Latent extinction risk and the future battlegrounds of mammal conservation

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Global conservation prioritization usually emphasizes areas with highest species richness or where many species are thought to be at imminent risk of extinction. However, these strategies may overlook areas where many species have biological traits that make them particularly sensitive to future human impact but are not yet threatened because such impact is currently low. In this article, we identify such areas for the world's mammals using latent extinction risk, the discrepancy between a species' current extinction risk and that predicted from models on the basis of biological traits. Species with positive latent risk are currently less threatened than their biology would suggest, usually because they inhabit regions or habitats still comparatively unmodified by human activity. Using large new geographic, biological, and phylogenetic databases for nearly 4,000 mammal species, we map the global geographic distribution of latent risk to reveal areas where the mammal fauna is still relatively unthreatened but has high inherent sensitivity to disturbance. These hotspots include large areas such as the Nearctic boreal forests and tundra that are unrepresented in most current prioritization schemes, as well as high-biodiversity areas such as the island arc from Indonesia to the south Pacific. Incorporating latent extinction risk patterns into conservation planning could help guard against future biodiversity loss by anticipating and preventing species declines before they begin.

conservation planning | hotspots | Red List

Systematic conservation planning seeks to optimize the allocation of scarce conservation funding by prioritizing areas for protection. Because biodiversity loss is now recognized as a global-scale phenomenon and many conservation decisions are taken at an international level, conservation planning is increasingly done on a global scale (1). Priority areas or hotspots are usually identified on the basis of species richness, the numbers of threatened or endemic (narrowly distributed) species, and the degree of habitat loss already incurred (2–8). This approach is necessarily a remedial one, responding to the need to minimize biodiversity loss in regions where human disturbance to natural habitats has already been severe or is ongoing. In this article, we present a more proactive extension to this approach by identifying areas where disturbance may be low at present but the potential for future loss of species is severe. To identify these areas, we use the concept of "latent extinction risk," i.e., the discrepancy between a species' current extinction risk and the risk predicted from its biological traits.

Species do not respond equally to human impacts such as habitat loss or hunting: some species are far more likely to become threatened with extinction than others (9, 10). Much of the variation in extinction risk is associated with species' biology so that predictive models of extinction risk can be constructed from sets of ecological and life-history traits (11–20). If the current extinction risk of a species is subtracted from the extinction risk predicted by its biology, the quantity remaining is the species' latent extinction risk. Strongly negative latent risk values indicate species in which current extinction risk is far in excess of that expected from their biology, most likely due to having been exposed to severe threatening processes. Conversely, high positive values of latent risk indicate species in which biology should make them relatively sensitive to human impact (e.g., they may have low reproductive rates) but that have not yet experienced human pressures that would cause this biological disadvantage to be expressed as a continuing population decline. Latent risk can be thought of as a measure of the potential for a species to decline rapidly toward extinction given exposure to levels of human impact equivalent to the present day average across species. It follows that areas in which a large proportion of species have high latent risk values have a particularly high potential for future species losses. Our aim here is to characterize the global geographic patterns of latent risk for mammals, the only major taxonomic group for which sufficient data currently exist for such an analysis.

Results and Discussion

We used large new databases of the biology and phylogeny of nearly 4,000 nonmarine mammal species to construct phylogenetically controlled comparative models of species-level extinction risk. The extinction risk response variable in our models was The World Conservation Union (IUCN) Red List (21) (www.redlist.org), converted to a numerical index from 0–5. Threatened species not listed under criterion A of the Red List were excluded; therefore, the index corresponds to a rate of recent and ongoing population decline (11, 12, 15, 19), determined by objective, quantitative criteria (22). We fitted separate predictive models of extinction risk for major mammal clades. The models typically explain between one-third and one-half of the variation in extinction risk and reveal a range of life-history and ecological predictors of risk (Table 1). In particular, the models highlight the importance of small geographic range size, large body mass, and "slow" life history as indicators of elevated risk. Latent extinction risk for each species was calculated as the predicted extinction risk value from the relevant within-clade model minus the current extinction risk from our index, based on the Red List. To summarize geographic patterns of current, predicted, and latent extinction risk, we calculated mean values of each for species occurring within each cell ($\approx$10,000 km^2) of a global equal-area grid. Summarizing extinction risk across species in this way reveals considerable geographic heterogeneity, with distinct areas of low and high values for each of the three extinction risk measures (Fig. 1 a–c). Latent risk is particularly low in many parts of the world already heavily modified by human activity, especially Europe, western Russia, Japan, Madagascar, and New Zealand (Fig. 1c). These areas are all regions where human impact on mammal species has already largely made itself felt, and thus, there are comparatively few surviving species with high latent risk.

