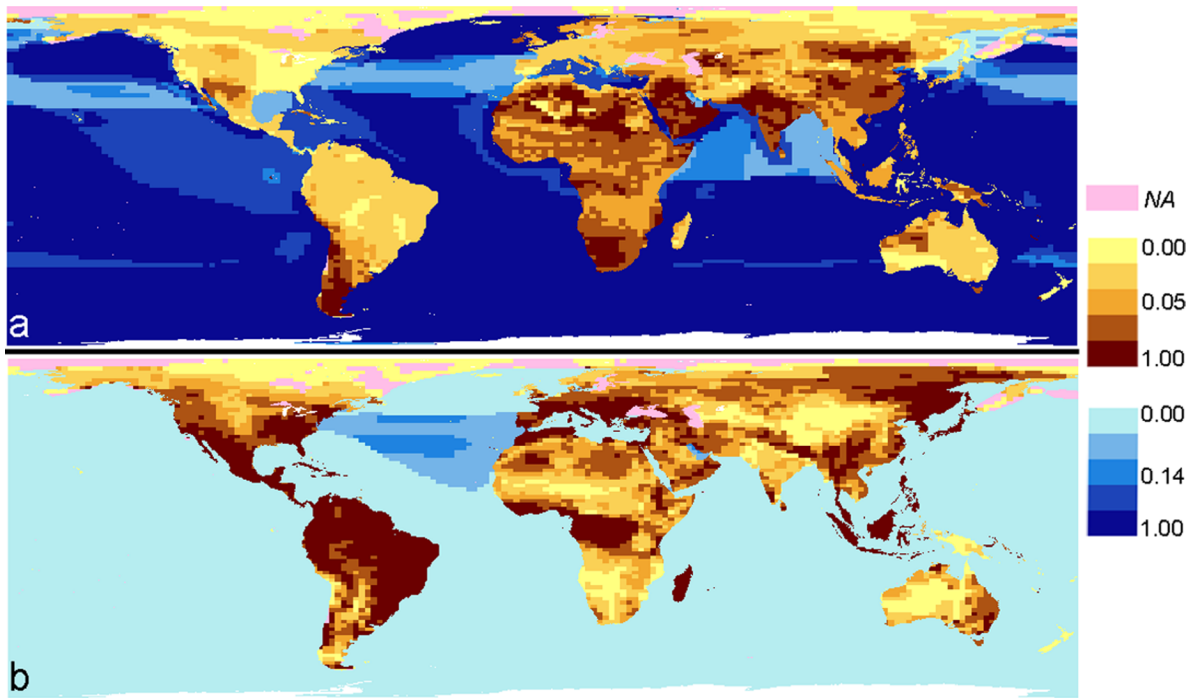
Fig. A3. Global distribution of the proportion of terrestrial and marine mammals at each site affected only by direct effects (a) and only by habitat effects (b). *NA* indicates areas with <3 species for which proportions were not estimated. For direct comparison both panels are plotted in the same scale.

Table A2. Coefficient estimates for univariate models.

Variable	N	Only-habitat effects		Only-direct effects	
		Precautionary	Relaxed	Precautionary	Relaxed
Specialization					
hab	132	−0.56 (0.175)*	−0.79 (0.274)*	−0.17 (0.344)	−0.16 (0.394)
diet	146	−0.27 (0.187)	0.12 (0.256)	−0.23 (0.337)	−0.27 (0.432)
Reproductive speed					
mass	150	−0.16 (0.029)**	−0.07 (0.040)†	0.26 (0.035)**	0.18 (0.044)**
litter	147	0.12 (0.114)	−0.45 (0.172)*	−0.95 (0.221)**	−0.84 (0.277)*
gest	130	−0.15 (0.080)†	0.25 (0.115)*	0.79 (0.146)**	0.46 (0.173)*
wean	129	−0.35 (0.090)**	0.08 (0.117)	0.67 (0.123)**	0.40 (0.157)*
matur	123	−0.26 (0.070)**	0.10 (0.099)	0.66 (0.119)**	0.41 (0.145)*

Note: Models describe how intrinsic species' traits influence the proportion of threatened species per family affected by each threat effect exclusively. N is the sample size in each model. These analyses excluded all species listed as threatened under the Red List criterion B (small range area). Data Deficient (DD) species are classified as threatened under the precautionary approach and as non-threatened under the relaxed approach.
*$P < 0.05$, ** $P < 0.001$, †$P < 0.10$.

Table A3. Coefficient estimates for multivariate models.

Variable	Only-habitat effects		Only-direct effects	
	Precautionary	Relaxed	Precautionary	Relaxed
Specialization				
hab	−0.73 (0.242)*	−1.11 (0.327)**	−0.59 (0.456)	−0.54 (0.525)
diet	−0.85 (0.327)*	−0.30 (0.434)	0.50 (0.460)	0.30 (0.545)
Reproductive speed				
mass	−0.27 (0.054)**	−0.17 (0.075)*	0.33 (0.081)**	0.31 (0.090)**
litter	−0.17 (0.290)	−0.20 (0.417)	−0.74 (0.479)	−1.24 (0.568)*
gest	0.33 (0.216)	0.62 (0.299)*	−0.24 (0.289)	−0.37 (0.314)
wean	−0.17 (0.164)	−0.14 (0.235)	−0.55 (0.288)†	−0.54 (0.328)†
VIF	<5.9	<5.6	<3.6	<3.7

Note: Models describe how intrinsic species' traits associated with specialization and reproductive speed influence the proportion of threatened species per family affected by each threat effect exclusively. The dataset for these analyses ($N = 109$ families) excluded all species listed as threatened under the Red List criterion B (small range area). Data Deficient (DD) species are classified as threatened under the precautionary approach and as non-threatened under the relaxed approach.

 *$P < 0.05$, ** $P < 0.001$, †$P < 0.10$.