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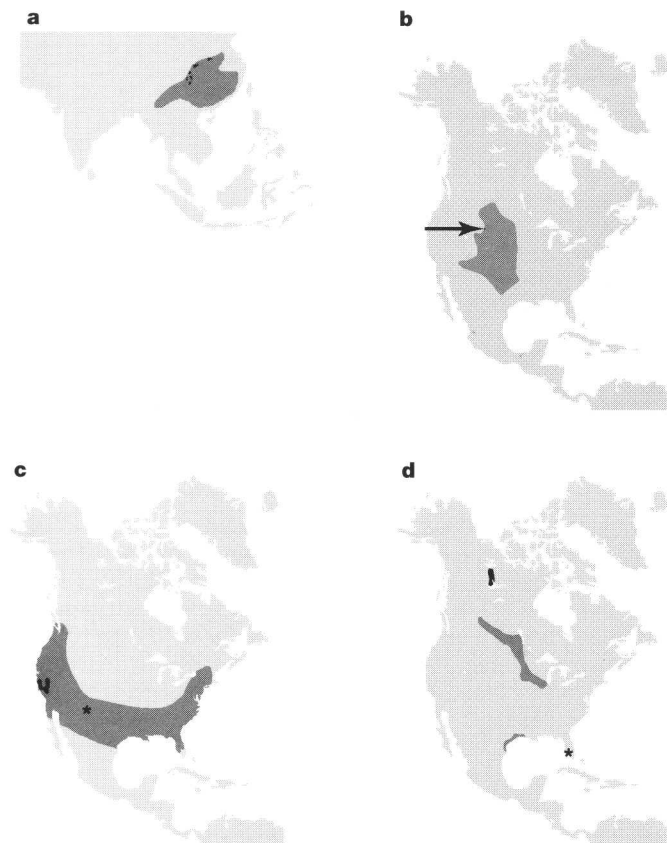


Figure 1 Patterns of range contraction in four endangered species. **a**, Giant panda, *Ailuropoda melanoleuca*; **b**, black-footed ferret, *Mustela nigripes*; **c**, California condor, *Gymnogyps californianus*; **d**, whooping crane, *Grus americana*. Historical range is in grey, extant range is in black or indicated by an arrow, and asterisks mark the locations of recent re-introduction sites for the California condor and the whooping crane.

Dynamic biogeography and conservation of endangered species

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As one moves from the core to the periphery of a species' geographical range, populations occupy less favourable habitats and exhibit lower and more variable densities^{1–4}. Populations along the periphery of the range tend to be more fragmented and, as a result, are less likely to receive immigrants from other populations. A population's probability of extinction is directly correlated with its variability and inversely correlated with density and immigration rate^{5–9}. This has led to the prediction that, when a species becomes endangered, its geographical range should contract inwards, with the core populations persisting until the final stages of decline^{2,10}. Convinced by these logical but untested deductions, conservation biologists and wildlife managers have been instructed to avoid the range periphery when planning conservation strategies or allocating resources for endangered species^{11–13}. We have analysed range contraction in 245 species from a broad range of taxonomic groups and geographical regions. Here we report that observed patterns of

