phorylation of BAD by Akt will preclude its binding to membrane-anchored Bcl-$x_L$, leading to increased cell survival. Thus, BAD phosphorylation by Akt is a mechanism by which growth factor receptors could deliver a survival signal that leads to the inhibition of apoptosis. However, these results do not rule out the possibility that Akt promotes cell survival by other mechanisms in addition to that mediated by phosphorylation of BAD. In this respect, it has been shown that Akt promotes expression of Bcl-2 in certain cell lines but not in others (*11*), which suggests that Akt mediates cell survival by at least one other mechanism. Previous studies have indicated that another kinase, Raf-1, could phosphorylate BAD in vitro (*16*). Unlike Akt, however, Raf-1 and another kinase, PKC, phosphorylated BAD in vitro at serine residues other than $Ser^{112}$ and $Ser^{136}$, which suggests that BAD is not a physiological target of Raf-1 in vivo (*3*). Akt was originally identified as an oncogene in mice and is overexpressed in some human tumors (*17*). Because Bcl-2 and Bcl-$x_L$ are known to deliver oncogenic signals that result in tumor development, these results suggest that active Akt promotes tumor development, at least in part, by acting on Bcl-2–related survival factors through phosphorylation and inactivation of BAD.

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# Population Diversity: Its Extent and Extinction


Jennifer B. Hughes,* Gretchen C. Daily, Paul R. Ehrlich



Genetically distinct populations are an important component of biodiversity. This work estimates the number of populations per area of a sample of species from literature on population differentiation and the average range area of a species from a sample of distribution maps. This yields an estimate of about 220 populations per species, or 1.1 to 6.6 billion populations globally. Assuming that population extinction is a linear function of habitat loss, approximately 1800 populations per hour (16 million annually) are being destroyed in tropical forests alone.


Much of the current scientific and public concern over the extinction crisis centers on the loss of species globally (*1*). Most of the benefits biodiversity confers on humanity, however, are dependent on large numbers of populations of species, because each population ordinarily provides an incremental amount of an ecosystem good or service. Examples of these goods and services are seafood, timber, water purification, generation of soil fertility, pest control, mitigation of floods and droughts, and regulation of biogeochemical cycles (*2*). Populations also supply the genetic diversity that is crucial for the development and improvement of pharmaceuticals and agricultural crops (*3*).

Here we make a crude first approximation of population diversity (defined as the number of populations on the planet) and then estimate the extinction rate at this level of biodiversity. We reviewed the literature on population differentiation from a variety of taxa and estimated the average number of mendelian populations per unit area for a species. We then estimated the average range size of a species from a sample of distribution maps. The product of these two numbers is an approximation of the average number of populations per species, which, multiplied by the total number of species, yields an estimate of the number of populations on Earth (*4*).

Populations are normally defined as geographical entities within a species, distinguished either ecologically or genetically (*5*). We adopted the genetically based definition, or mendelian population (*6*), defined here as a group of individuals evolving independently of other groups because of limited gene flow and genetically distinguishable from other populations.


Department of Biological Sciences, Stanford University, Stanford, CA 94305–5020, USA.

*To whom correspondence should be addressed.

To estimate the number of populations per unit area, we searched 15 journals from 1980 to 1995 for genetic studies on population differentiation (*7*). The studies selected had sampled the same species from more than two geographic locations and reported the geographic distances between sampling locations. We excluded articles that compared populations across islands, used domesticated species, or sampled species with average outcrossing rates of less than 10%.

Of over 400 articles found on population differentiation, 81 present appropriate data for a calculation of population numbers per unit area (*8*). Of these, 69 use allozyme data and the remaining articles use restriction fragment length polymorphisms (RFLPs) and DNA sequences. We were able to make an estimate for 82 species. Most of the species are vertebrates ($n = 35$), followed by plants ($n = 23$), arthropods ($n = 19$), mollusks ($n = 4$), and one platyhelminth.

To quantify the number of populations per unit area of a species, we scored articles in terms of whether the sampling locations were distinct populations or were within one population. If statistically significant differentiation among localities was found in the paper, we considered all of the localities to be separate populations (*9*). We then calculated the number of populations per area as the number of sampling locations divided by the extent of the entire sampling area. If the researchers did not find significant differentiation between the localities, we assumed that they had sampled from within one population and that the extent of the population was that of the sampling area. Many studies found an intermediate amount of differentiation. For instance, if a number of sites were sampled, and a significant difference was found only between two clusters of sites, we assumed that there were two populations within the sampling area.

