On the Challenge of Comparing Contemporary and Deep-Time Biological-Extinction Rates

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To assess whether Earth is currently experiencing a human-induced "sixth" mass extinction, scientists over the past 20 years have compared modern rates of extinction with the widely accepted average global background rate of 1 extinction (E) per million species-years (MSY). The application of the comparative method has led to the widely iterated estimate that contemporary global extinction rates are 100–1000 times higher than the background rate. Recent analyses indicate that the average background rate is closer to 0.1 E/MSY, suggesting that the difference between contemporary and background extinction is actually about 10 times greater than previously thought. Here, we review the historical development and mathematical underpinning of these estimates and show that, regardless of the baseline measure, there have been fewer documented extinctions in the recent 100–500 years than the comparative measure implies. Although anthropogenic activities have reduced the abundance and distribution of countless species and have caused more species extinctions than would be expected in the absence of humans, we conclude that the most appropriate interpretation of the existing data is that the global rate of contemporary extinction is closer to 100 times greater than the (revised) background rate of extinction rather than 1000 times greater.

In coming to grips with the magnitude of contemporary global biological extinction, it has been widely suggested that Earth has entered the early stages of a mass extinction rivaling the "big five" of the geological past, during which more than half of all species went extinct over the course of thousands or millions of years (Bambach et al. 2004). A commonly cited indicator that a modern mass extinction is underway is the estimate that contemporary rates of global extinction are 100–1000 times greater than the average global background rate of extinction gleaned from the past (Pimm et al. 1995, MEA 2005, Wagler 2007, Kolbert 2015). For these comparisons, the background rate derives from estimated lifespans of species in the fossil record during nonmass extinction intervals (Raup 1991). Mean lifespans range from approximately 0.2 million–16 million years depending on taxonomic group, which yields an average background longevity generally expressed as approximately 1 million–10 million years (summarized in May et al. 1995, May 2002). For the last two decades, the lower value, 1 million years, has been the accepted benchmark lifespan from which background extinction is inferred and against which contemporary rates of extinction are evaluated. This shorter lifespan has been favored because it translates into a higher rate of background extinction than does a longer lifespan and therefore yields a more conservative

estimate of the difference between background and contemporary extinction (May et al. 1995, Pimm et al. 1995, 2006, Burkhead 2012). Furthermore, for practical reasons related to preservation and the state of species-level taxonomy in the fossil record, direct assessments of longevity based on first and last appearances over the sweep of the Phanerozoic eon have generally been conducted at or above the genus level and extended for species (Raup 1991, May et al. 1995). The million-year estimate, therefore, is more likely than a 10-million-year estimate to reflect the lifespan of a species, the desired taxonomic level for comparing background and contemporary extinction.

In separate but related articles, Pimm and colleagues (2014) and deVos and colleagues (2014) summarized several lines of evidence supporting a longer lifespan (10 million years) as a more appropriate benchmark for inferring historical background rates. Both papers cited observations that genus-level lifespans for major groups (e.g., Cenozoic mammals) tend to be longer (Alroy 1996), not shorter, than a million years, with major marine groups typically having genus lifespans longer than 10 million years (e.g., cetaceans, marine carnivores, and brachiopods; Harnik et al. 2012). In addition, they relayed Russell and colleagues' (1998) suggestion that species- and genus-level background extinction should not differ appreciably because most extinctions

documented in the fossil record are based on monotypic or species-poor genera and furthermore that species of the same genus tend to have similar vulnerabilities to extinction. Finally, de Vos and colleagues (2014) presented results from molecular phylogeny analyses that showed low rates of extinction (most approaching 0 extinctions per lineage per million years) and diversification (less than 0.2 species per species per million years) within five major taxonomic groups as additional evidence that the longer (10-million-year) rather than the shorter (million-year) lifespan is the more appropriate benchmark from which to infer background extinction. Extinction, after all, cannot have been greater than diversification, or else species richness in the fossil record would not increase over time (Rosenzweig 1995). Given the recent controversy pertaining to whether molecular phylogenies confer reasonably accurate estimates of extinction and diversification (Rabosky 2010, Beaulieu and O'Meara 2015, Rabosky 2015), it is relevant to note that de Vos and colleagues (2014) omitted dubious phylogenies and included a broad range of scenarios in their analysis to show that their results were not dependent on a narrow range of assumptions.

