

## Emergence of a sixth mass extinction?

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Recently, two articles were published in leading scientific journals, each calling attention to an emerging mass extinction. The two are complementary in that they reached the same conclusion by using data from contrasting environments. But, the important question in each case is, can the beginning of a mass extinction be confidently predicted from the evidence presented? The two articles are the latest of several publications that have stated the Earth is in the beginning of a great extinction episode that will eventually result in the loss of at about 75% of all living species. The most recent extinction of this magnitude occurred at the close of the Cretaceous about 65 million years ago. The new mass extinction prognosis began about 22 years ago and was based on estimates of species extinction, due to human activities, that had reached thousands of species per year. Although such unsupported estimates soon gave way to more realistic approximations based on documented records, the spectre of a mass extinction has remained. However, I have found evidence that human-caused extinctions have amounted to only about 1.5 species per year for the last 500 years and that these losses have probably been equalled or surpassed by species born (speciation) during that time. Without evidence of substantial net species loss, mass extinction becomes a speculation without substance. The world's greatest conservation problem is not species extinction but population decline to the point where many species exist only as remnants of their former abundance.

ADDITIONAL KEYWORDS: insects – marine species – mass extinction – species gain – species loss – terrestrial vertebrates.

### INTRODUCTION

According to [Ceballos \*et al.\* \(2015\)](#) and [Payne \*et al.\* \(2016\)](#), the Earth is at the beginning of a sixth mass extinction, a catastrophic event whereby about 75% of its species will be lost. The first article utilized evidence from extinctions that had taken place among terrestrial vertebrates, and the second article relied on evidence from marine animals that were under threat but not extinct. The concept of another mass extinction, following a fifth one which took place 65 Mya, was apparently instigated by [Leakey & Lewin's \(1995\)](#) volume entitled *The Sixth Extinction*, in which the authors estimated an annual extinction rate between 17 000 and 100 000 species. The idea that the planet was losing so many species and that the irresponsible use of natural resources by humans was the evident cause, was shocking to many scientists and the general public. The theory of a new mass extinction

was based on numerous books and articles that had described biodiversity loss in terms of thousands of species that were disappearing each year. Considering that the recent history and practice of conservation biology has been strongly influenced by the impression of huge biodiversity losses, it seems appropriate to ask: what is the evidence for losses of such magnitude? If a mass extinction has really started to have its effect, this question is of basic importance to the future of the conservation enterprise and indeed to all of humanity.

Previous to the book by [Leakey & Lewin \(1995\)](#), [Myers \(1979\)](#) had published a volume that predicted the extinction of 1 million species between 1975 and 2000. By the 1990s, numerous books and articles had described biodiversity loss in terms of thousands of species that disappeared each year. Among the most notable were [Gore's \(1992\)](#) book, in which he estimated that 40 000 species were disappearing each year, and [Wilson's \(1992\)](#) prediction of about 27 000 rain forest extinctions per year. Other huge species loss estimations soon followed and eventually led to declarations that the Earth had started to undergo a sixth mass

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extinction. To date, almost all biodiversity loss (extinction) estimates have been made without considering that biodiversity gains (speciation) may have occurred over the same time period. This is the equivalent of calculating one's financial status by looking only at expenditures without taking income into consideration.

The conservation problem is twofold: first, can one find dependable data on the extent of global species loss, say over the past 500 years, attributable to human influence? Second, how many species came into being during that time and how do the losses compare to the gains? In regard to the first question, my recent review (Briggs, 2016) called attention to the fact that almost all species loss estimates were greatly exaggerated, some of them deliberately so in order to attract public attention (Hannah & Phillips, 2004; Ladle & Jepson, 2008). Within the past few years, the exaggerations have tended to become less and some attention has been paid to the extinctions that have been documented by the IUCN Red List (2014). The newer articles attempted to compare contemporary extinction estimates with those found in the geologic record. Pimm *et al.* (1995) introduced a method called the E/MSY (extinctions per million species-years). Using this method, background rates are estimated from fossil extinctions that took place in million year or more time bins. For current rates, the proportion of species extinct in a shorter time (one to a few centuries) is extrapolated to predict what the rate would be over a million years. However, both theory and empirical data indicate that extinction rates will vary markedly depending on the time over which they are measured (Barnosky *et al.*, 2011). More recently, MacLeod (2013) approached the problem of determining background extinction in a more straightforward manner. He utilized average longevities for different taxonomic groups as estimated from the fossil record. Based on these data, he estimated an average longevity for all species with a medium to high fossilization potential. This translated roughly to a historical, background extinction of about one species per year. A 'very rough' rate of about one species per year had also been suggested by May *et al.* (1995).