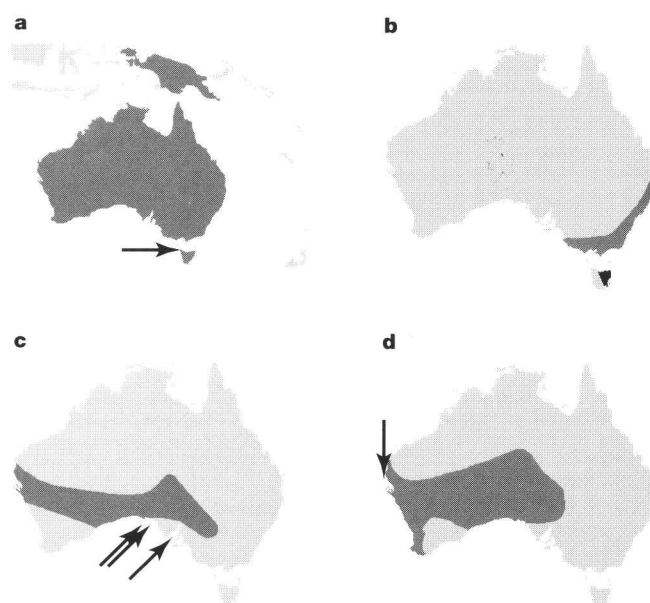


Figure 2 Patterns of range contraction in four species whose historical range included islands as well as much larger areas on the Australian mainland. **a**, Tasmanian tiger, *Thylacinus cynocephalus*; **b**, Tasmanian bettong, *Bettongia gaimardi*; **c**, greater stick-nest rat, *Leporillus conditor*; **d**, Shark Bay mouse, *Pseudomys fieldi*. Historical range in grey, and extant or final range is in black or indicated by an arrow.

Table 1 Number of species studied from different taxonomic groups and geographical regions

	North America	Australia	Eurasia	South America	Africa	Islands	Subtotal
Birds	12	6	19	2	3	45	87
Mammals	8	36	30	5	20	1	100
Reptiles	1		2	1		1	5
Amphibians	3		1				4
Fishes	1		1				2
Mollusks	1		1			20	22
Arthropods	2		1		1		4
Plants	4					17	21
Subtotal	32	42	55	8	24	84	245

See ref. 24.

range contraction do not support the above predictions and that most species examined persist in the periphery of their historical geographical ranges.

Table 1 shows the number of species studied and their geographical distribution. We found that 240 (98%) of the 245 species maintained populations in at least a portion of their peripheral range. Furthermore, 167 (68%) maintained a greater than expected portion of their range in the periphery, not the core ($P < 0.001$, binomial test). In fact, remnant populations of 91 species occurred exclusively in the periphery of their historical range, whereas populations of only five species persisted solely in the core of their historical range ($P < 0.001$, binomial test). We detected no significant difference in the patterns of range contraction between birds and mammals (63 (72%) of 87 birds and 70 (70%) of 100 mammals exhibiting greater persistence along the periphery). Most species, including some of the flagship species of conservation biology (Fig. 1), persist along the edge of their range.

Consistent with contemporary theory in ecology^{6,7,9}, persistence was greater for populations occupying larger patches of their historical range. On the mainland, 12 (75%) of 16 species persisted in larger patches of their historical range, whereas 15 (83%) of 18 insular species persisted in larger patches. However, if a species' historical range included both mainland and insular sites, population persistence was highest on the islands, despite their smaller size (23 [68%] of 34 species exhibited greater than expected persistence on islands; $P = 0.029$, binomial test; Fig. 2).

We found two additional patterns that seem contrary to the general tendency for greater persistence along the range periphery—Africa and the Hawaiian Islands. Africa was the only continent with an adequate sample size whose species failed to exhibit a significant peripheral bias in persistence (14 (58%) of 24 species persisted in the periphery; $P = 0.271$, binomial test). In contrast, 42 (78%) of 54 Eurasian species, 34 (81%) of 42 Australian species and 26 (81%) of 32 North American species persisted in their range peripheries ($P < 0.001$, 0.001, 0.001, respectively, binomial tests). In a similar fashion, whereas 11 (92%) of the 12 species we studied from New Zealand, and all of the 6 species from the Mariana Islands (including Guam) persisted more in the periphery than expected by chance, only 43% of the 54 Hawaiian species exhibited a peripheral bias.

These apparently exceptional results and the more general tendency for persistence along the periphery indicate that range contraction is strongly influenced by anthropogenic extinction forces (for example, habitat degradation, biocides and introduced species) which render historical density patterns irrelevant. Populations that persist the longest are those last affected by the contagion-like spread of extinction forces; that is, those along the edge of the range, on an isolated and undisturbed island, or at high elevations. African species failed to show any peripheral bias in range decline because, instead of moving across species' geographical ranges like a contagion, humans having a significant ecological effect became established in many places across the continent before the earliest record of historical extinctions. We actually predicted this result for Africa, based largely on Martin's^{14,15} explanation for the absence of a

post-Pleistocene collapse of the African megafauna: large mammals and birds shared a long evolutionary and ecological history with prehistoric humans. The 'exceptional' pattern for Hawaiian species is also entirely consistent with the above hypothesis concerning the contagion-like spread of extinction forces. Polynesians and, later, Europeans colonized most of the beach front and lowlands of these islands, and then spread, along with their commensals, upward. Persistent populations of Hawaiian species are either those that can cope with these anthropogenic disturbances, or those whose final populations remain in the least disturbed and most isolated sites; that is, in the montane areas. In short, the geography of recent extinctions is largely the geography of humanity. Thus, our ability to understand patterns in recent extinctions and to predict those of future ones depends to a very large degree on our ability to reconstruct and predict the spatial dynamics of humans and associated extinction forces.