Following these guidelines, the three authors separately reviewed each article and estimated the order of magnitude of the number of populations in 10,000 $km^2$ for each species. For example, an estimate of "0" represents 1 to 9 populations in a 10,000-$km^2$ area, "2" represents 100 to 999 populations in 10,000 $km^2$, and "–2" represents 0.01 to 0.099 populations in 10,000 $km^2$ or 1 to 9.9 populations in 1 million $km^2$. In the few cases in which our initial estimates disagreed, we studied the article together until we arrived at a consensus.

To illustrate these methods, we describe the reasoning behind our estimates for two different species. Lavery *et al.* (*10*) sampled coconut crab (*Birgus latro*) populations from seven islands in the Indo-Pacific. (Because the crab has a marine planktonic larval stage, we did not exclude the study for sampling only on islands.) The locations spanned an area of approximately 40 million $km^2$. Lavery *et al.* found seven polymorphic allozyme loci, and the mean $F_{ST}$ (a measure of population differentiation) was 0.078, which was significantly different from zero. From this information, we concluded that the seven sampling locations were separate populations and that there are approximately 1.75 populations of *B. latro* per 10 million $km^2$. Thus, we estimated that there are –3 orders of magnitude of coconut crab populations per 10,000 $km^2$. Rasmussen and Brødsgaard (*11*) studied the weedy perennial *Lotus corniculatus* (Fabaceae) in Denmark. Using RFLPs, they investigated the genetic variation of 30 plants from a 5-$km^2$ area of dune heathland. The plants were significantly differentiated among six patches within this area. We concluded that there were six populations in these 5 $km^2$ and extrapolated that there may be as many as 12,000 populations per 10,000 $km^2$. We conservatively estimated that on average the order of magnitude of the number of populations in a 10,000-$km^2$ area is 3, or from 1000 to 9999 populations per 10,000 $km^2$.

To estimate the average range size of a species, we digitized range maps from guidebooks for birds, mammals, fish, and butterflies from a number of geographical regions (*12*). We used the graphics program Canvas 3.5 to calculate the area of the range depicted on each map and converted the scanned area to the actual area by calibrating the range to a known geographic area on the same map, usually an island or country (*13*). We excluded books that had maps with a very large (>20%) projection error (*14*).

The average order of magnitude of the number of populations per 10,000 $km^2$ is reported by arbitrary taxonomic groupings in Table 1. There are several ways to combine these estimates of population differentiation to arrive at an estimate for all species. One method is to weight all the species equally. For the 82 species, there are on average 1.2 populations in a 10,000-$km^2$ area of a species' range. Another method is to weight the groups according to their estimated species richness. This method is approximately equivalent to using the arthropod estimate of 2.1 populations per 10,000 $km^2$, because the other groups for which data exist are not very speciose (*15*). By any of these weighting schemes, the estimate of number of populations per species per 10,000 $km^2$ falls within the same order of magnitude of $10^0$. Given that the standard error of these estimates encompasses orders of magnitude, these numbers are essentially the same. Thus, we use 1 as our estimate of the number of populations per species per 10,000 $km^2$.

The average range per species varies from 790,000 $km^2$ for Indomalayan mammals to 6.6 million $km^2$ for East African mammals (Table 2). As with the calculation of populations per unit area, there are a number of ways to distill the range results into an average range size for all species. Equally weighting the four taxonomic groups, the mean range size of a species is 2,572,000 $km^2$. Averaging the range size estimates of arthropods only (here just butterflies) leads to a range of 2,195,000 $km^2$ per species. These numbers are quite similar, so we conservatively use the lower number, 2.2 million $km^2$, as our estimate of the average range size of a species.

Multiplying the number of populations per area (1 population per 10,000 $km^2$) by the average range size of a species (2.2 million $km^2$) yields an average of 220 populations per species. Using three estimates of global species numbers (5, 14, and 30 million) (*16–18*, respectively), we arrive at three estimates of the total number of populations: 1.1, 3.1, and 6.6 billion populations.

It is difficult to evaluate the accuracy of our estimate of population diversity, yet there is reason to believe it is conservative. First, the estimates of populations per unit area from the literature are restricted by the sampling intensity of each study. It is likely that, in most cases, heavier sampling in the study area would have revealed further differentiation, thus increasing the estimated

**Table 1.** Estimates of the mean order of magnitude of population diversity and the number of populations per 10,000 $km^2$ by arbitrary taxonomic groupings. *N* is the number of species used for the estimate in each group.

| Taxonomic group | *N* | Number of populations per 10,000 $km^2$ |
|---|---|---|
| Plants | 26 | 1.7 |
| Conifers | 5 | 0.06 |
| Platyhelminthes | 1 | 10 |
| Mollusks | 4 | 20 |
| Freshwater | 2 | 1.0 |
| Land | 2 | 316 |
| Arthropods | 19 | 2.1 |
| Crustaceans | 5 | 4.0 |
| Insects | 13 | 0.83 |
| Vertebrates | 35 | 0.49 |
| Fish | 8 | 0.05 |
| Freshwater | 3 | 10 |
| Marine | 5 | 0.003 |
| Birds | 11 | 0.06 |
| Mammals | 12 | 5.6 |
| Reptiles | 1 | 0.01 |
| Amphibians | 3 | 50 |
| All species* | 85 | 1.2 |

