

Figure 4 Active tectonic erosion by seamount tunnelling. The seismic image is a prestack depth migration of a segment of Sonne-81 line 6 over a subducting seamount. Dots mark the plate boundary, with black dots delineating the seamount flanks. This segment of the seismic line is parallel to the continental margin, and shows lateral variations in margin wedge thickness. The margin wedge is 0.5–0.7 km thinner above the subducting seamount. Extension of the upper plate by uplift above the seamount is too small to explain the thinning. Thus, thinning is probably due to tectonic erosion produced by mechanical wearing of the upper plate. The location of this cross-section is shown on Figs 1 and 3.

that hydrofracturing and piecemeal stoping^{2,4,8} (an underground mining process) of the base of the upper plate by overpressured fluids may also contribute to upper-plate thinning. A body of Plio-Pleistocene sediment at the front of the margin from southern Costa Rica to Guatemala is limited to a prism less than 10 km wide^{11,14,22}. Although underplating at the rear of the frontal prism might be active or an older relatively small body of accreted material may be present¹⁹, accretion of sediment must be limited in space and time. Subduction erosion at present dominates processes off Costa Rica, and probably also extends into the Nicaraguan margin. □

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Quantitative evidence for global amphibian population declines

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 Although there is growing concern that amphibian populations are declining globally^{1–3}, much of the supporting evidence is either anecdotal^{4,5} or derived from short-term studies at small geographical scales^{6–8}. This raises questions not only about the difficulty of detecting temporal trends in populations which are notoriously variable^{9,10}, but also about the validity of inferring global trends from local or regional studies^{11,12}. Here we use data from 936 populations to assess large-scale temporal and spatial variations in amphibian population trends. On a global scale, our results indicate relatively rapid declines from the late 1950s/early 1960s to the late 1960s, followed by a reduced rate of decline to the present. Amphibian population trends during the 1960s were negative in western Europe (including the United Kingdom) and North America, but only the latter populations showed declines from the 1970s to the late 1990s. These results suggest that while large-scale trends show considerable geographical and temporal variability, amphibian populations are in fact declining—and that this decline has been happening for several decades.

Over the past several decades, there have been reports of catastrophic declines and extirpations of amphibian species in Australia, South and Central America^{13–16}, and in high-altitude regions of the western United States¹⁷. Ancillary evidence has pointed to several possible underlying causes, including changes in local climate¹⁸, acid precipitation¹⁹, disease^{20,21}, increased UV-B irradiation²² or various combinations thereof^{23,24}. Because these reports usually document the disappearances of species from small geographical regions, extrapolations to 'global' amphibian declines are tenuous at best. To address this problem of restricted geographical coverage, we have analysed 936 amphibian population data sets collected from journal publications and technical reports, as well as unpublished data provided by herpetologists from around the world. Every effort was made to be exhaustive, and we believe

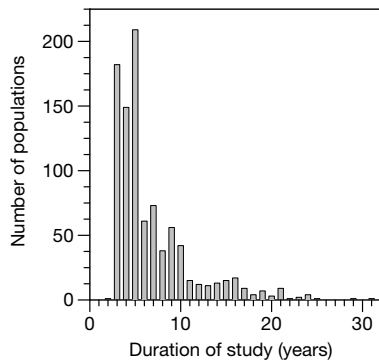


Figure 1 Frequency distribution of study durations.

that our sample represents the most complete collection of amphibian population time series to date. In total, over 200 researchers have contributed data from 37 countries and 8 regions of the world, including population data for 157 species from 21 families (Table 1). The studies range from 2 to 31 years in duration (Fig. 1).

Using a procedure (ΔN , see Methods) that we developed to detect population trends across multiple populations, and considering all 936 populations together (referred to here as the 'global' set), we find significant declines from approximately 1960 to the present (Fig. 2). There was no significant trend from 1950 to 1960 ($\beta = -0.003 \pm 0.013$, $t = 0.23$, $P = 0.50$), a steep decline from 1960 to 1966 ($\beta = -0.070 \pm 0.018$, $t = -3.96$, $P < 0.001$) followed by a shallower decline from 1966 to 1997 ($\beta = -0.008 \pm 0.001$, $t = -11.49$, $P < 0.001$). The trends from 1960–1966 and 1966–1997 represent annual declines of approximately 15% and 2%, respectively (Fig. 2). This apparent difference in rates of decline for the two time periods should be treated cautiously because of the relatively small sample sizes for the early years (Fig. 2).

To address potential biases introduced by the large number of short time series and variable data quality, we have in addition analysed trends in three non-independent subsets of the data, as described in the Methods section. These additional analyses are available as Supplementary Information. Although there are quantitative differences, the population patterns for these three subsets are qualitatively similar to the patterns found in the 'global' set (see Figs 1, 3, 5 in Appendix 2 of Supplementary Information).