Although the background rate of one species per year may be a convenient reference, it must be used with caution. There is a background extinction gradient over geological time (MacLeod, 2013) so the rate will vary according to the interval selected. Upward through the Cenozoic, the rate gradually became smaller and less variable. For the Pleistocene epoch, the extinction rate was less than any other stage in the geological record (MacLeod, 2013). This became evident despite the well-publicized megafaunal extinctions on the continents and the slaughter of endemic, oceanic island species by the early explorers. For the purpose

of comparing background extinction rates with those caused by humans, the Pleistocene fauna is the best known and most similar to that of the present day. How low was the rate for the past 2.5 Myr? Using the graph published by MacLeod (2013, p. 47), I determined that a rate of about 0.5 species per year would be appropriate (Briggs, 2016). This reduced background rate removes some of the incongruence that occurred when short-term extinctions were compared to long-term rates in the geological record (Regan *et al.*, 2001).

## TERRESTRIAL ENVIRONMENT

If we accept a Pleistocene background extinction rate of about 0.5 species per year, it can then be used for comparison to apparent human-caused extinctions. For the past 500 years, this rate means that about 250 species became extinct due to non-human causes. According to the IUCN Red List (2014), 338 terrestrial vertebrate species have become extinct since the year 1500. If we subtract the Pleistocene background rate for about the same time (338 minus 250 = 88), we have an approximate figure for human-caused extinctions in that group which amounts to about 0.18 species per year. How can the apparent loss of 88 species over the past 500 years be interpreted to show the beginnings of a mass extinction? The answer, as illustrated by the papers of Pimm *et al.* (1995), Barnosky *et al.* (2011), De Vos *et al.* (2014), Pimm *et al.* (2014) and Ceballos *et al.* (2015), is to use the E/MSY, a fashionable but questionable statistical procedure (Briggs, 2016). For example, De Vos *et al.* (2014) concluded that human-caused extinction rates are 1000 times higher than natural background rates and future extinctions were likely to be 10 000 times higher. When sensational estimates like these appear in reputable journals, they are repeated by other media and public alarm is caused by results that are equivocal at best.

I found that Ceballos *et al.* (2015) offered little evidence that a mass extinction can be predicted from recent extinctions among vertebrate animals (Briggs, 2016). However, further information that pertains to terrestrial vertebrates is available. The times and locations of mammal and bird extinctions for the past 500 years have been documented by the IUCN Red List and a bird extinction list maintained at the American Museum in New York. The lists were analyzed by Loehle & Eschenbach (2012) who found that more than 95% of all the extinctions had taken place on oceanic islands. In their analysis, the authors considered Australia (a physiographic continent) to have functioned as a biogeographic island during the latter half of the Cenozoic. If we use the mammals and birds as surrogates for all the vertebrates, extinctions

on the world's continents must have been very few. For instance, only three of the 61 mammal extinctions and only six of the 128 bird extinctions took place on continents. The loss of isolated island species, while regrettable, had little or no effect on continental ecology and evolution.

