

References and Notes

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15. Cove Mountain in eastern Tennessee (Great Smokey Mountains National Park), Giles County (150 km south of Nashville), Land between the Lakes (Tennessee Valley Authority reservation between Tennessee and Cumberland rivers, KY), and Mammoth Cave (Mammoth Cave National Park, KY). These stations cover an area of about 7700 km².
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26. The model resolution was 1° in longitude and latitude. The model domain covered more than one-third of the Northern Hemisphere (170° to 20°W) from the surface to the top of the atmosphere. The advection was calculated grid-free, and there was no numerical diffusion. Diffusion in the boundary layer was parameterized, and boundary layer heights were computed with Richardson number profiles. The concentration evaluation grid consisted of 10 boxes from the surface to 11 km, with the lowest box from surface to 150 m.
27. Area 1, Northwest Territories; area 2, Northeastern Alberta; area 3, northern central Saskatchewan; area 4, northern central Manitoba; and area 5, Ontario (James Bay).
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41. This study was performed during a visit of the corresponding author to the NOAA Aeronomy Laboratory made possible by a grant provided by the Max Kade Foundation, New York. Surface CO, NO_x, and O₃ measurement data came from SOS95 and NARSTO sites. Airborne measurements were made by D. Parrish and J. Holloway. The modeling was based on data from the European Centre for Medium-Range Weather Forecasts, provided by A. Krieger from the University of Agricultural Sciences, Vienna, Austria. We are grateful to A. Stohl, Technical University of Munich, who developed the FLEXPART model and was always open for discussion of the results.

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Nonrandom Extinction and the Loss of Evolutionary History

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The hierarchical nature of phylogenies means that random extinction of species affects a smaller fraction of higher taxa, and so the total amount of evolutionary history lost may be comparatively slight. However, current extinction risk is not phylogenetically random. We show the potentially severe implications of the clumped nature of threat for the loss of biodiversity. An additional 120 avian and mammalian genera are at risk compared with the number predicted under random extinction. We estimate that the prospective extra loss of mammalian evolutionary history alone would be equivalent to losing a monotypic phylum.

Current and projected species extinction rates exceed geologically normal background rates by several orders of magnitude (1–3), indicating that we face an extinction episode equivalent to mass extinctions of the paleontological past. When biodiversity is measured by evolutionary history, expressed as the total length of all the branches in the tree of life, a surprisingly high proportion is likely to survive even a massive extinction episode. This is because most species have close relatives and thus contribute little to the total branch length: Whole clades are lost only when all their species go extinct, which is unlikely under an assumption of phylogenetically random extinction. However, historical extinctions and current extinction risk are often not randomly distributed among species. For example, the 85 mammalian species extinctions since 1600 include at least five members of the extinct family Nesophontidae (4, 5), and the prevalence of current threat varies signif-

icantly among orders of mammals (6) and birds (7). This nonrandomness will result in the loss of more branch length and more higher taxa than predicted by random extinction (8). Here, we quantify how the clumping of extinction risk affects the amount of evolutionary history under threat in mammals and birds, using two measures of biodiversity: the number of higher taxa (genera) and the total phylogenetic branch length [commonly referred to as “phylogenetic diversity” (PD)] (9).

Nee and May (10) showed that surprisingly little PD is lost under even catastrophic extinction scenarios. In one of their simulations, 81% of the phylogenetic branch length remained even when only 5% of the species survived an extinction episode. Their simulations assumed that extinction was random—the “field of bullets” scenario—or could be optimized through management (so as to minimize loss of branch length) and indicated that the amount preserved would be influenced by the topology of the phylogenetic tree.