*Calculated giving equal weight to all species.

number of populations. Second, molecular markers may not always reveal notable differences between groups (*19*). Finally, our estimates of populations per area ultimately rely on the use of a mendelian population definition. Butterfly distributions mapped by Thomas and Webb (*20*) provide some insight into the relation between the diversity of mendelian and ecologically defined populations, or demographic units (populations with independent dynamics) (*5*, *21*). They map the presence and absence of the butterflies of Dorset county, England, in 1-km squares. Even at this scale, many isolated patches are apparent. We estimated that an average species contained one mendelian population in 10,000 $km^2$. These maps suggest, however, that the number of demographic units in the same-sized area may easily be an order of magnitude higher.

The most likely source of inflation of the total population diversity estimate is the quantification of species' range size. The shaded areas of the distribution maps are very rough and virtually always encompass unsuitable habitat where populations do not occur (*22*). Also, most of the sources we used were limited to temperate regions, even though it is estimated that two-thirds of species diversity exists in the tropics (*23*). This regional bias may inflate the population estimates, given that in some taxa species' range sizes tend to increase toward the poles (*24*).

Perhaps the most prominent source of bias in our estimate is the taxonomic focus inherent at each step. Arthropods comprise an estimated 65% of the planet's species, whereas birds account for probably less than 0.01% (*17*). Of the available data on population structure, however, arthropods and birds accounted for 22 and 13% of the species, respectively. In addition, some groups were notably absent. The diversity of fungi, nematodes, and microorganisms remains virtually unexplored but is thought to be enormous (*25*).

Estimates of current species extinction rates are largely based on species-area relationships and the rate of habitat loss due to deforestation (*1*, *26*). Given the current rate of tropical deforestation of roughly 0.8% per year (*27*), the rate of committing tropical forest species to extinction is predicted to lie between 0.1 and 0.3% each year (*28*). Assuming that there are 14 million species globally and that two-thirds of all species exist in tropical forests, tropical forest species diversity is declining by roughly 14,000 to 40,000 species per year, or two to five species per hour.

There is no comparable work relating numbers of populations to area. Although a wide range of relationships could be justified, depending on the spatial and time scales considered, in the absence of information we use the simplest and most intuitive here: namely, that changes in population diversity and area correspond in a roughly one-to-one fashion in ecological time. That is, when 90% of an area is destroyed, about 90% of the populations in the original area are exterminated (as opposed to roughly 50% of the species as predicted by the species-area relationship). Clearly, the destruction of 90% of the area occupied by a population may not force that population to extinction; however, one would expect the extinction of all of the populations entirely contained, and some of those partially contained, within the destroyed area.

If indeed a one-to-one relationship holds, population extinction rates in tropical forest regions are estimated at 0.8% per year, directly proportional to habitat loss. Using our midrange estimate of global population diversity (3 billion populations) and assuming that two-thirds of all populations exist in tropical forest regions, we estimate that 16 million populations per year, or roughly 1800 per hour, are being exterminated in tropical forests alone. This is an absolute rate three orders of magnitude higher, and a percentage rate three to eight times higher, than conservative estimates of species extinction. The consequences for human well-being of the rapid loss of populations will depend in part on the degree to which their functions can be replaced by populations of "weedy" species, but they are likely to be severe.

**Table 2.** Range size summary statistics sorted by taxonomic group and calculated using only every other map of each book. Estimates are rounded to the nearest 10,000 $km^2$.

| Taxon and geographic region | Number of families | Number of species | Mean area per species ($km^2$) | SD ($km^2$) |
|---|---|---|---|---|
| Mammals | | | | |
| North America | 21 | 137 | 2,900,000 | 3,860,000 |
| Indomalayasia | 38 | 493 | 790,000 | 1,510,000 |
| East Africa | 39 | 167 | 6,550,000 | 9,160,000 |
| Butterflies | | | | |
| North America | 6 | 269 | 2,240,000 | 2,930,000 |
| South East Asian Islands | 6 | 368 | 2,150,000 | 6,240,000 |
| Birds | | | | |
| North America | 53 | 306 | 3,010,000 | 3,630,000 |
| South America | 12 | 347 | 1,640,000 | 2,640,000 |
| Fish | | | | |
| North America | 42 | 334 | 850,000 | 1,670,000 |
| Total* | 217 | 2421 | 2,572,000 | 1,340,000 |

*Total mean and SD are calculated by equally weighting the four taxa.