ECOLOGY

Table 1. Extinction risk models for nonmarine mammal clades

	Marsupials	Afrotheria	Carnivora	Ungulates	Primates	Chiroptera	Rodentia	Lagomorpha	Minor clades
No. of species in model	87	39	87	60	67	765	290	64	54
Degrees of freedom	71	26	69	46	52	372	159	56	44
R^2	0.45	0.93	0.41	0.33	0.46	0.41	0.16	0.71	0.39
Adult mass	3.28**	−5.95***			4.48***	−2.22*		2.05*	4.87***
Adult mass†	−3.89***	11.08***				2.69**			
Weaning age					3.64***				−2.38*
Sexual maturity age					−3**		2.01*		
Litter size			−2.48*						
Litters per year			−3.18**	−2.96**					
Gestation length			2.32*						
Population density	−2.64*			−2.06*					
Arboreality					−3.06**				
Geographic range size	−5.65***		−4.25***		−3.79***	−16.03***	−5.01***	6.72***	4.87***
Geographic range size†								−6.86***	
Geographic range size‡								6.83***	
Geographic range size × adult mass								−2.85**	

Values shown in the columns are t values. Degrees of freedom are based on the number of phylogenetically independent contrasts and, therefore, are considerably lower than the number of species in most cases. Arboreality is an index reflecting the degree to which a species is tree dwelling. Full definitions of the variables are in ref. 11. *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$; †, quadratic term; ‡, cubic term.

It is the areas where mean latent risk is highest, however, that have the greatest potential for future species losses, based on current correlates of extinction risk. These regions are, in general, areas where the mean current extinction risk of species is relatively low but the predicted risk is high: most obviously, the northern regions of North America and the arc of islands between the Bay of Bengal and the southwest Pacific. To define the geographic hotspots of latent risk, we selected grid cells with the highest 10% of values (Fig. 2). This value is an arbitrary cutoff, selected to match the approximate proportion of the world's land area currently protected within reserves (23) (http://sea.unep-wcmc.org/wdbpa/) rather than to represent some biologically meaningful dichotomy. Setting the cutoff at 5% and 15% produced hotspots that varied in extent but occupied the same basic locations. The 20 hotspots thus identified (Table 2) are not simply reflections of those parts of the world in which human impact has been less extensive than elsewhere: the Amazon region, for example, is still largely undisturbed but has relatively low latent risk. Rather, the hotspots reflect a combination of comparatively low human impact and a mammal fauna consisting of species that have (on average) high inherent sensitivity to disturbance. For example, the hotspots of Arctic North America contain largely intact habitats in which few species are currently threatened but have many large-bodied ungulates and carnivores with slow life histories, and hence low maximum rates of population growth. Islands also figure prominently as areas of high mean latent risk. This pattern is unsurprising given the preponderance of narrowly distributed endemic species on islands and the importance of a small geographic range as a predictor of high extinction risk for most clades (Table 1), giving many islands a high level of predicted extinction risk (Fig. 1*b*). There is a possibility that the low current levels of extinction risk on some islands (Fig. 1*a*) is the result of a filter effect (24), whereby the most extinction-prone species have already disappeared. However, we consider it unlikely that filter effects have driven high latent risk levels on islands. In a postfilter assemblage, both current and predicted extinction risk levels should be low; therefore, such assemblages would not be expected to have high latent risk.