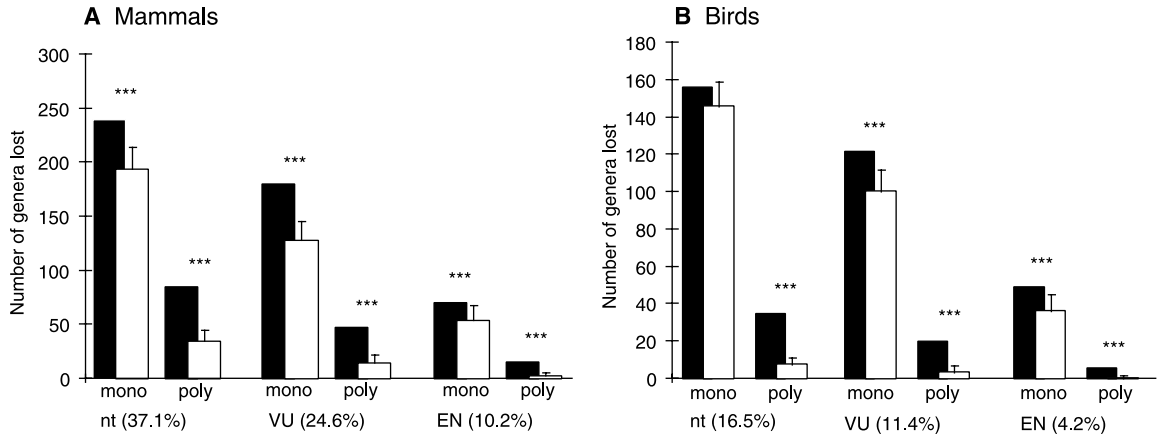
In principle, we can envisage two natural scenarios that would result in nonrandom distribution of extinction risk. First, any phylogenetic clumping of factors that promote risk would increase the chance of all species in polytypic taxa—and hence those taxa as a

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Fig. 1. Numbers of monotypic and polytypic genera lost under different extinction regimes for (A) mammals and (B) birds. Dark bars: extinction of all species listed at or above the indicated threshold level of threat [see note (12); numbers in parentheses are percentages of species culled]. Light bars: random extinction of same intensity (mean of 1000 trials). Error bars: 2 standard deviations of the simulation distribution. *** $P \leq 0.001$ (P values obtained directly from distribution of simulation results). For overall genus loss (monotypic + polytypic), all $P \leq 0.001$. DD species were treated as being at no risk of extinction; treating them as EN led to qualitatively very similar results (33).



whole—being lost. Second, if such phylogenetically distributed traits have already mediated considerable extinction, then many monotypic genera or families might be the last survivors of once-larger clades. This could lead to a higher proportion than expected of monotypic genera, or species on long phylogenetic branches, being threatened. Nonrandom extinction risk has been documented in many groups (6–8, 11), but its impact on biodiversity loss has not hitherto been assessed.

We estimated the loss of biodiversity expected according to current assessments of species extinction risk and compared it with the loss that would result from a random extinction episode of equal severity. We used assessments of extinction risk from the 1996 World Conservation Union (IUCN) Red List (4), which is comprehensive in its coverage of mammals and birds. Three levels of extinction risk were selected for the analysis:

endangered and higher (EN), vulnerable and higher (VU), and near threatened and higher (nt) (12). For each of these levels in turn, we imposed extinction of all species of at least that level, with all species at lower levels surviving (13). Species for which no threat classification can be made because of a lack of information are classified as data deficient (DD) by IUCN (14). We dealt with DD species in two ways. First, we assumed that they had no risk of extinction: Here a genus containing a DD species is never lost, a treatment that is therefore conservative. Second, we classified DD species as EN, so that they are all lost in all extinction regimes. This errs in the opposite direction but is probably nearer the truth: It is likely that disproportionately many DD species are at high risk of extinction (4).

For each threshold and each clade, we calculated the numbers of species, the num-

bers of genera (overall, monotypic, and polytypic), and (for primates and carnivores, the only two clades whose complete species-level phylogenies are available) the total phylogenetic branch length that stand to be lost (15). For comparison, we conducted simulations (1000 trials) in which the same numbers of species were removed at random (16).

Figure 1 shows the results for mammals and birds; Table 1 shows the taxonomic and phylogenetic results for Primates and Carnivora. The same general trends are apparent whether DD species are treated as highly threatened or secure. Three of the four data sets show far more genera to be at risk than would be predicted by the random extinction model. The fourth data set (Carnivora) shows a weaker tendency in the same direction (17). Within each data set, the difference between observed and expected loss (the “extra” loss) tends to increase with the proportion of species culled, at least until a

Table 1. Numbers of genera and phylogenetic diversity (PD) lost under different extinction regimes in primates and carnivores, for two treatments of data-deficient (DD) species. Level, threshold threat level [see (12)]; %spp, percentage of species culled; Obs., loss incurred with extinction of all species

listed at or above threshold level; Mean, mean loss from 1000 random extinctions of same severity; #SDs, difference between Obs. and Mean, expressed in standard deviations of simulation results.