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the ratio of the scanned areas of two known geographic regions to the ratio of their actual areas. From this comparison, we calculated a projection error as $1 - k$, where $k$ is a constant such that

$$\left\{\frac{\text{scanned area of region1}}{\text{actual area of region 1}}\right\} = k \times \left\{\frac{\text{scanned area of region 2}}{\text{actual area of region 2}}\right\}$$

For consistency, the regions were arranged in this formula (assigned as region 1 or region 2) so that $k$ was always less than 1. To be conservative, we tried to choose reference areas as different in latitude as possible but covering a large latitudinal range.

15. From projections of estimated species richness for these groups (*17*), arthropods should account for 94% of the estimate, versus 3.4% for plants, 2.1% for mollusks, and 0.5% for all chordates combined. Using these exact proportions changes the arthropod estimate by +0.02 populations in 10,000 km$^2$.
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# Extinction and the Loss of Evolutionary History

Sean Nee* and Robert M. May

**Extinction episodes, such as the anthropogenic one currently under way, result in a pruned tree of life. But what fraction of the underlying evolutionary history survives when *k* of *n* species in a taxon are lost? This is relevant both to how species loss has translated into a loss of evolutionary history and to assigning conservation priorities. Here it is shown that approximately 80 percent of the underlying tree of life can survive even when approximately 95 percent of species are lost, and that algorithms that maximize the amount of evolutionary history preserved are not much better than choosing the survivors at random. Given the political, economic, and social realities constraining conservation biology, these findings may be helpful.**

We approach questions about pruning the tree of life and the calculus of biodiversity (*1*), so forcefully raised by the current extinction crisis (*2*), in the context of theoretical clades that either have been growing exponentially throughout their history or have been of constant size, such that each time a new lineage has appeared by speciation another lineage has gone extinct. These extremes bracket the plausible dynamical histories of real clades. The radiations of both the New World and Old World monkeys are consistent with the exponential growth model (*3*), whereas the history of the Plethodontid salamanders is consistent with the constant size model (*4*). Logistic growth, in which diversity rises to some maximum, is a convenient model for macroevolutionary clade expansion as well as population growth (*5*). In this framework, exponential growth is the early phase of logistic growth, and the constant size model describes a clade that has been at its maximum size for some time. From the data of marine families compiled by Benton (*6*), to which the logistic model has been fitted (*5*), the number of families appears to have been roughly constant for about 200 million years before the Late Permian mass extinction.

Suppose $k$ species are saved from a total of $n$. This may be done in many ways. At one extreme, the species may be picked at random with respect to their phylogenetic relationships—the "field of bullets" scenario (*7*); at another extreme, useful for comparison, the species may be chosen according to the following algorithm, which maximizes the amount of evolutionary history preserved. The $k - 1$ lowest nodes in a tree (counting from the root) are selected. These define $k$ clades. One species from each clade is picked; if a clade has more than one species in it, then one is picked at random. Figure 1 illustrates the relation between species loss and the loss of evolutionary history and shows that this algorithm optimizes the amount of evolutionary history preserved.

If $k$ species out of a total of $n$ are saved, it is natural to express the amount of history preserved as a fraction of the total amount that could have been preserved if all $n$ species had been saved. How can this "amount of evolutionary history" be measured? For many purposes, it may be best simply to count species as such. But, as emphasized by Vane-Wright and others (*1*, *8*), it is often useful to measure the loss at a more fundamental level; ultimately, it would be best to assess this loss at the genetic level, by some measure of underlying information molecularly coded in DNA. Proximally, we work here with the tree structure. The above algorithm clearly works whether the actual "lengths" of the branches are known, or merely the branching order of the nodes (although firmer estimates of the fraction saved can be made in the former case). Also, note that we assume all branch tips are equidistant from the root; more details of molecular evolution could give a picture in which such lengths varied, although it seems likely that our general conclusions will remain valid in these more general circumstances.

We now present approximate equations for the average fractional amount of evolutionary history preserved, $f(k,n)$, when we save $k$ of the original $n$ species, under various assumptions about the history of the clade (*9*). For a random set of species from a clade that has been of constant size (indicated by the subscript r, const.), the equation for $f(k,n)_{\text{r, const.}}$ is

$$f(k,n)_{\text{r, const.}} \approx \frac{\ln(k-1) + C}{\ln(n-1) + C} \qquad (1)$$

where C is Euler's constant, with a value of ~0.577. This is obviously only meaningful for $k > 1$. Numerical simulations show that this analytical approximation performs very well for $k > 3$.

For a random set of species from a clade

Department of Zoology, Oxford University, South Parks Road, Oxford, OX1 3PS, UK.

*To whom correspondence should be addressed. E-mail: sean.nee@zoo.ox.ac.uk