



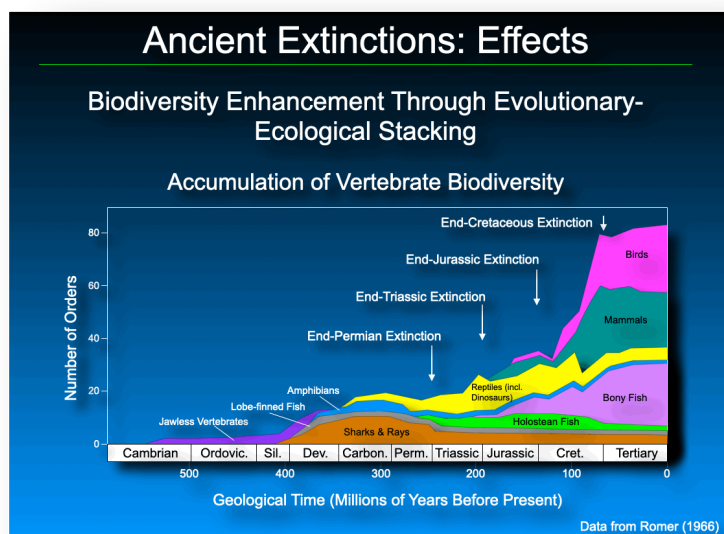
Responses to Questions on Extinction

On 13 November 2013 I received a request from a free-lance journalist for responses to a series of questions regarding the character and potential causes of extinction events in the geological past and what implications such events might have for our understanding of the current biodiversity crisis. This constituted background information the journalist was collecting for a commissioned article he was writing for a major US news magazine. The questions, along with my responses, are provided below.

1. If extinction events are necessary for subsequent evolutionarily radiation, are we thinking about them the wrong way when we assume them to be catastrophes? That is to say, of course to live through such an event would be catastrophic, much as dying is, but just as dying is necessary for life, is it fair to say that extinction is necessary for evolution? At the same time, I want to be very careful here, because I don't want to be suggesting we take a blithe approach to biodiversity loss.

Extinction is not necessary for evolution except in the sense of anagenetic evolution – when an evolving population changes its genotype or phenotype so much it either (i.) becomes impractical to continue referring to it using the same name or (ii.) there is a (hypothetical) suspicion that members of the evolved population at time₂ could not have interbred successfully with members of the same population at time₁. But this is more a case of taxonomic bookkeeping than a evolutionary phenomenon.

What extinction is necessary for, however, is taxon richness increase. Extinction removes the advantages of ecological incumbency from established clades, and so opens up new opportunities for clades whose diversification has been held back by the incumbents (who were able to take advantage of a previous episode of rapid diversification, often in the wake of an extinction event). This can happen across all ecological levels and across all extinction events, not just the so-called “mass extinction” events. The environmental changes that drive extinction events also change the character of selection. This unpredictable change in selection regimes can, in turn, open up new opportunities for diversification through adaptation. Through these mechanisms extinction has increased the overall range of diversity in the biosphere over time; a phenomenon known as evolutionary stacking. This happens because, after the Cambrian explosion, it seems to have been quite rare for older higher taxonomic categories (= major body plans) to have disappeared entirely whereas newer taxonomic categories have appeared and diversified quite regularly throughout the Phanerozoic. Here's an older diagram that I still use in my lectures to illustrate evolutionary stacking.



We still have modern members of Sepkoski's Cambrian Evolutionary Fauna with us despite all the extinction and diversification that has taken place since the Cambrian.

All these factors underscore the creative role extinction has played in promoting biodiversity. If there had been no extinction over the course of earth history our planet would be home to a far less diverse array of species than it is.

2. However damaging anthropogenic global warming and biodiversity loss (and other environmental problems such as microplastic pollution, nitrogen pollution, etc) may be to ecosystem services upon which humans depend, to the rest of nature, all of these phenomena are just the latest evolutionary selection pressures. Upon realizing this: What do you think we humans should do? My own feeling would be that we should still attempt to reverse the damage to these ecosystem services (thus act to mitigate climate change, biodiversity loss, etc), but for our own sake, not because these new selection pressures are “bad” for the rest of nature. For some of these issues, a recognition that we are acting in our own interest, not that of the rest of nature, wouldn’t mean abandonment of environmental policies and behaviours with respect to arresting these problems. But for a few of them, it would: for example, halting the advance of ‘invasive species’ would now only be a policy necessary where it undermined ecosystem services, not everywhere on the basis that there was some pristine nature that invasives are disturbing. What do you think about this? Do you think my line of argumentation there basically makes sense?