Another reason to avoid using vertebrate animals to predict global events is that the vertebrates comprise a very small fraction of the fauna that inhabits the terrestrial Earth. Land vertebrates (mammals, birds, reptiles, amphibians) represent a total diversity of only about 25 000 species (Jenkins, Pimm & Joppa, 2013). In comparison, some 90% of the terrestrial world's fauna are insects and they powerfully influence the overall state of biodiversity. A recent review (Stork *et al.*, 2015) has indicated a mean of 5.5 million for all insects (range 2.6–7.8 million). Four insect groups (butterflies, tiger beetles, dragonflies, damselflies) have been of special interest to amateur and professional entomologists. Each group is well known, it has a worldwide distribution and its species extinction during the past 500 years is documented. Among these four groups, 25 260 species have been evaluated, and only three were found to have become extinct (Briggs, 2016). This result seems consistent with the work of Coope (2004) who noted a virtual absence of insect extinctions during the Pleistocene. By using the foregoing groups as surrogates for insects as a whole, and employing the ratio of 3 to 25 260, we can conclude that about 653 insect species may have been lost. According to the IUCN Red List, 66 insect extinctions have taken place over the past 500 years, mainly on oceanic islands. However, in this case the IUCN figure is deficient because so few insects have been evaluated.

We can now observe that, during the past 500 years, the Earth has lost ~1009 species from three faunal groups: 338 terrestrial vertebrates (documented), 653 insects (based on surrogates), and 18 marine species (documented, see following section on marine environment). The expected background loss of 250 species (0.5 species per year), when subtracted from the 1009 total, leaves 759 extinctions or a rate of about 1.5 species per year, probably attributable to human-caused effects. For the terrestrial world only (including oceanic islands), the figures on insects and the vertebrates minus the background loss, yield 741 extinctions, also about 1.5 species per year. One may compare these realistic losses to the previous estimates of hundreds or thousands of extinctions per year as claimed in some of the scientific literature, and repeated by conservation societies, messages on the internet and reports by the print media.

Although it has been known since Darwin's time that speciation, as well as extinction, are continuous processes, the papers by Ceballos *et al.* (2015) and

Payne *et al.* (2016) and almost all of their predecessors have ignored the gains and decried the losses. An objective evaluation of global biodiversity over time needs to include data on both loss and gain. I published evidence that global biodiversity gain was concurrent with declining population sizes (Briggs, 2014), and I cited several cases whereby molecular research had revealed rapid adaptive divergence resulting in ecological speciation. A new study of generic richness trends in Phanerozoic bivalves (Mondal & Harries, 2015) indicated a steep increase that began in the early Triassic and continued through the Cenozoic. Their finding is significant for our purposes because genus-level alpha and beta diversity measures are highly correlated with species-level data (Flessa & Jablonski, 1995). The absence of any large-scale extinction during the Pleistocene suggests that the marine, and probably the global species diversity, is still increasing (MacLeod, 2013).

There are also contemporary data that illustrate net gains in biodiversity. In the past few centuries, terrestrial species diversity has increased on oceanic islands and in many continental regions; in addition, no general decreases in diversity have been known to occur at regional scales (Sax & Gaines, 2008). Human introductions for agricultural and ornamental purposes have produced substantial gains in continental plant diversity (Ellis, Antill & Kreft, 2012). De Vos *et al.* (2014), who examined a series of individual phylogenies, found that average extinction rates were less than average diversification rates. An assemblage time series study (Dornelas *et al.*, 2014) gathered data on 35 613 species from 100 individual series. The data were extracted from marine, freshwater, and terrestrial biomes from the poles to the tropics. Most of the time series were concentrated within the past 40 years. The results did not indicate a negative trend in species richness. For these reasons, and in view of minimal losses, I conclude that, over the past 500 years, speciation has continued and that biodiversity gain by this means may have equalled or even surpassed the losses.

## MARINE ENVIRONMENT

The new publication by Payne *et al.* (2016) recognizes an emerging mass extinction in the oceans. The authors point to the fact that terrestrial biodiversity is declining rapidly (with reference to Ceballos *et al.*, 2015) and suggest that the oceans are poised to follow suit. They observed that this sixth mass extinction may approach or exceed the magnitude of the five major extinctions of the past 550 million years, if current loss rates persist. However, there is no evidence that current marine losses are more than one species per year, if that much.