Level	%spp	All genera			Monotypic genera			Polytypic genera			Phylogenetic diversity (My)		
		Obs.	Mean	#SDs	Obs.	Mean	#SDs	Obs.	Mean	#SDs	Obs.	Mean	#SDs
<i>Primates, treating DD species as not at risk</i>													
nt	52.1	25****	15.12	3.798	17****	10.58	2.856	8**	4.54	2.068	607.4	602.4	0.1
VU	38.2	18****	9.87	3.404	13****	7.88	2.192	5***	1.99	2.398	489.7**	425.1	2.0
EN	16.2	10****	3.94	3.736	7**	3.57	2.160	3****	0.37	4.922	209.1*	173.1	1.5
<i>Primates, treating DD species as EN</i>													
nt	59.8	27****	18.81	2.790	17****	12.39	2.000	10**	6.43	1.953	749.8	703.4	1.2
VU	45.9	18**	13.07	1.927	13**	9.64	1.680	5	3.43	1.191	615.2***	520.5	2.7
EN	23.9	10*	6.27	1.856	7	5.48	0.837	3**	0.33	2.603	329.6**	260.9	2.4
<i>Carnivores, treating DD species as not at risk</i>													
nt	30.2	32****	25.68	1.628	28	24.51	0.934	4****	1.17	4.095	505.6	473.1	0.8
VU	26.1	28*	22.59	1.372	26*	21.59	1.191	2	1.00	1.405	441.2	405.4	0.9
EN	10.7	9	9.75	-0.250	8	9.58	-0.517	1	0.16	2.240	181.7	164.3	0.6
<i>Carnivores, treating DD species as EN</i>													
nt	37.3	37	32.86	1.131	33	30.23	0.218	4	2.62	0.802	574.9	592.4	-0.4
VU	33.2	33	29.18	1.114	31	27.16	0.164	2	2.02	-0.014	510.5	528.0	-0.4
EN	17.9	14	15.85	-0.818	13	15.25	-0.837	1	0.60	0.512	246.3	275.3	-0.8

*, $P \leq 0.1$; **, $P \leq 0.05$; ***, $P \leq 0.01$; ****, $P \leq 0.001$ (P values calculated directly from the 1000 simulation trials).

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large proportion (around 50%) of the species are lost. For mammals, birds, and primates, loss of all threatened (threshold at VU) species would lead to the loss of about 50% more genera than expected under the null model. About half of these additional genera are monotypic, indicating that members of monotypic genera tend to be more threatened than average species. The pattern is in fact more general: Across both mammals and birds, the probability of a species being threatened declines with the number of species in its genus, family, or order (18). Like clustering of threatened species within clades, this distribution will tend to counteract the ability of hierarchically structured phylogenies to retain diversity in the face of impending extinctions.

There are also many mammal and bird genera—far more than expected under the null model (Fig. 1)—in which all two to six species are threatened (19). The extinction of all threatened species would lead to the loss of whole genera of unusual and highly valued groups, such as chimpanzees, golden-lion tamarins, chinchillas, manatees, and kiwis. The loss is not limited to the genus level: Several species-poor families (either monotypic, such as the aye-aye and kagu, or polytypic, such as rhinos and kiwis) and even orders (Microbiotheriidae, Proboscidea, Sirenia, and Apterygiformes) would also be lost, along with their unique biological characters. Although it is true that smaller proportions are lost of PD and genera than of species—an almost inevitable consequence of the hierarchical nature of phylogenies—the extra loss of biodiversity (relative to random extinction) is considerable. Loss of all threatened species of mammals and birds would lead to the loss of at least 85 and 38 extra genera, respectively (from the conservative simulations). Only three mammalian orders (Chiroptera, Carnivora, and Rodentia) have more than 85 genera, and there are only around 1150 mammalian and 2100 avian genera altogether.

The results for primates make it possible to estimate very roughly the extra PD that stands to be lost in mammals as a whole (20). The three thresholds of extinction risk and two treatments of DD species give six estimates of the extra PD lost per genus, averaging around 10 million years (My) per genus. Mammals as a whole stand to lose 85 extra genera, corresponding to an estimated 850 My of extra PD. The added loss of PD incurred through nonrandom extinction in mammals alone would therefore roughly equate to the loss of a monotypic phylum.