This has always seemed to me to involve the “What is to be done?” side of the extinction issue in which the most prominent points-of-view involve economic, cultural and moral considerations. First, it seems to me that many on the conservation side appear to think extinction is, in some sense, “unnatural” and must be eradicated. This is a patently absurd notion. Other than speciation, extinction is likely the most common evolutionary process on Earth. We could not “stop” all extinction even if we wanted to and, for the reasons I’ve given above, we should not want to. We are a species, just like any other species on the planet and our activities cannot avoid putting pressure on other species. It is true that, in many cases, our rampant population growth and careless economic activities have put undue pressure on other species as well as having already driven a comparatively small number to extinction. That is lamentable and should be lamented. But, as with all things in life, the solution to this problem involves finding a justifiable balance between the damage human populations do and the mitigation/conservation measures they are able to enact. Generally speaking, I believe we (humans) should strive to reduce our extinction footprint to the point where it heads back down to pre-industrialization levels. However, I’m not so naïve to think we will ever get back to pre-industrialization levels unless/until human populations agree either to de-industrialize en mass or sharply reduce our collective population size. I see no social or political consensus for either of these alternatives.

In terms of convincing humans to forego some of their industry-provided comforts, some argue that we need either to prioritize conservation of the services natural processes deliver to human populations or develop either technological alternatives for, or ways to prop-up, those services. But this school of thought seems to presume we know how the natural world delivers these services to human populations. Aside from blatantly obvious (e.g., don’t allow water companies to pollute all the watercourses in your country, such as the UK has) we do not possess this knowledge. This lack of understanding makes it difficult to know how or when any interventions we might be able to manage would be effective, much less successful. However, our lack in this area does present a strong case for funding ongoing research. Until we know more about how nature delivers these services I’ve long believed the best thing we can do is take as much land as possible out of development/agricultural-centered private or public ownership and set it aside to let it recover. While there have been some movements in this direction (e.g., national parks program, Nature Conservancy), I see no serious national consensus for this alternative.

The cultural arguments are, for me the most complex and, possibly, the most likely to make a big impact in the medium term. As Ursula Heiss has argued in her 2016 book *Imagining Extinctions*, understanding the cultural narratives that underpin how people approach the extinction question is absolutely indispensable in the design of effective advocacy programs. Cultural issues shape how all of us regard and react to specific issues, including various extinction-related controversies — even among scientists, lawyers, politicians and economists. The sooner we understand this the sooner we’ll be able to make the arguments that need to be made in terms various socio-economic and cultural groups can understand.

Then there’s the moral dimension. For me, this is an aspect of culture, but it’s often broken out as a separate consideration. On one hand there seems to be little argument that it is immoral to keep ignoring the biodiversity crisis and/or pretending species numbers will stabilize in line with some new techno-industrial normal. On the other, moral arguments against taking any serious steps to do anything other than preserve the status quo (e.g., such steps are claimed to be too authoritarian, too costly, too bad for business, too likely to increase economic disparity, too likely to effect the worse off in society detrimentally, too likely to be unpopular, too urban-centric) are made with equal fervor and are more focused on the wants/needs/desires particular constituent groups. Rather than forcing interest groups to come together in the common purpose of biodiversity conservation, the enormity of the challenge is driving them apart into trans-national philosophical tribes.

I'm afraid I don't believe any one line of argument will be more "correct" or more effective in turning this situation around. Different people respond to different motivations. Increasingly though, I'm struck by the way western democracies have lost the trust of their national publics, a trend that has only been exacerbated by the distracting and divisive content promoted by social media. Perhaps it's appropriate to think of the fact that we have not been able to come to a consensus on biodiversity loss not as a problem that has some efficient techno-economic-political solution, but rather as a symptom of something far deeper that's gone very badly wrong in the dominant (western) culture. Progress on biodiversity conservation, as well as many other issues, might not be possible unless/until this deeper issue can be addressed.

3. Is my above argument, that novel anthropogenic selection pressures are just the latest in a long line of novel selection pressures, both biotic and abiotic (from the novelty of lignin that allowed vascular plants to conquer land and then drive the late Devonian mass extinction(s) to large igneous provinces and a bolide impact that prompted other Big Five extinctions), actually correct? Or are human activities so extreme that they stand outside this series of selection pressures, and are geologically unique in scale?