Separate analyses of population data from North America and western Europe suggest that, while both showed declines between 1960 and the late 1960s, only in North America did populations appear to decline during the period 1966–1997 (North America, 1960–1997: $\beta = -0.026 \pm 0.002$, $t = -16.79$, $P < 0.001$; western

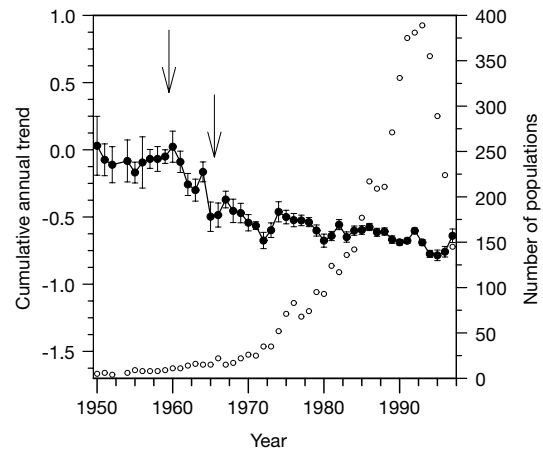


Figure 2 Amphibian population trends from 1950 to 1997 using all 936 populations. (Filled circles, $\Sigma \Delta N$; open circles, number of populations used to calculate ΔN). Arrows indicate the 'switchpoints' (see text).

Europe, 1960–66: $\beta = -0.158 \pm 0.027$, $t = -5.96$, $P < 0.001$; western Europe, 1966–1997: $\beta = 0.001 \pm 0.001$, $t = 1.18$, $0.2 < P < 0.4$) (Fig. 3a, b). The decline from 1960 to 1966 was much more pronounced in western Europe than in North America, but, because the negative trend has persisted over the past several decades in North America, the cumulative change in population size from 1960 to 1997 is similar for both regions. Results for the three subsets, again, show qualitatively similar patterns to analyses presented here despite minor quantitative differences (see Figs 2, 4, 6 in Appendix 2 of Supplementary Information). Regional analyses of low-latitude areas such as South America, Africa and Australia were not possible with this method because most of the populations are from North America and Europe (areas of low to intermediate amphibian diversity). Although there is increasing awareness of the need for more research on amphibian population dynamics²⁵, one clear message of our research is the pressing need for more studies from high-diversity regions of the world, such as the tropics.

A second method for assessing declines based on the ratio of declining to increasing populations (see Methods) indicates that, across all regions included in the analysis, there were significantly more declines than increases (56.6% declines, $\chi^2 = 15.94$, d.f. = 1, $P < 0.001$) (Table 2). However, there was no statistically significant difference in the ratio of declining to increasing populations among regions ($\chi^2 = 4.12$, d.f. = 4, $P = 0.39$). The data in the Supplementary Information also show significantly more declines than increases across all included regions. However, the peer-reviewed/published

Table 1 Summary information of 936 amphibian populations

Region (no. of populations, species and families)	Study duration Mean \pm 1 s.d. (range)	1940–49	1950–59	1960–69	1970–79	1980–89	1990–98
W. Europe (511, 21, 7)	6.9 \pm 4.2 (3–29)	0	0	7	45	171	419
N. America (240, 75, 12)	6.0 \pm 4.1 (3–20)	2	6	15	61	120	110
UK (75, 6, 3)	10.3 \pm 5.3, (3–25)	0	6	6	13	59	59
S./C. America (51, 34, 4)	4.7 \pm 2.2 (3–15)	0	0	0	0	23	31
Australia/NZ (24, 8, 3)	3.9 \pm 1.2 (3–6)	0	0	0	1	15	8
Asia (21, 12, 5)	5.7 \pm 5.7 (3–22)	0	1	8	5	9	5
E. Europe (9, 6, 3)	9.9 \pm 8.4 (4–31)	1	1	3	3	5	3
Africa/Middle East (5, 4, 4)	53.5 (2–11)	0	1	1	1	3	0

Shown are number of studies and study duration for each decade and geographical region. Populations contribute to more than one decade total if they were studied over more than one decade.

