The hierarchical nature of phyla 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.

Neave 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 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
whole—being lost. Second, if such phyleogenetically distributed traits have already medi-
ated considerable extinction, then many monotypic genera or families might be the last sur-
vivors of once-larger clades. This could lead to a higher proportion than expected of monotypic
genera, or species on long phyleogenetic branch-
es, being threatened. Nonrandom extinction risk
has been documented in many groups (6–8,
11), which is comprehensive in its coverage
of mammals and birds. Three levels of ex-
tinction risk were selected for the analysis:

<table>
<thead>
<tr>
<th>Level</th>
<th>%spp</th>
<th>All genera</th>
<th>Monotypic genera</th>
<th>Polypytic genera</th>
<th>Phylogenetic diversity (My)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Obs. Mean #SDs</td>
<td>Obs. Mean #SDs</td>
<td>Obs. Mean #SDs</td>
<td>Obs. Mean #SDs</td>
</tr>
<tr>
<td>nt</td>
<td>52.1</td>
<td>25**** 15.12 3.798</td>
<td>17**** 10.58 2.856</td>
<td>8** 4.54 2.068</td>
<td>607.4 602.4 0.1</td>
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<tr>
<td>VU</td>
<td>38.2</td>
<td>18**** 9.87 3.464</td>
<td>13**** 7.88 2.192</td>
<td>5*** 1.99 2.398</td>
<td>489.7** 425.1 2.0</td>
</tr>
<tr>
<td>EN</td>
<td>16.2</td>
<td>10**** 3.94 3.736</td>
<td>7** 3.57 2.160</td>
<td>3*** 0.37 4.022</td>
<td>209.1* 173.1 1.5</td>
</tr>
<tr>
<td>nt</td>
<td>59.8</td>
<td>27**** 18.81 2.790</td>
<td>17**** 12.39 2.000</td>
<td>10** 6.43 1.953</td>
<td>749.8 703.4 1.2</td>
</tr>
<tr>
<td>VU</td>
<td>45.9</td>
<td>18**** 13.07 1.927</td>
<td>13** 9.64 1.680</td>
<td>5 3.43 1.191</td>
<td>615.2*** 520.5 2.7</td>
</tr>
<tr>
<td>EN</td>
<td>23.9</td>
<td>10**** 6.27 1.856</td>
<td>7 5.48 0.837</td>
<td>3** 0.33 2.603</td>
<td>329.6** 260.9 2.4</td>
</tr>
<tr>
<td>nt</td>
<td>30.2</td>
<td>32**** 25.68 1.628</td>
<td>28 24.51 0.934</td>
<td>4**** 1.17 4.095</td>
<td>505.6 473.9 0.8</td>
</tr>
<tr>
<td>VU</td>
<td>26.1</td>
<td>28* 22.59 1.372</td>
<td>26* 21.59 1.191</td>
<td>2 1.00 1.405</td>
<td>441.2 405.4 0.9</td>
</tr>
<tr>
<td>EN</td>
<td>10.7</td>
<td>9 9.75 0.250</td>
<td>8 9.58 0.217</td>
<td>1 0.16 0.157</td>
<td>181.7 164.3 0.8</td>
</tr>
<tr>
<td>nt</td>
<td>37.3</td>
<td>32**** 32.86 1.131</td>
<td>33 30.23 0.218</td>
<td>4 2.62 0.802</td>
<td>574.9 592.4 0.4</td>
</tr>
<tr>
<td>VU</td>
<td>33.2</td>
<td>33 29.18 1.114</td>
<td>31 27.16 0.164</td>
<td>2 2.02 0.104</td>
<td>510.5 528.0 0.4</td>
</tr>
<tr>
<td>EN</td>
<td>17.9</td>
<td>14 15.85 0.818</td>
<td>13 15.25 0.837</td>
<td>1 0.60 0.512</td>
<td>246.3 275.3 0.8</td>
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</tbody>
</table>

* P < 0.1, ** P < 0.05, *** P < 0.01, **** P < 0.001 (P values calculated directly from the 1000 simulation trials).
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-tion 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 Aepypterygiformes) 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, respectivevly (from the conservation 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 phyllum.

References and Notes
9. 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 species (22–27).
10. Conversely, PD is a measure of the total amount of evolutionary change that is independent of the number of recognized taxa in a phylogeny.
13. All bird and mammal species have been classified into one of seven categories of threat. Six of these categories represent a sequence of declining extinction risk (extinct, extinct in the wild, critically endangered, endangered, vulnerable, and lower risk), with vulnerable and all higher taxa being lumped into the general category of “threatened.” Lower risk has three subcategories (conservation-dependent, near threatened, and least concern). Because conservation-dependent species qualify for threatened status but are secure as a result of ongoing conservation actions, we included these with the vulnerable species for our analyses. Lower risk (near threatened) species are close to qualifying for threatened status and so represent a lower potential threshold for threatened status. See (28).
14. We did not set a higher threshold because (i) only 2% of birds and 4% of mammals are listed as more threatened than EN (ii) although it is probably a reasonable approximation that DD species are at least VU or EN II. It is probably unreasonable to assume they are all CR.
15. A total of 208 mammalian and 66 bird species are DD (4.4% and 1%, respectively) (4).
16. Species listed on the IUCN Phylodiversity were species-level conservative 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).
17. The phylogenies, data sets, and programs used to conduct simulations are available from www.bio.ic.ac.uk/evolve/.
18. There are several reasons why carnivores might not show significant extinction. Unlike primate genera, many carnivore genera are ecologically 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, 2.1 (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.
19. Mammals: Otomops (six species); Bos, Bubalus, Ceratotherium, Leptotaphirus, Mesocapromys, Pterolopex, Rhinopithecus (four species); Caprocynus, Dasycercus, Hemicyopus, Megalopygus, and Tachypus, Eubalaena, Callicotis, Cerop Sawyer, Hippoglopus, Hyroceti r, Hyperoodon, Kusma, Leptoceros, Macrurus, Microtomonogale, Monachus, Notoryctes, Pan, Pera melanis, Platynota, Pogonomys, Podomys, Rhinoceros, Rhynchohyus, Scyllium, Solenodon, Sordirox, Tateotes, Tokudalia (two species); Birds: Pomarea (five species); Apteryx, Dasyurus, Goura, Heteromura (three species), Astrichis, Brachypteryx, Geronticus, Gennhis, Hylorchilus, Laxops, Mesotismus, Moho, Nesospiza, Oreoptyxius, Pauhi, Pigartchates, Rhynchoptilla, Telegraphia, Tesmisa, Trogocerus, Xylops (three species).
20. 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).
28. IUCN, IUCN Red List Categories (IUCN, Cland, Switz erland, 1994).
33. A. Purvis, P.-M. Agapow, J. L. Gittleman, G. M. Mace, data not shown.
37. We thank J. Baillie, R. Grenyer, N. Isaac, S. Nee, C. Nunn, D. Orn, W. Sew, and anonymous referees for help, comments, and suggestions. This work was supported by the Natural Environment Research Council (NERC) through grant GR3/17526 (A.P. and D.M.A.) and a fellowship (M.J.D.) and by the National Center for Ecological Analysis and Synthesis (NCEAS) through NSF grant DEB-94-21535 (J.L.G.).
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