Acceptance of the longer lifespan implies that the background rate of extinction used for the aforementioned comparative purposes is 10 times lower than the previously accepted benchmark, which, in turn, implies that the difference between contemporary and background extinction is 10 times greater than previously thought (deVos et al. 2014). Nevertheless, the authors did not revise the benchmark range of contemporary extinction from 100–1000 times the background rate (Pimm et al. 1995) to 1000–10,000 times background. Instead, they and various secondary authors (Alford 2014, Gutierrez 2014, Orenstein 2014) maintained that the finding suggested that contemporary extinction was 1000 times the background rate, with future rates expected to be as high as 10,000 times the background rate (deVos et al. 2014). Nevertheless, because the upper bound of the previous estimate was already 1000 times the background rate, it is not surprising that authors in the popular press have interpreted the 10-fold increase to mean that the rate of global extinction is now thought to be 1000–10,000 times the background rate (Jivanda 2014, Spotts 2014). As the scientific community and general public become increasingly accustomed to the much higher value, it is worthwhile to consider the historical development and mathematical underpinning of this family of estimates. In doing so, we illustrate why decreasing the background rate of extinction does not significantly increase the contemporary rate beyond the previous upper bound of 1000 times the background rate. In addition, we show that, regardless of the baseline measure, there have been fewer documented extinctions in the last 100 to 500 years than the comparative measure implies (Smith et al. 1993, IUCN 2015). We fully accept that anthropogenic activities have reduced the abundance and distribution of countless species and have caused more species extinctions than would be expected in the absence of humans. However, the most appropriate interpretation of the data is that the global rate of contemporary extinction is closer to 100 times greater than the (revised) background rate of extinction rather than 1000 times greater.

Calculating a background rate of extinction from the fossil record

Inferring background extinction from taxonomic longevity in the fossil record follows the straightforward logic that if the average lifespan of a species in the fossil record is 1 million years, then in a pool of one extant species, there would be, on average, one extinction every 1 million years. If the size of the species pool were enlarged, say, to one million species, each of independent origin, then a rate of extinction on par with background would be 1 extinction per year (Raup 1991). Pimm and colleagues (1995) used this logic to compare deep-time and contemporary rates of extinction in terms of "species-years," equivalent to the product of the number of species and the number of years (see also Nott et al. 1995). The background rate in terms of this novel unit, given an average species lifespan of 1 million years, is 1 extinction per million species-years (1 E/MSY). The format is convenient because it expresses the rate of extinction in species and years simultaneously, so neither the number of species nor the number of years must be constant to compare rates.

The application of "species-years" to compare contemporary and deep-time extinction

The magnitude of the difference between contemporary and deep-time extinction had been considered prior to the publications by Pimm and colleagues (1995), but the estimate was either inferred as a function of habitat loss (e.g., Wilson 1988) or was communicated in terms less clearly conveyed than E/MSY. For example, Reid (1992) estimated that the 60 bird and mammal extinctions between the years 1900 and 1950 "greatly exceeds" the background rate of "1 extinction per 100–1000 years" for those taxonomic groups—but with the caveat that broad extrapolation of these numbers to claim an extinction crisis may not be appropriate. Rather, Reid (1992) suggested that it would be more productive to estimate extinction as a function of habitat loss (i.e., species–area relationships). Early estimates of species loss derived from species–area relationships helped bring attention to the accelerating rate of tropical deforestation in the 1970s–1980s, but the uncertainty associated with the indirect measure of species loss was widely recognized as a limitation to conferring more accurate estimates (Burgman et al. 1988, Reid 1992). Predictions of species extinctions based on species–area relationships, such as the loss of 15%–20% of all species between the years 1980 and 2000 (Lovejoy 1979), eventually proved excessive (table 1).

The application of "species-years" to compare contemporary and deep-time extinction (Nott et al. 1995, Pimm et al. 1995) was an appealing methodological advance relative to previous methods used to estimate species loss because

Table 1. Early estimates of species extinction rates as a consequence of habitat destruction.