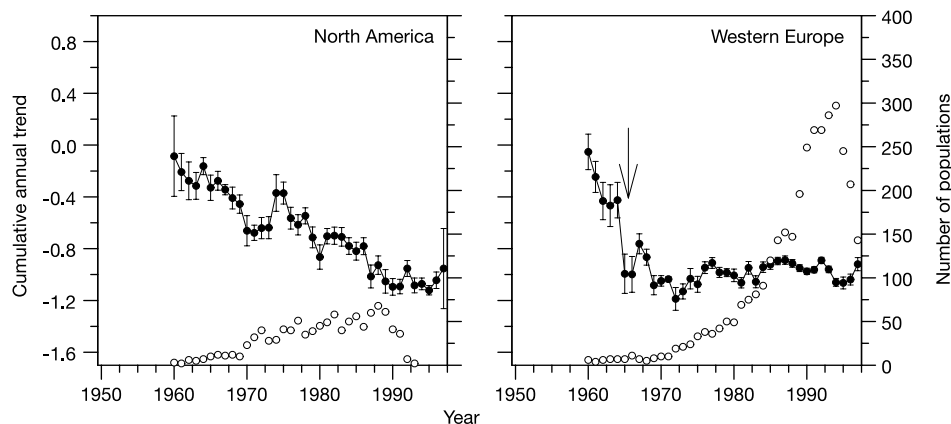


Figure 3 Amphibian population trends from 1960 to 1997 for North America and western Europe (including the United Kingdom). (Filled circles, $\Sigma, \Delta N$; open circles, number of populations used to calculate ΔN). Arrows indicate the 'switchpoints' (see text).

and the published data sets do show significant differences in the ratio of declining to increasing populations among regions (see Tables 1–6 in Appendix 3 in Supplementary Information). An examination of the standardized deviates of the log-linear models for the published and peer-reviewed/published subsets shows that North America and Australia/New Zealand have relatively more declines than other regions.

Our analysis of amphibian population trends from around the world suggests that while there is considerable geographical and temporal variability, at a global scale amphibians have declined over the past several decades and continue to do so. Most of the evidence to date for global amphibian declines has involved documentation of local extirpations of populations^{5,18}. Only 61 of the 936 populations that we studied went extinct (without subsequent recolonization during the study), and only one of those was during the period of most significant decline (1960–66), providing evidence that even extant populations have undergone strong declines. Our analysis

further suggests recent declines, especially in North America and Australia/New Zealand, two regions where anecdotal evidence of declines is perhaps the strongest^{26,27}. We also found evidence for historical declines in both Europe and North America. Indeed, our results suggest that the most dramatic declines—from which amphibian populations and communities seem not to have recovered—occurred several decades before herpetologists sounded the alarm. □

Methods

Data description and selection

Data from 936 amphibian populations were used in this study (for supporting documentation, see Appendix 1 of Supplementary Information). In combining results from many studies, there must be explicit criteria for deciding which studies to include. Recent work on meta-analytic techniques suggests that the more restrictive the criteria for inclusion, the greater the potential bias²⁸. On the other hand, some attempt must be made to evaluate the robustness of the results to changes in inclusion criteria (see Table 3). To address this issue, we analysed the 'global' set and three different subsets of the 'global' set defined by (1) the duration of the population time-series; (2) whether the data were published; and (3) whether the published data had been peer reviewed. Here we present the results of our analysis of the 'global' set; all results for analyses using the three subsets (that is, data sets with more restrictive criteria) are presented in Appendices 1–3 in Supplementary Information.

For all population data, estimates given as a range (for example, 35–40 individuals) were converted to the mean of the upper and lower values of the range. Where estimates were a minimum (for example, 50+), we have taken the minimum estimate as the population estimate (this occurred in fewer than ten populations). Some populations were counted more than once a year. For breeding aggregations, the maximum abundance estimate was used, and for non-breeding populations the average of all abundance estimates in a calendar year was used.

Analysis

Two types of analyses were used: we called one the 'ΔN method' and the other 'the proportion declining' method. The former method combines measurements of

Table 2 Individual population trends by region

Region	No. of declining populations	No. of increasing populations	No. of no-trend populations
Western Europe	309	248	29
North America	130	96	14
South America	31	19	1
Australia/New Zealand	17	6	1
Asia	10	10	1
Eastern Europe	4	5	0
Africa/Middle East	2	2	1

Trends of individual populations were calculated using Kendall's τ , Pearson correlation and Spearman rank correlation. All three techniques gave qualitatively the same result, so only Kendall's τ results are presented here.

Table 3 Selection criteria

Selection criteria	Data Set			
	'Global'	Subset 1	Subset 2	Subset 3
Population or relative abundance estimates were available for at least two years	X		X	X
No change in methodology*	X	X	X	X
No experimental manipulation	X	X	X	X
At least 10 animals counted in at least 1 year of the study	X	X	X	X
No categorical measures†	X	X	X	X
Study initiated since 1950	X	X	X	X
Estimates were available for at least seven years		X		
Published‡			X	
Peer-reviewed§				X

* Studies with changes that would lead to obvious biases in population trends, for example, trends over time in search/capture effort, were excluded. Techniques for taking censuses of amphibian populations included egg mass counts, visual encounter surveys, quadrat and transect sampling, drift fence/pit trap counts, removal sampling, mark-recapture estimates, calling male counts and aquatic traps³⁰.