Our calculations of latent risk do, of course, rely on the accuracy of the extinction-risk models. One possible source of bias is the incompleteness of the biological data matrix, which means that not all species in our data set were represented in the models. For most clades, 33–100% of the species in our data set were included in the models; the figure is somewhat lower for Rodentia (17%) and the "minor clades" (18.2%). We must therefore assume that the subset of species included are an unbiased sample. This assumption could be violated if threatened species are the focus of more research attention so that the amount of information available on the biology of a species is not independent of its extinction risk status. This hypothesis does not, in fact, appear to be the case for our data set: the correlation among species between extinction risk status and the number of traits for which data exist is very low ($P = 0.96$). Moreover, the hotspots appear to be robust to uncertainty in the model parameter estimates. Recalculating latent risk values by using the upper and lower 95% confidence bounds of predicted extinction risk values produced hotspots with 98.6% and 97.5% congruence, respectively, with the hotspots shown in Fig. 2. Nevertheless, we expect that the extinction risk models can be updated and refined as information on the biological traits of mammal species continues to accumulate.

Our use of detailed models of extinction risk based on species biology is a more powerful method of assessing sensitivity of species assemblages than the common approach of mapping the occurrences of rare, endemic, or currently threatened species (2, 4, 25–27). The latter approach assumes that current relative rankings of species on the extinction risk scale are maintained through time: that is, the most highly threatened species today will be the first to disappear in the future. This is not necessarily a reasonable assumption, however. Synergistic effects of biology with human impact (11, 12, 28) mean that some species are expected to decline much more rapidly toward extinction than others as levels of disturbance increase. Hence, many species currently considered relatively safe could leapfrog other species on the extinction risk scale to become the most highly threatened in the next few decades (12). In fact, this phenomenon has already occurred in a number of recent cases. The Guatemalan howler monkey *Alouatta pigra*, for example, has rapidly advanced several stages along the Red List, from Least Concern in 2000 to Endangered in 2004; this shift is considered a genuine change in status, not simply the product of new or better information (21).

An important feature of the distribution of latent risk hotspots is their lack of congruence with hotspots of mammal species
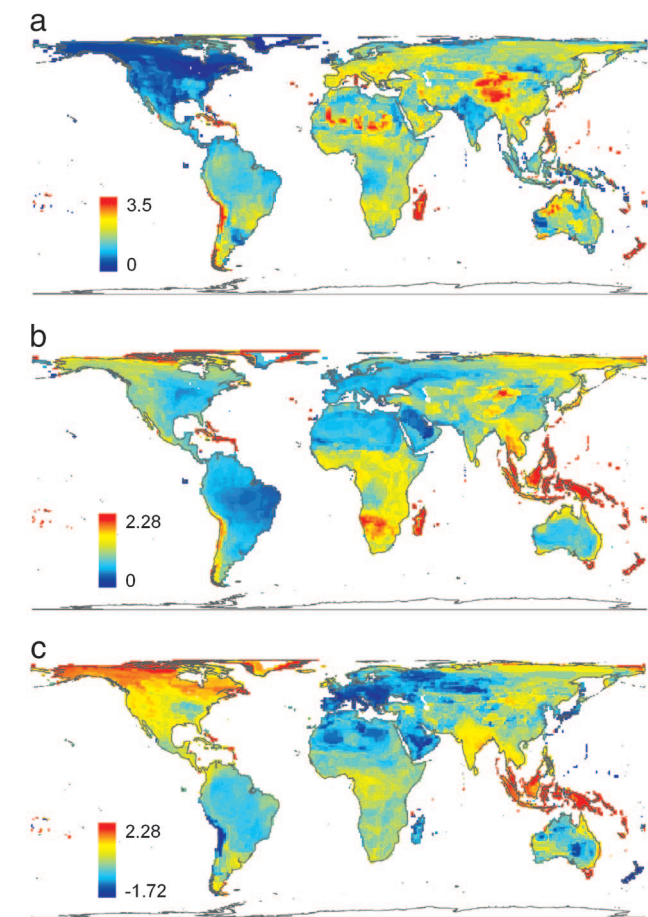
Fig. 1. Global geographic distribution of extinction risk in nonmarine mammals. Current extinction risk (*a*), predicted extinction risk (*b*), and latent extinction risk (*c*) is shown. Values are averages of species found within each grid cell; cell size is ≈10,000 km².