These results have strong implications for conservation biology. Although they may have represented suboptimal habitats in historical times, areas along the range periphery and on remote islands and mountain ranges often provide valuable opportunities for conserving endangered species^{16,20}. We find it very encouraging, therefore, that a number of recent conservation programmes have broadened their options by including peripheral sites for re-introductions and areas to search for undiscovered populations of endangered species (asterisks in Fig. 1c, d). Although once viewed as the land of the living dead^{21,22}, sites along the range periphery may now hold great promise for conserving endangered species and biological diversity in general. □

Methods

We obtained range maps for 245 species from the literature or through personal correspondence with authorities (see Supplementary Information). We include only those species with maps available for both historical and extant ranges (or final site in the case of extinct species), and with extant ranges that were less than 25% of the species' historical distribution. We digitized the range maps into Idrisi, a geographical information system²³. For each species, we first located the centre, which was the point within the species' historical range that was most distant from all edges of the range. The distance from this point to the nearest edge was then calculated. We defined the region that was within half of this distance to an edge as periphery and the remaining portion of the range as central. We then calculated an index of centrality (C), which is a measure of the proportion of the extant or final range that fell within the central region of the historical range.

First, we calculated the area of the extant range expected to occur within the central region (C_{EE}) as follows:

$$C_{EE} = \left(\frac{C_H}{T_H} \right) T_E,$$

where T_E is the total area of the extant (or final) range; T_H is the total area of the historical range; and C_H is the area of the central region of the historical range. We then calculated C as follows. If $C_{EO} \leq C_{EE}$, where C_{EO} is the area of the extant range observed within the historical central region, then

$$C = \left(\frac{C_{EO}}{C_{EE}} \right) 0.5$$

If $C_{EO} > C_{EE}$, then

$$C = 0.5 + \left[0.5 \left(\frac{C_{EO} - C_{EE}}{T_E} \right) \right].$$

The index of centrality (C) ranged from 0, where the extant range fell completely outside the central portion of the historical range, to 1, where the extant range fell completely within the central portion of the historical range. We designated species with C values greater than 0.5 as 'central species', and those species with C values less than 0.5 as 'peripheral species'. We then used a binomial test to determine whether the ratio of central to peripheral species differed significantly from 1 : 1.

We used maps for species with multiple patches in their historical range to test whether persistence was higher for populations inhabiting larger patches. We first assigned patches to one of two size categories ('large' or 'small'), based on their area relative to the median patch size. If a species had an odd number of patches in its historical range, the median-sized patch was excluded from the analysis. For each species, we counted the number of large and small patches maintaining persistent populations (P_L and P_S , respectively). We counted the number of species (S_L) for which P_L was greater than P_S and the number of species (S_S) where P_S was greater than P_L . Species with ties ($P_L = P_S$) were excluded from analysis. We used a binomial test to determine whether the ratio of S_L to S_S differed significantly from 1 : 1. This analysis was done for 124 continental and 44 insular species²⁴.

To compare the relative persistence of mainland and island patches, we first calculated the total area of all of the historical patches (A_{TH}) and the area of the historical mainland patches (A_{MH}) for 44 species. We multiplied A_{MH}/A_{TH} by the total number of persisting patches (P_{TP}) to generate the expected number of patches persisting on the mainland. If the number of patches persisting on the mainland (P_{MP}) was greater than expected, we classified the species as a mainland species, otherwise it was classified as an island species. There were no ties ($P_{MP} = \text{expected number of patches}$). We tested whether the ratio of mainland species and island species differed significantly from 1 : 1 using a binomial test.

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Supplementary information is available on Nature's World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial offices of Nature.

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