† Abundance estimates were derived from integer counts of individuals, egg masses, or vocalizations.

‡ Data had to have been published in peer-reviewed journals or in government or technical publications.

§ Data had to have been published in a peer-reviewed journal. Where there was any doubt as to whether a publication was peer-reviewed, the data were excluded from the analyses.

population change across multiple populations, and asks how large the 'average' change in population size is over time; the latter method simply measures trends in individual populations, and asks whether the ratio of declining populations to increasing populations is significantly different from 1:1. The first method is preferable, because it allows us to assess potential changes in the rate of decline over time, but it requires large sample sizes that were not available for some regions. The second method allowed us to test for declines in those regions with small sample sizes.

ΔN method

This method was used to test for trends in the 'global' set, and to test for 'regional' trends in North America and western Europe (including the UK). For 'global' and 'regional' trends we calculated $\log(N+1)_{t+1} - \log(N+1)_t = \Delta N$ for successive yearly intervals. For this analysis, only populations having at least two consecutive years of data could be used. We then calculated $\Delta N \equiv (\sum_{t=1}^n \Delta N_t) / n$ based on all populations (*n*) for which there were data for the time interval (*t*, *t* + 1) in question (because the number of studies increases over time, so does the sample size for ΔN). This procedure was repeated for each year from 1950 to 1997, and the annual averages used to compute the cumulative average change, $\bar{\Delta N} \equiv \sum_{t=1}^T \Delta N_t / T$, from *T* = 1950 to *T* = 1997. More than 200 western European population time series come from two large studies in Sweden and Switzerland. Analyses of population trends with and without these data indicate they had no qualitative effect on the results.

Visual examination of a plot of ΔN for the global set suggests three qualitatively different time periods, corresponding roughly to 1950–1960, 1960–1970 and 1970–1997. To estimate switchpoints between periods, we fitted regression models including dummy (categorical) variables defining the period intervals (for example, period 1: 1950–1960; period 2: 1961–1970, and so on). Changing the beginning and end points for a given period results in a change in model fit, with the best estimate of the switchpoints derived from the model with the lowest residual mean square. The initial switchpoints were selected by examination of the data, with subsequent fitting based on moving the switchpoints forwards and backwards from the initial estimate(s). Model fitting ended when models with switchpoints two years earlier and later than the best model had higher residual mean-square values. Our best-fit model partitioned the global set into three time periods: 1950–1960, 1960–1966 and 1966–1997. The best model for the western European data showed two distinct time periods (1960–1966 and 1966–1997), while the best model for North America showed a single trend from 1960 to 1997.

ΔNs are summary data. As such, using it as the dependent variable in regression underestimates the true error sums of squares. We have corrected for this by including the error contribution of each ΔN to ΔN (ref. 29), and all significance tests use this true error sum of squares and the corresponding true degrees of freedom.

Proportion of declining populations method

In a second analysis, we evaluated trends in population size over time using the Spearman correlation, the Pearson correlation coefficient and Kendall's τ. Irrespective of the test statistic used, results were qualitatively the same. We present our results using Kendall's τ because it avoids some of the assumptions about data distribution. We calculated the correlation (Kendall's τ) between population size and year for each population in a particular geographical region. Populations were then classified as to whether they were declining (negative correlation), increasing (positive correlation) or had no trend (correlation = 0). For a population to show no trend, the correlation must be exactly 0. A log-linear model was fitted using the independent variables region, trend and their interaction (region × trend). Populations showing no trend were not included in the log-linear model. For the 'global' dataset and the three subsets, the Eastern European and African/Middle Eastern regions are presented but not included in the log-linear model; for the ≥7 year data set, Asia, South America and Australia/New Zealand are also presented, but excluded from the log-linear model because of low sample sizes.

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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 office of Nature.

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The metapopulation capacity of a fragmented landscape

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Ecologists and conservation biologists have used many measures of landscape structure^{1–5} to predict the population dynamic consequences of habitat loss and fragmentation^{6–8}, but these measures are not well justified by population dynamic theory. Here we introduce a new measure for highly fragmented landscapes, termed the metapopulation capacity, which is rigorously derived from metapopulation theory and can easily be applied to real networks of habitat fragments with known areas and connectivities. Technically, metapopulation capacity is the leading eigenvalue of an appropriate 'landscape' matrix. A species is predicted to persist in a landscape if the metapopulation capacity of that landscape is greater than a threshold value determined by the properties of the species. Therefore, metapopulation capacity can conveniently be used to rank different landscapes in terms of their capacity to support viable metapopulations. We present an empirical example on multiple networks occupied by an