In a sense, the uniqueness – or not – of the environmental changes driving the present biodiversity crisis is unknowable. Human populations were not involved in previous episodes of "mass extinction". But our actions are affecting species through changes in the environment and there is copious evidence changes as large as the ones humans are now causing – and larger, much larger – have happened before in earth history. In some cases these changes are associated with large extinction events, but in many other cases they are not. Take the Pleistocene. Half the northern hemisphere was covered by ice, some of it kilometers thick. On a proportionate basis it's one of the smallest extinction events. Quite large bolide impacts have occurred repeatedly during the Phanerozoic. Most are not associated with any extinction events (local or global) whatsoever, and the only one that is happened at a time of dramatic sea-level lowstand and a quite a large LIP eruptive event. The fact that both of these environmental events are known to be associated with other large extinction events, doesn't strike me as an irrelevant coincidence. especially since there are many other instances where their singular presence in the environment is not associated with high extinction levels. BTW, since there is little evidence the end-Ordovician event was associated with an LIP event, I would dispute your assertion that the LIP-"mass extinction" score is 5/5. Anyway, what about all those other LIP events that aren't associated with any extinction activity at all so far as we can tell?

I think the larger story here lies in human psychology and/or socialization. We seem to be programmed either sociobiologically or culturally to look for a single cause for any substantial misfortune suffered by any individual or group. If there's a crime there's a perpetrator. If a company fails there's an unprincipled competitor who's to blame. If some group is being taken unfair advantage of there's an oppressor. If a nation feels hard done by there's an external enemy. It often seems (to me) that, as a species, we are uncomfortable (perhaps unable to deal) with contingent complexity. Some one thing always has to be "responsible" for our personal and collective misfortunes and we project that habit of mind onto everything we do and see, irrespective of the evidence to hand and/or any source of uncertainty. The guilty party has to be identified. Then the books can be closed. In my personal and professional experience life's not like that. Pretending it's all a matter of singular action-reaction is a caricature of real life, for individual, populations, and species. It's kind of a narrative we tell each other so we can try to make sense of the world. But that doesn't mean these stories are accurate.

This is not to say we will always be at the mercy of our prejudices. Science, when practiced correctly, is the best means by which we can overcome them. But scientists are a subject to confirmation bias as much anyone else (see Donald Mair's 2012 book *What's so Good About Biodiversity*). In conversations such as this a quote made – or at least attributed to – Max Planck often comes to mind, to wit "Science progresses one funeral at a time."

To me extinction events occur whenever factors forcing irregular environmental change come into the frame. When single factors are operative the extinction intensity is local and small. When multiple factors operating at low levels are come along middle-sized regional extinctions result. And when multiple factors operating at high levels align the result can be devastating. But the key to understanding extinction doesn't lie in the factors themselves, it lies in their coincidence. From my point-of-view, human activities are just another irregular environmental-change factor, no more or less important in and of itself than any other such factor. In order for our activities to cause a large extinction event we will need to sustain our current level of intense disruption over an ecologically long time scale. The jury is out as to whether human populations will be able to maintain its present level of environmentally disruptive intensity over a sufficient time scale to cause the extinction of large numbers of species. Current estimates suggest that could take anywhere from 200 to 2,000 years at present levels. A lot can change in 100 years, much less 2,000. In this simple fact I find hope.

Coming back to the question of contingency, over the last 100 years we have weakened the biosphere

substantially. As a result, its resilience is lower than it might have been. In a sense our world now occupies a vulnerable position, prone to respond extremely to any other external shocks that may come along. Today the news from Iceland is that volcanologists predict there will be a substantial eruption there shortly. What if that eruption is unexpectedly large? Eventually one will come along that is.

4. What do you think of Peter Ward's Medea Hypothesis, that life is actually responsible for most of the mass extinction events (thus the LIPs may have kicked things off, but they also drove the microbial activity that produced the anoxia and euxinia that were so devastating for many mass extinctions)? I get where he's going with this, but this seems to equate ultimate and proximate causes.

I think I've covered this partially above. There are a large number of factors that can put selection pressure on populations and correlations between these factors exist. In his example I suppose Peter is arguing that an LIP eruption could inject greenhouse gases into the atmosphere, which could raise global average temperatures, which could raise sea surface temperatures, which could stimulate phytoplankton productivity, which could then lead to anoxia/euxinia. But this is a pretty long and fraught chain of events, subject to modification by all sorts of other factors Peter is not mentioning. To make this case Peter would need to have positive and independent evidence that each stage was operative as his theory predicts and that no other factors were involved (e.g., sluggish marine circulation, preponderance of shallow ocean basins). Then he would need to show that all, or the majority, of large extinction events exhibit the a similar chain of events that involve biotic feedbacks. Does he have such evidence? I'm unaware of it.

It's easy to spin scenarios like this and, in the absence of evidence one way or the other, no way to prove they could not have caused any particular extinction event. But science doesn't regard the impossibility of proving a negative as strong evidence supporting any particular scenario. To me Peter's is just another attempt to hang a complex planet-wide event on a single cause, with the – not even novel – tweak of implying nature is to blame for its own demise across extinction intervals. Again, what about all those LIP events that are not associated with anoxia/euxinia events?