richness. If species richness hotspots are defined conservatively as the most species-rich 10% of grid cells, the overlap with the latent risk hotspots in Fig. 2 is only 2.7%, restricted to a small area of Peninsular Malaysia and northern Borneo. Hotspots

defined as the 10% of grid cells with the highest numbers of "endemic" species [those in the lower quartile of geographic range size (4)] overlap with the latent risk hotspots by only 9.1%. Hotspots defined as the 10% of grid cells with highest numbers of species listed as threatened in the Red List overlap with latent risk hotspots by only 1%. Hence, areas within the latent risk hotspots will be poorly represented under conservation prioritization schemes that seek to maximize total species numbers, or numbers of endemic or threatened species, represented in reserve networks or otherwise protected (25–27, 29). Nevertheless, in many of the latent risk hotspots, current levels of protection within reserves >1,000 hectares [the smallest reserves are less likely to sustain viable mammal populations (30)] are well below the global average of 11.9% (23) (Table 2). Furthermore, many of the latent risk hotspots are expected to undergo rapid increases in human population density (Table 2), with mean projected annual rates of human population growth from 2000–2015 far in excess of the global average of 1.13% (31) (http://sedac.ciesin.columbia.edu/plue/gpw). Human population density is a general indicator of threats to biodiversity (12, 32); therefore, species in these areas will come under rapidly increasing pressure in coming decades.

We see the latent extinction risk approach as an extension, not an alternative, to existing conservation prioritization schemes. The strategy of prioritizing hotspots of total, endemic, or threatened species richness has many advantages as a cornerstone of efforts to stem global biodiversity loss (5). Nevertheless, identifying areas of highest latent risk offers the best chance to anticipate species losses before they begin and, thus, to implement effective preemptive conservation measures. By definition, latent risk hotspots tend to be in less heavily disturbed regions with comparatively high wilderness value. In such areas, the benefit-to-cost ratio of conservation is often higher than in more developed regions (33). Therefore, incorporating latent risk patterns into global conservation planning may be one of the most cost-effective means of protecting biodiversity in the long term. High latent risk areas could also play a role in guiding efforts to monitor the state of wild nature for the Convention on Biological Diversity's 2010 target to reduce the rate of biodiversity loss (34) (www.biodiv.org/decisions/default.aspx). Monitoring the indicators of progress toward the 2010 target, such as the abundance and distribution of selected species, cannot be done everywhere and must be undertaken selectively (35). It makes sense, therefore, to include in monitoring schemes those areas in

Fig. 2. Hotspots of latent extinction risk in nonmarine mammals. Hotspots are defined as the 10% of grid cells with the highest mean latent risk values.

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Table 2. Hotspots of latent extinction risk in nonmarine mammals

Hotspot	Area, km²	Total species no.	Mean latent risk (±SE)	Proportion protected in reserves >1,000 hectares, %	Projected annual human population growth 2000–2015, %
New Guinea	714,175	205	0.36 ± 0.001	10.78	2.91
Melanesian islands	119,611	96	0.54 ± 0.01	7.22	2.78
Indian Ocean islands	1,438	10	0.54 ± 0.14	7.29	2.15
Andaman and Nicobar Islands	6,948	20	0.61 ± 0.04	7.55	1.96
Sulawesi	178,114	130	0.31 ± 0.001	11.35	1.92
Borneo	519,625	224	0.27 ± 0.001	19.64	1.82
Patagonian Coast	33,292	26	0.25 ± 0.001	0	1.64
Sumatra and Peninsular Malaysia	616,746	284	0.26 ± 0.001	17.52	1.62
Western Java	71,109	131	0.25 ± 0.001	4.48	1.30
Nusa Tenggara	87,735	86	0.34 ± 0.003	9.03	0.80
East Indian highlands	15,548	70	0.23 ± 0.001	3.53	0.69
Lesser Antilles	3,889	16	0.35 ± 0.02	14.19	0.51
Southern Polynesia	566	3	0.97 ± 0.05	0.07	0.46
Northern Canada and Alaska	4,694,500	96	0.32 ± 0.001	13.33	0.09
Maluku	76,331	99	0.51 ± 0.01	7.05	0.05
Tasmania and Bass Strait	73,002	49	0.31 ± 0.002	31.35	−0.11
Siberian tundra	235,597	35	0.27 ± 0.001	11.34	−0.56
Bahamas	8,241	8	0.41 ± 0.02	1.14	−0.65
Greenland	882,468	9	0.63 ± 0.002	18.55	−0.76
Eastern Canadian Forests	884,833	57	0.26 ± 0.001	6.38	−0.84