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- These two measures are representative of the many that have been proposed (21). Although numbers of species (or higher taxa such as genera) are obvious empirical measures, they do not quantify the evolutionary history represented by the species (22–27). Conversely, PD is a measure of the total amount of evolutionary change that is independent of the number of recognized taxa in a phylogeny.
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- We did not set a higher threshold because (i) only 2% of birds and 4% of mammals are listed as more threatened than EN and (ii) although it is probably a reasonable approximation that DD species are at least VU or even EN, it is probably unreasonable to assume they are all CR.
- A total of 208 mammalian and 66 bird species are DD (4.4% and 1%, respectively) (4).
- Species lists were as used by IUCN. Phylogenies were species-level composite estimates (29, 30), with the primate phylogeny modified to match the IUCN list (31, 32). Use of the species list from (31) made no qualitative difference to either the taxonomic (primates and mammals) or PD (primates) results (33).
- The phylogenies, data sets, and programs used to conduct simulations are available from www.bio.ic.ac.uk/evolve/.
- There are several reasons why carnivores might not show significance. Unlike primate genera, many carnivore genera are geographically very widespread. Given that extinction risk varies significantly among geographic regions (4), species in widespread taxa might have less similar predispositions to extinction than those in narrowly distributed genera. Second, carnivore genera are unusually species-poor, with most being monotypic and only 2.1 species per genus on average, compared with 4.2 (median = 2) in primates, 4.2 (median = 2) in mammals as a whole, and 4.7 (median = 2) in birds. Third, recent simulations (34) suggest that a critical determinant of the extent of biodiversity loss is the correlation between speciation rates and extinction risk, with a negative correlation giving greatest loss.
- Species were coded as threatened if listed (4) as at least conservation-dependent and were coded as nonthreatened otherwise (DD species were excluded from analysis). Logistic regression was used to regress the binary codes against the number of species in the genus, family, and order, for mammals and birds in turn, with the following model: $T = e^{(1+A+BlnN)}$, where T is a binary variable that is true when a species is threatened and N is the number of species in the genus, family, or order to which each species belongs. Results were as follows. Mammals (4553 species): species within genera, $b = -0.138$, $a = -0.664$, $\chi^2_1 = 32.0$; species within families, $b = -0.173$, $a = -0.090$, $\chi^2_1 = 79.7$; species within orders, $b = -0.320$, $a = 1.121$, $\chi^2_1 = 147.8$; all $P < 0.001$. Birds [9689 species; higher level classification, following IUCN, from (35)]: species within genera, $b = -0.067$, $a = -1.812$, $\chi^2_1 = 6.6$, $P < 0.05$; species within families, $b = -0.058$, $a = -1.684$, $\chi^2_1 = 5.6$, $P < 0.05$; species within orders, $b = -0.187$, $a = -0.598$, $\chi^2_1 = 89.9$, $P < 0.001$.
- Mammals: *Otomopsis* (six species); *Bos*, *Bubalus*, *Croteromys*, *Leontopithecus*, *Mesocapromys*, *Pteralopex*, *Rhinopithecus* (four species); *Capricornis*, *Dasyercus*, *Hemitragus*, *Myomimus*, *Oryx*, *Propithecus*, *Redunca*, *Rynchocyon*, *Trichechus* (three species); *Alcelaphus*, *Berardius*, *Bison*, *Brachyteles*, *Chinchilla*, *Chlamyphorus*, *Chrysospalax*, *Connochaetes*, *Cryptochloris*, *Eubalaena*, *Galidictis*, *Geocapromys*, *Hippotragus*, *Hyosciurus*, *Hyperoodon*, *Kunsia*, *Leptonycerus*, *Macruromys*, *Micropotamogale*, *Monachus*, *Notoryctes*, *Pan*, *Perameles*, *Platanista*, *Podogymnura*, *Pseudohydromys*, *Rhinoceros*, *Rynchocyon*, *Scolomys*, *Solenodon*, *Surdisorex*, *Tateomys*, *Tokudaia* (two species). Birds: *Pomarea* (five species); *Apteryx*, *Dasyornis*, *Goura*, *Heteromirafra* (three species); *Anodorhynchus*, *Atrichornis*, *Brachypteracias*, *Geronticus*, *Hemignathus*, *Hylorchilus*, *Loxops*, *Mesitornis*, *Moho*, *Nesospiza*, *Oreomystis*, *Pauxi*, *Picathartes*, *Rhynchopsitta*, *Telespiza* (two species).
- We did not extrapolate from carnivores because their pattern of extinction risk, unlike mammals as a whole, is not greatly different from random. We did not extrapolate to birds because bird and mammal genera may have different average ages (36).
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