In evolutionary morphology research we call these “just so” stories (with apologies to Rudyard Kipling). I don't think just so stories work as explanations for extinction events. Besides I think any attempt to single out one cause as being the “true” culprit is to miss the take-home message of over 40 years of intense extinction-cause research.

5. In your textbook on The Great Extinctions, you write: “The Big Five mass extinctions [cannot] be separated from background extinction events by a noticeable discontinuity in extinction intensity.” Would it be correct for me to say that the major mass extinction events and the background extinction rate are not discrete phenomena but instead one continuous phenomenon? Or put another way: there is no real sharp distinction, only continuity, between mass extinction and background extinction.

The way I describe this is to invoke the metaphor of a spectrum. When you rearrange proportional extinction-intensity data you see a continuous spectrum of intensities with no break that would allow anyone to distinguish large (= “mass”) events from background events. Raup and Sepkoski's distinction relies on a descriptive statistical argument that (i.) requires selective data culling (elimination of the Cambrian events), (ii.) assumes the significance level used to make the separation has some sort of profound biological significance (used a different significance level, you get a different answer) and (iii.) wasn't even applied consistently to the data they analysed (the Tithonian event was above their background/mass-extinction cut-off, but was not identified as a mass extinction event; same for the Eifelian data point, which was not included in the suite of Late Devonian mass-extinction stages). It's clear to me what they were actually doing was trying to reproduce Normal Newell's speculation about the existence of mass extinctions in the Phanerozoic in a way that confirmed, and perhaps extended, his identifications. When Dave and Jack found a way to do that in the analysis of Jack's data, they stopped looking. We now know that the internal structure of major Phanerozoic extinction events is way more complex than Jack's data, or Dave and Jack's analysis, implied (see Fan et al., 2020). If you're allowed to pick and choose which data you include, and which results you pay attention to, you can make up any story you want.

To me the story the extinction-intensity spectrum tells is that there is no substantive difference between the causes of background and the causes of mass extinction events. These events are caused by the same suite of events just operating in different combinations and levels of intensity at different points in earth history.

6. How do you feel in general about the current discourse about extinction and mass extinction? Do you feel that the public, politicians and environmental campaigners are broadly getting it right, or would you offer some corrections to the discourse?

I think I've made a variety of different points related to this issue in my responses above. The public is confused and, with the exception of the young, doesn't much care one way or the other. Politicians are reluctant to be honest with the public regarding what we know how to do and what we don't, what societal changes the achievement of particular targets will require, how much it's all going to cost, etc. (= they know what they need to do, they just don't know how to do it and still get elected). Some environmental campaigners seem bent on dragging human populations back into modes of living the public at large is not willing to accept (a socio-political agenda that has nothing to do with conserving biodiversity per se), at least at present, while others among this group seem just to be along for the ride capitalizing on the opportunity to thumb their noses at their elders and attract media attention to themselves. As for the media, it seems only to be just interested in endlessly stoking arguments among various advocacy groups, as if endlessly arguing about what should be done has ever solved any problem.

7. What do you feel are the most important unanswered questions within extinction studies?

Extinction researchers need to get past their preference for finding a single cause responsible for a particular, some, or all large extinction events and ignoring the study of extinction as a comprehensive topic. It also needs to learn to ignore the media. The media's biased involvement in extinction research has, if anything, made it harder to make genuine progress than otherwise would have been the case. More data need to be collected from all extinction events (as well as inter-extinction event intervals) and brought into a consistent taxonomic/phylogenetic framework (see the work done by Gerta Keller, my former colleague at Princeton, for an example). At the moment there are far too many people thinking the way forward for paleontological extinction research is to endlessly analyze the same (bad) data.

More generally though, I can do no better than repeat what I've referred to as "Raup's Dictum"

"There is no way of assessing cause and effect except to look for patterns of coincidence—and this requires multiple examinations of each cause-and-effect pair. If all extinction events are different the deciphering of any one of them will be next to impossible." David Raup, *Bad Genes or Bad Luck*, p. 151.

Raup's challenge to us cannot be met by making biased interpretations based on incomplete data collected only from sediments proximate to single extinction event horizons and then simply announcing that you've "solved" the riddle of extinction. Moreover, any credible explanation for any single extinction event needs to be a bit more sophisticated than, "Well, you see, this <insert whatever single cause you like> happened and, as a result, everything died ... except the things that didn't die."

Norman MacLeod

School of Earth Sciences and Engineering
Nanjing University
Nanjing, China
210023

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