

Uncertainties in extinction rates

SIR — The rate at which species of plants and animals are likely to become extinct in the near future is very uncertain^{1–6}. We believe these uncertainties are compounded by difficulties in defining what is meant by 'becoming' extinct, as different authors attach quite different meanings to this deceptively simple word.

For the comparatively well-studied birds and mammals (around 13,000 species), extinction rates this century have run around one species per year; were this rate maintained, it would correspond to an average 'species lifespan' of roughly 10⁴ yr. This is two to three orders of magnitude shorter than the average species lifetime of 10⁶ to 10⁷ yr seen over the sweep of the fossil record⁷, but it is almost two orders of magnitude longer than the impending extinction times — characteristically 200–400 yr — which have been deduced in three independent ways: (1) from observed rates of habitat loss combined with heuristic species–area relations^{4,8,9}; (2) by extrapolating the rates at which species appear to be 'climbing the ladder' of IUCN-defined categories of threat¹⁰ from "vulnerable" to "endangered" to "extinct"²; and (3) by using the assessments of species-by-species extinction probability distributions, as functions of time, which underly the new draft IUCN criteria^{11,12} for categories of threat, to calculate the expected times when half the species in each of 10 vertebrate taxa will be extinct (three, four, three orders or families of reptiles, birds, mammals, respectively; these 10 average extinction times range from 100 to 1,000 yr, but are characteristically 300–400 yr for mammals and birds)^{10,12}. All three of these theoretical estimates are admittedly shaky: it is doubtful to what extent the effects of habitat fragmentation, especially in the tropics, are described by species–area relations based on empirical observations of species distributions among island archipelagoes^{9,13}; and estimates based on IUCN "category-ladder-climbing" or extinction probability distributions may tell us much more about patterns of human concern, the taxonomic group in question,

and rates of data entry than about extinction rates^{2,3}. Even so, the discrepancy between three different but concordant theoretical estimates of impending extinction rates, and the rates currently documented, is disturbing.

This discrepancy largely disappears if we are more careful in recognising that the species–area or 'ladder-climbing' estimates are projected numbers of species that, on current trends, are 'committed' to extinction. In particular, species–area relations suggest that destroying 90% of a habitat will eventually lead to loss of around half the species in it, but the time taken to attain this new, impoverished state is not specified, and will depend on details that vary from place to place and species to species. In general, the notion of 'committed' to extinction recognizes that extinction is a gradual process on an uncertain timescale, but that the end point is nevertheless certain once a species' demographic and genetic base has been sufficiently eroded by habitat destruction or other processes.

Simberloff¹⁴, for example, used a species–area approach to estimate that about 1,350 species of birds would be committed to extinction by the year 2015. If this figure were misinterpreted as the predicted number actually to become extinct between 1986 and 2015 (which was not Simberloff's intent), it would imply an average of 45 extinctions per year, which seems implausibly high. A more empirical approach is to examine the 1,029 entries in Collar and Andrews¹⁵ list of threatened bird species. Interpreting 'committed' to extinction as referring to any species whose populations in the wild are no longer viable and will inevitably become extinct, unless major conservation actions reverse current trends (by habitat restoration, elimination of introduced predators, captive breeding and re-introduction, and so on), Two of us estimated¹³ that 450 bird species will be committed to extinction by 2015, with 27 of these already probably extinct (in addition to the 12 listed as almost certainly extinct¹⁵). Although this empirically based estimate is still one-

third the theoretically based one, the disparity is not the worrying two orders of magnitude noted earlier.

In short, projected extinction rates are beset by many uncertainties. But theoretical estimates and species-by-species studies for birds give answers that are roughly concordant, provided we are clear about the stages involved in 'becoming' extinct. Broadly similar answers pertain to the insect fauna of the United Kingdom^{16,17}, although in general our knowledge of the endangered status of invertebrates is woefully inadequate¹⁸. The situation is less clear for plant species, and seems to depend a lot on the area in question. Moreover, the genetic erosion of plant species which are not yet committed to extinction is a major concern, yet is generally overlooked in the extinction debate.

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Atmospheric CO₂ and plants

SIR — Under low atmospheric-CO₂ concentrations (*p*CO₂), C4 plants have a physiological advantage over C3 plants¹. Collatz *et al.* have published models^{2,3} appropriate for predicting the magnitude of this advantage. These (*a* in the figure) give C4 plants a major advantage at *p*CO₂ values characteristic of the Pleistocene glaciations (190–240 p.p.m.; ref. 4). Experimental work confirms that *p*CO₂ of the order of 200 p.p.m. is stressful to C3 plants, reviewed in ref. 5. Hence, all other things being equal, one would expect C4 niche expansion during the ice ages. C4 physiology, however, is inefficient at low temperatures^{1,2}, and in many regions, shrinkage of the C4 niche due to ice-age cooling probably outweighed expansion due to CO₂ starvation.

The claim that low CO₂ promotes C4 expansion at high altitude is equivocal¹. Historical δ¹³C data may offer a stronger line of evidence. Data from ref. 6 on δ¹³C for a 20,000-year southern Indian peat core are juxtaposed to *p*CO₂ history as reconstructed from ice cores^{4,7} (*b* in the figure). As shown, and as would be anticipated if C4 plants displaced isotopically lighter C3 competitors under CO₂ starvation, δ¹³C and *p*CO₂ are inversely related.

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