Therefore, the danger of an emerging mass extinction in the ocean is no more real than it is on land. So far, only 18 marine species (Briggs, 2016), compared to a total of about 2.21 million eukaryotic species (Mora *et al.*, 2011), are recorded to have become extinct during the past 12 000 years. Of course, undetected extinctions have probably been taking place in the sea, but speciation has also been active. A common source of increase is from species that continuously originate in high diversity centres. They are known to spread out and invade peripheral communities and therefore increase or maintain outlying diversity as part of a worldwide, dynamic system (Briggs & Bowen, 2013).

Aside from its emphasis on an emerging mass extinction, which is unsupported by data, the paper by Payne *et al.* (2016) makes a useful contribution to marine ecology and management of ocean resources. Because so few marine extinctions have been recorded and none within the past 30 years (Dulvy, Pinnegar & Reynolds, 2009), the authors relied on the distribution of threat as defined by the IUCN. There is a difficulty in using threat as equivalent to imminent extinction. Biologists often classify rare species with small populations as threatened even though they may not actually be at risk. Even so, Payne *et al.* (2016) made comparisons between the modern threatened fauna (fishes and molluscs) and fossil extinctions. The comparisons were made at the generic level because many extant genera are also known as fossils. Fossil extinction intensity was calculated as the percentage of genera that did not survive from one time interval to the next. The primary conclusion of the study was that extinction threat to living genera was most strongly associated with body size, the larger the size the greater the threat, but the fossil series did not indicate an extinction/size relationship. The authors also concluded that their results illustrated the 'unique selectivity of the emerging mass extinction'. Selection for larger size by humans who harvest from animal populations does have evolutionary consequences, but there are no indications that this kind of selection causes extinctions that would foretell a mass extinction.

Aside from the reference to a mass extinction, the primary conclusion is important because body size among predatory species had been recognized by fishery biologists as a critical factor in management application. It has been found that the presence of large-size predators has importance beyond the prevention of trophic cascades. Research by Berkeley, Chapman & Sogard (2004) has shown that larval viability varies with size, and larvae produced by larger (and older) females have increased survival. Selective harvesting of larger individuals leads to an exponential reduction in the number of larvae produced, a shortening of the reproductive season, a decrease in

larval viability and a selection for reproduction at a younger age. In response to these reproductive and genetic effects, the body size of fishes has consistently declined under fishing pressure, even in situations where total diversity (species richness) has remained high (Birkeland & Dayton, 2005). Size-selective fishing may impact ecosystems more rapidly and more profoundly than declines in species richness (Fisher, Frank & Leggett, 2010). The finding by Payne *et al.* (2016) provides more evidence that predator size is an important evolutionary factor in ecology and fishery management.

### CONSERVATION IMPLICATION

By now, it should be evident that the world's greatest conservation problem is not huge annual extinctions and the beginning of a mass extinction. On both land and sea, species diversity (richness) has remained high, but the critical conservation problem is population decline. Many formerly abundant populations have been reduced to small remnants by overexploitation, loss of habitat and various kinds of pollution. As populations become smaller, they lose genetic diversity, are denied the protection of large population size (Allee effect) and tend to become inbred. Unless they are protected to the extent that their populations can rebound, such species are vulnerable to extinction and are often considered to comprise an extinction debt that will be paid when they can no longer cope with environmental change. Population declines over time have been reported by Butchart *et al.* (2010) and by the Living Planet Index (2014). The latter has been supported by the World Wildlife Fund, Zoological Society of London, Global Footprint Network and the Water Footprint Network. The Index provided information on the status of 10 380 terrestrial vertebrate populations belonging to 3038 species. On average, population sizes had undergone a 52% decline between 1970 and 2010. The greatest decline was in freshwaters where the loss was 76%.