Estimate	Reference
Extinction of 1 million species by 2000	Myers 1979
Extinction of 1/5 of all species by 2000	Lovejoy 1980
Extinction of 50% of all species by 2000	Ehrlich and Ehrlich 1981
Extinction of 25%–30% of all species by 2000	Myers 1983
Extinction of 20%–25% of species by 2010	Norton 1986
Extinction of 27,000 species a day in the tropics	Wilson 1988

(a) the results were based on *documented* extinctions versus predicted extinctions and (b) the new unit allowed for direct comparison between contemporary and deep-time extinction. The results derived from the application of the method were used to convey that recent extinction rates were 100–1000 times higher than the background rate of 1 E/MSY (Pimm et al. 1995). This finding bolstered the notion that the degree of species loss driven by anthropogenic activities was, as was previously suggested (e.g., Myers 1979, Wilson 1988), causing the Earth's sixth mass extinction (e.g., Leakey and Lewin 1995, Zimmer 1996). The following example clarifies the method.

In a pool of 297 North American freshwater mollusk species, 21 extinctions were recorded during a 100-year time span (Williams et al. 1992). Therefore,

$$\frac{21 \text{ extinctions}}{297 \text{ species} \times 100 \text{ years}} = \frac{x \text{ extinctions}}{1,000,000 \text{ species years}}; x = 707 \text{ E}/\text{MSY}$$

Although this result indicated that the contemporary rate of extinction for these freshwater mollusks, indeed, fell within the range of 100–1000 times greater than the background rate, the measures for the remaining taxonomic groups considered by Pimm and colleagues (1995) were all less than 200 E/MSY. Their conclusion that contemporary extinction could range up to as high as 1000 times greater than the background rate of one E/MSY was derived by averaging their estimates with those previously derived from species–area relationships (e.g., Myers 1979, Lovejoy 1980, Wilson 1988), the latter of which conferred much higher rates of 1000 E/MSY or more (Pimm et al. 1995 figure 2). Subsequent comparisons between contemporary and deep-time extinction based on extrapolating the number of documented extinctions over 100- or 500-year time spans, however, found extinction rates within most taxonomic groups to be less than 100 E/MSY (table 2). Higher rates are commonly encountered when the estimate is extrapolated from a small species pool covering a limited area (e.g., the freshwater mussel example above; island species). Lower rates are commonly encountered when the estimate is extrapolated from species that occupy a broad range (e.g., continental species) or from a longer time interval (e.g., the recent 500 versus 100 years; table 2).

Despite the extrapolation method providing a more direct estimate of global extinction rates than species–area relationships provided, the upper bound of the decades-old estimate that extinction rates are 100–1000 times above background nevertheless was based on species–area relationships (Pimm et al. 1995). Therefore, it would have been logical for a researcher interested in communicating extinction rates based on documented extinction to focus on only the lower bound. By doing so, it would follow logically that, compared with a background rate of one E/MSY, contemporary extinction is 100 times the background rate, but compared with a background rate of 0.1 E/MSY, contemporary extinction is 1000 times the background rate. Those who suggest that the rate of contemporary extinction is now

Table 2. Estimates of extinction rates for various taxonomic groups.

Taxonomic group	Estimate (E/MSY)	Reference
Vertebrates	30	Ceballos et al. 2015
Mammals	39	Ceballos et al. 2015
	72 (1900–2014: 243)	Pimm et al. 2014
	82–702 (island species)	Loehle and Esenbach 2012
	0.89–7.4 (continental species)	
	36–78	Regan et al. 2001
Birds	30	Ceballos et al. 2015
	49 (1900–2014: 132)	Pimm et al. 2014
	98–844 (island species)	Loehle and Esenbach 2012
	0.69-5.9 (continental species)	
	26 (1850–2006: approximately 100)	Pimm 2006
Amphibians	45	Ceballos et al. 2015
	66 (1900–2014: 132)	Pimm et al. 2014
	12	McCollum 2007
Reptiles	16	Ceballos et al. 2015
Freshwater fish of North America	305 (1900–2010)	Burkhead et al. 2012
Freshwater gastropods of North America	954 (1900–2010)	Johnson et al. 2013
Angiosperms of Australia	3.6–7.1	Regan et al. 2001

Note: Contemporary extinctions from 1500 through publication year unless otherwise noted. Background rate of comparison may be slightly higher or lower than 1 extinction per million species-years (E/MSY).