Hotspots are listed in descending order of projected human population growth.

which free-ranging populations appear likely to be especially sensitive to future human impacts.

Materials and Methods

Data Sets. Biological trait data were from a database compiled from around 3,300 literature sources, containing data on 25 ecological and life-history traits for 4,030 mammal species. The extinction risk index was based on the 2004 The World Conservation Union Red List (21) converted to an index from 0–5, following protocols found in refs. 11, 12, 15, 19. Our data set included threatened species only where they were listed under criterion A of the Red List (a recent or ongoing decline in population size) (21) to avoid the circularity of including species listed on the basis of small population size or narrow distribution (19). To calculate phylogenetically independent contrasts (see below), we constructed a dated, composite supertree phylogeny of 4,497 mammal species, using a standardized methodology (11, 36). To map the geographic distributions of current, predicted, and latent extinction risk, we overlaid mammal species distribution maps (37) onto a Behrmann-projected global equal-area grid, with a resolution of 96.486 km. We then calculated the mean value of each extinction risk measure for the set of species thus indicated as occurring within each grid cell.

Statistical Models. Separate regression models of extinction risk were fitted for the following mammal clades: Carnivora, Primates, Rodentia, marsupials, ungulates (Artiodactyla + Perissodactyla), Lagomorpha, Afrotheria (Hyracoidea + Macroscelidea + Tubulidentata + Chrysochloridae + Tenrecidae), and Chiroptera. Because the remaining clades (Xenarthra, Scandentia, Eulipotyphla, and Monotremata) each had too few species with data values for reliable model fitting, we pooled these as "minor clades" and analyzed them together. Models were fitted by using phylogenetically independent contrasts to eliminate the pseudoreplication that would otherwise result from the nonindependence of species (28). Before calculating contrasts, polytomies (unresolved nodes in the phylogeny) were resolved to a series of bifurcating nodes separated by zero-length branches. The contrast calculated at

each of these new nodes was given reduced weighting in the regression model such that each polytomy contributed only a single degree of freedom to the model. Phylogenetic branch lengths were transformed by raising them to a power (κ), then optimizing the value of κ to minimize the correlation between contrasts and their standard deviations (38). Minimum adequate regression models were then found by using heuristic procedures (12, 19) to simplify them from the list of biological traits. Having thus identified the set of independent biological predictors of extinction risk for each mammal clade using phylogenetically independent contrasts, we then fitted the same set of predictors in standard, nonphylogenetic regressions and used these equations to calculate predicted values of extinction risk. This method was necessary because regressions on independent contrasts do not estimate an intercept and because the procedure used to optimize phylogenetic branch lengths renders slope estimates noncomparable (38). All analyses were carried out by using functions written in R (39) (www.R-project.org).

Hotspot Identification. Hotspots of latent extinction risk were identified as those grid cells in which the mean latent risk value was ≥0.2248, the 90th percentile value of the distribution of latent risk values across grid cells. We only identified contiguous or closely spaced clusters of at least six such grid cells as hotspots; hence, there are several isolated, single, or small clusters of grid cells with high latent risk values that we have not assigned to hotspots. In delineating separate hotspots (Fig. 2), we erred on the side of splitting rather than aggregating island groups to capture the heterogeneity in latent risk values, human population growth rates, and reserve coverage. For example, the area corresponding to the "Sundaland" hotspot of Conservation International (6) is here divided into four separate latent risk hotspots: Sumatra and Peninsular Malaysia, Borneo, Sulawesi, and Western Java.

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ECOLOGY