For the marine environment, a Living Blue Planet Report (2015) has been published by the World Wildlife Fund and the Zoological Society of London. This report provided information on 7829 populations from 1243 species of birds, mammals, reptiles and fishes. An overall population decline of 49% was shown to have taken place between 1970 and 2012. For the same time, an index of 17 species of large pelagic fishes indicated a 74% decline, 2501 reef fish populations demonstrated a 34% decline and 350 fish populations in seagrass habitats suffered a more than 70% drop. Many formerly abundant food fishes have undergone population collapses, meaning that about 90% of their original

populations have been lost, primarily to overfishing. They continue to exist as remnant populations that so far have not been able to recover (Roberts, 2007).

### CONCLUDING REMARKS

Two recent articles published in leading scientific journals have once again called attention to an emerging mass extinction. Although both articles referred to extinction in a global sense, each concentrated on a different environment. The first article attempted to demonstrate the beginning of a great extinction by exaggerating the relatively small numbers of terrestrial vertebrate species that became extinct within the past 500 years, and neglecting the fact that most of the extinctions had taken place on oceanic islands. The second article recognized the start of an oceanic mass extinction on the basis of some marine species that were under threat, and were demonstrating a reduction in body size. Whether or not threat status, as determined by the IUCN Red List (2014), or body size reduction (or both) indicate imminent extinction is problematic. Documented marine extinctions have been few (18) and none has occurred within the past 30 years. In order to demonstrate the beginning of a mass extinction, there needs to be evidence that the global biodiversity is decreasing due to a rise of extinctions above the rate of speciation. Instead, we have indications that the extinction rate has been very low and may have been matched or exceeded by species coming into existence over the same time period. The idea that another mass extinction is emerging is based on speculation derived from unsupported estimations of large extinctions, and where the possibility of concurrent species gain was not considered. The species that have been reduced to remnant populations constitute our greatest conservation problem. Many can still be rescued if there is sufficient public interest in doing so.

The best way to keep track of biodiversity loss in the terrestrial world is to continue monitoring the well-known groups of insects and use them as surrogates to estimate the overall extinction rate. The number of recorded extinctions in the marine environment seems suspiciously low, which indicates the need for long-term monitoring of familiar groups such as the fishes and the corals. The low Pleistocene extinction rate apparently continued upward through the past 500 years, and if species were created at more than the extinction rate, the net global biodiversity must have continued to rise. The immediate threat to this scenario is climate change. The global temperature increase due to atmospheric pollution is likely to result in the extinction of numerous species, especially small populations that are already at risk.

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### REFERENCES

- Barnosky AD, Matzke N, Tomiya S, Wogan GO, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC, Mersey B, Ferrer EA. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* **471**: 51–57.
- Berkeley SA, Chapman C, Sogard SM. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* **85**: 1258–1264.
- Birkeland C, Dayton PK. 2005. The importance in fishery management of leaving the big ones. *Trends in Ecology & Evolution* **20**: 356–358.
- Briggs JC. 2014. Global biodiversity gain is concurrent with declining population sizes. *Biodiversity Journal* **5**: 447–452.
- Briggs JC. 2016. Global biodiversity loss: exaggerated versus realistic estimates. *Environmental Skeptics and Critics* **5**: 20–27.
- Briggs JC, Bowen BW. 2013. Marine shelf habitat: biogeography and evolution. *Journal of Biogeography* **40**: 1033–1035.
- Butchart SHM, Walpole B, Collen B, van Strien A, Scharlemann JP, Almond RE, Baillie JE, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Hernández Morcillo M, Oldfield TE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié JC, Watson R. 2010. Global biodiversity: indicators of recent declines. *Science* **328**: 1164–1168.
- Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. *Science Advances* **1**: e1400253.
- Coope GR. 2004. Several million years of stability among insect species because of, or in spite of, ice age climatic instability? *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **359**: 209–214; discussion 214.
- De Vos JM, Joppa LN, Gittleman JL, Stephens PR, Pimm SL. 2014. Estimating the normal background rate of species extinction. *Conservation Biology* **29**: 452–462.
- Dornelas M, Gotelli NJ, McGill B, Shimadzu H, Moyes F, Sievers C, Magurran AE. 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science* **344**: 296–299.
- Dulvy NK, Pinnegar JK, Reynolds JD. 2009. Holocene extinctions in the sea. In: Turvey ST, ed. *Holocene extinctions*. Oxford: Oxford University Press, 129–150.
- Ellis EC, Antill EC, Kreft H. 2012. All is not loss: plant biodiversity in the anthropocene. *PLoS ONE* **7**: e30535.