1000–10,000 the background rate (Jivanda 2014, Spotts 2014) are likely unaware that the higher bound of the estimate was based on expected rather than documented extinction.

The extrapolation problem

Broad acceptance that contemporary extinction rates are 1000 times higher than the background rate (i.e., 100 E/MSY) relies on extrapolation of both species and time, and it follows that the relative weights of the size of the species pool and the span of time influence the overarching significance of a 100 E/MSY. For example, a contemporary rate of extinction equal to 100 E/MSY could be derived from 100 extinctions out of 200 species in 5000 years *or* 10,000 extinctions out of one million species in 100 years:

$$\frac{100\,\text{extinctions}}{(200\,\text{species})\,(5000\,\text{years})} = \frac{10,000\,\text{extinctions}}{(1,000,000\,\text{species})\,(100\,\text{years})}$$

The latter might convey a stronger impression than the former of a mass extinction in progress.

Given that approximately 1.9 million (mostly multicellular) contemporary species have been named (Chapman 2009, as used in Pimm et al. 2014), it follows that at a rate of 100 E/MSY, we should have lost 19,000 named species over the last century (i.e., 190 species per year, or one species every 2 days):

$$\frac{19,000\,\text{extinctions}}{(1,900,000\,\text{species})\,(100\,\text{years})} = \frac{100\,\text{extinctions}}{1,000,000\,\text{species} \times \text{years}}$$

However, according to the IUCN (2015), there have been fewer than 1000 documented extinctions since 1500 (834 extinct + 69 extinct in the wild), resulting in a global extinction rate that approximates one E/MSY:

$$\frac{1000\,\text{extinctions}}{(1,900,000\,\text{species})\,(500\,\text{years})} = \frac{1.05\,\text{extinctions}}{1,000,000\,\text{species} \times \text{years}}$$

Considering that most of these extinctions occurred in the last 100 years and that an additional 950 species are suspected of being extinct because they have not been detected for decades, a more reasonable estimate of global extinction would be about 10 E/MSY:

$$\frac{1950\,\text{extinctions}}{(1,900,000\,\text{species})\,(100\,\text{years})} = \frac{10.26\,\text{extinctions}}{1,000,000\,\text{species} \times \text{years}}$$

Adding the approximately 20,000 species presently threatened with extinction (IUCN 2015) in the next 100 years to the 1950 species already lost, the estimate of global extinction still falls below 100 E/MSY:

$$\frac{21,950\,\text{extinctions}}{(1,900,000 \times 200\,\text{years})} = \frac{57.76\,\text{extinctions}}{1,000,000\,\text{species} \times \text{years}}$$

The point is not to suggest that current rates of extinction are not high but rather to demonstrate the difficulty of extrapolating between short and long time spans and/or small and large species pools. We are not the first to recognize the difficulties of comparing contemporary and background

extinction. Barnosky and colleagues (2011) used the highly resolved mammalian record for the most recent 1000 years to estimate E/MSY from documented extinctions spanning 1- to 1000-year time bins and found that shorter intervals yielded higher estimates of mammalian extinction than longer intervals. Similarly, we show that when considering the entirety of documented species on earth, there have been fewer documented extinctions in the last 100 to 500 years than would be expected from the estimate that the average contemporary global extinction rate is 1000 times the background rate. Although many species have become extinct without recognition, this estimate is based on documented extinction and therefore should reasonably align with those numbers.

It has long been understood that the nature of contemporary, anthropogenic extinction is qualitatively different from what we observe for mass extinctions in the fossil record. Whereas the "big five" are known to have affected taxa with broad, often global geographic distributions, anthropogenic activities in recent time have resulted primarily in the extinction of endemic species with narrow distribution (Jablonski 2001). In the same vein, despite incontrovertible consensus that biodiversity is in a state of deepening crisis caused by human activities, it is risky to proclaim that contemporary global extinction rates are 1000 times greater than background when the data suggest otherwise. The future of biodiversity rests on the ability of financial, political, social, environmental, and academic leaders to collectively acknowledge this crisis and then devise sweeping societal shifts that prioritize healthy ecosystems (MEA 2005). In today's politically volatile atmosphere, the development of such a consensus is proving problematic, and it might be prudent to avoid presenting estimates that, perhaps ironically, may one day provide grist for those who seeking to undermine broad conservation efforts.

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