

Background- population decline

The Living Planet Index (LPI; WWF 2020) recently reported an average 68% decline in populations of vertebrates. This decline represents global average population size (abundance) losses per species for 20,811 populations of 4,392 species, between 1970 and 2016. The Index notes that species-rich regions are given greater weight in the calculation. It also notes wide variation among regions with Latin America and the Caribbean having suffered 95% population declines (<https://www.livingplanetindex.org/>). For simplicity, our analysis will utilize the average 68% decline of individuals for a given species or population.

Metrics of genetic diversity:

We present here a simple calculation of the expected change in two indices of genetic diversity- heterozygosity and allelic diversity- when populations decline by 68% of individuals. Heterozygosity is relevant as an index of genetic diversity because it mediates immediate response to natural selection through variation among, and within, individuals and reflects inbreeding rates and genetic 'drift' due to unequal family size. Allelic Diversity (AD) is relevant because it is the raw number of units available to be selected upon and thus, to some degree, the range of trait values- in other words, the evolutionary potential.

Assumptions and formulas:

We assume populations have achieved an equilibrium between mutation and genetic drift, and that the population size is measured in terms of effective population size, N_e . We also assumed an effective mutation rate of $10E-4$, which is equal to a per base mutation rate of $10E-8$ on a sequence of length 10,000 base pairs (a realistic size for a functional "gene"). Calculations are based on well developed population genetic theory (Formulas 1 and 2) whose predictions have been validated in hundreds of empirical studies and simulations.

Formula 1: At equilibrium between mutation (increasing genetic diversity) and genetic drift (reducing genetic diversity), the effective population size N_e predicts the amount of gene diversity H_e as

$$H^{\wedge}_e = \frac{4N_e\mu}{1+4N_e\mu}$$

with N_e the effective size and μ the mutation rate of the locus (Kimura & Crow 1964). Calculating gene diversity at mutation-drift equilibrium gives values that range from close to 0 to close to 1. This metric predicts the likelihood of being homozygous versus heterozygous at a certain locus, and thus pertains to inbreeding levels.

Formula 2: To express this H_e in the same units of measurements as allelic richness (number of alleles), we convert the diversity index H_e to its true diversity equivalent, the effective number of alleles, aka Allelic Diversity, AD, calculated as

$$AD=1/(1-H_e)$$

(Jost 2010). The metric expresses how many effective alleles there are in the population, which represents the raw material on which natural selection can act, or as we stated, "genetic variation that helps populations adapt".

As shown in Table S1, we applied these two formulas to N_e before and after a population reduction, for N_e of varying sizes. Specifically, we applied the formulas to N_e from one thousand to one million as the starting population size and applied the same formula to populations reduced by 68%.

Further assumption and point on metapopulations

We assume mutation-drift equilibrium for these calculations. The time to reach a new equilibrium depends on the presence of population substructure, the average size of subpopulations and the migration rate among subpopulations (Crow & Aoki 1984). The eventual losses to be expected at equilibrium, however, are relatively insensitive to subdivisions of populations, as long as subpopulations are interconnected through genetic exchange (Wright 1951). Under the assumption of some genetic exchange, a decline of X% of a panmictic population yields the same decline in genetic diversity as a X% loss of subpopulations where each remaining subpopulation remained at a stable size, or a X% decrease in every subpopulation without population extinction.

Below, we present the expected loss of genetic diversity for a 68% decline in population size at equilibrium. These losses in genetic diversity have not been fully achieved yet, but assuming no further declines nor recovery of population sizes, these numbers represent eventual outcomes expected. A subset of these findings are reported in the main manuscript, Table 1.

As one example we can examine a population of $N_e=10000$ (row 2 below), as might exist for a medium or large size vertebrate in a geographic region (for example, wolves in the Apennines before human impact). For a given allelic diversity of 5 at mutation-drift equilibrium (which is a realistic number of effective alleles at a locus of 10000 base pairs under selection), a 68% population size reduction yields a decrease in heterozygosity of 30%, and a loss of allelic diversity of 54%. Thus very significant losses are to be expected. The good news is that losses take place over time, so this expected loss of genetic diversity can still be mitigated by rapidly restoring population sizes and ensuring migration among populations.

Table S1: loss of genetic diversity that can eventually be expected to be associated with the reported 68% reduction in population sizes (e.g. the current LPI in WWF 2020). The Table presents both the expected gene diversity at mutation-drift equilibrium (H_{exp}), and the associated effective number of alleles (Allelic diversity, AD_{exp}) for the reference situation in 1970, and for a 68% population reduction. Note: These values assume mutation-drift equilibrium. The current situation is likely not at mutation-drift equilibrium, so the observed losses up to this point will be smaller. But this is what the future will bring in a constant N scenario without further deterioration or improvement.

Values prior to population decline, e.g. in 1970			Values after 68% population decline			Percentage losses	
$N_{e_{pre}}$	H_{exp}	AD_{exp}	$N_{e_{post}}$	H_{exp}	AD_{exp}	Loss of H	Loss of AD
1000	0.2857	1.4	320	0.1135	1.1	60.3%	19.4%
10000	0.8000	5	3200	0.5614	2.3	29.8%	54.4%
100000	0.9756	41	32000	0.9275	13.8	4.9%	66.3%
1000000	0.9975	401	320000	0.9922	129.0	0.5%	67.8%
10000000	0.9998	4001	3200000	0.9992	1281.0	0.1%	68.0%

Note: For any given mutation rate μ , the loss of allelic diversity (effective number of alleles) that results from a X% population decline converges to X% when $N\mu > 10$.

Citations

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