- Fisher JAD, Frank KT, Leggitt WC. 2010.** Global variation in marine fish body size and its role in biodiversity ecosystem functioning. *Marine Ecology Progress Series* **405**: 1–13.
- Flessa KW, Jablonski D. 1995.** Biogeography of Recent bivalve molluscs and its implications for paleobiogeography and the geography of extinction: a progress report. *Historical Biology* **10**: 25–47.
- Gore A. 1992.** *Earth in the balance*. New York: Rodale Books.
- Hannah L, Phillips B. 2004.** Extinction-risk coverage is worth inaccuracies. *Nature* **430**: 141.
- IUCN Red List. 2014.** Switzerland: Gland. Available at: [www.iucnredlist.org](http://www.iucnredlist.org) (accessed October 2016).
- Jenkins CN, Pimm SL, Joppa LN. 2013.** Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Science of the United States of America* **110**: E2602–E2610.
- Ladle RJ, Jepson P. 2008.** Toward a biocultural theory of avoided extinction. *Conservation Letters* **1**: 111–118.
- Leakey R, Lewin R. 1995.** *The sixth extinction*. New York: Doubleday.
- Living Blue Planet Index. 2015.** London: World Wildlife Fund. Available at: [www.livingblueplanetindex.org](http://www.livingblueplanetindex.org) (accessed October 2016).
- Living Planet Index. 2014.** London: World Wildlife Fund. Available at: [www.livingplanetindex.org](http://www.livingplanetindex.org) (accessed October 2016).
- Loehle C, Eschenbach W. 2012.** Historic bird and mammal extinction: rates and causes. *Diversity and Distribution* **18**: 84–91.
- MacLeod N. 2013.** *The great extinctions*. Buffalo: Firefly Books.
- May RM, Lawton JH, Stork NE. 1995.** Assessing extinction rates. In: Lawton JH, May RM, eds. *Extinction rates*. Oxford: Oxford University Press, 1–24.
- Mondal S, Harries PJ. 2015.** The effect of taxonomic corrections on Phanerozoic generic richness trends in marine bivalves with a discussion on the clade's overall history. *Paleobiology* **42**: 157–171.
- Mora C, Tittensor DP, Adl S, Simpson AGB, Worm B. 2011.** How many species are there on the Earth and in the ocean? *PLoS Biology* **9**: e21001127.
- Myers N. 1979.** *The sinking ark: a new look at the problem of disappearing species*. New York: Pergamon Press.
- Payne JL, Bush AM, Heim NA, Knope ML, McCauley DJ. 2016.** Ecological selectivity of the emerging mass extinction in the oceans. *Science* **353**: 1284–1286.
- Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JL. 2014.** The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**: 1246752.
- Pimm SL, Russell GJ, Gittleman JL, Brooks TM. 1995.** The future of biodiversity. *Science* **269**: 347–350.
- Regan HM, Lupia R, Drinnan AN, Burgman MA. 2001.** The currency and tempo of extinction. *The American Naturalist* **157**: 1–10.
- Roberts C. 2007.** *The unnatural history of the sea*. Washington: Island Press.
- Sax DF, Gaines SD. 2008.** Species invasions and extinctions: the future of native biodiversity on islands. *Proceedings of the National Academy of Science of the United States of America* **105**: 11490–11497.
- Stork NE, McBroom J, Gely C, Hamilton AJ. 2015.** New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *Proceedings of the National Academy of Science of the United States of America* **112**: 7519–7523.
- Wilson EO. 1992.** *The diversity of life*. Cambridge: Harvard University Press.