BRIDGING THE GAP BETWEEN THE FOSSIL RECORD AND THE MODERN DAY

Interview with Professor Seth Finnegan

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Seth Finnegan *is an Associate Professor in the Department of Integrative Biology at UC Berkeley and a curator at the University of California Museum of Paleontology. He studies marine paleobiology and processes which shape marine ecosystems over time. We asked Dr. Finnegan about his favorite mass extinction event at the end of the Ordovician period (488 to 443 million years ago) and about the relationships that we can draw between past extinction patterns and the current anthropogenically caused extinction.*

Professor Seth Finnegan.

BSJ: What interests you specifically in the late Ordovician period?

SF: The Ordovician is a very interesting period of time for a number of reasons. Most of the major animal groups that still exist today—mollusks, arthropods, etc.—make their first appearance during the Cambrian explosion. However, the majority of these groups are not particularly diverse. In the Ordovician period, which follows the Cambrian explosion, a number of these groups begin to diversify. By the end of the Ordovician period, most of the groups that ecologically dominate marine ecosystems for the next two hundred million years are in place. Then many members of these groups go extinct in a very unusual, rapid mass extinction event. Ultimately, the Ordovician an interesting period because it contains both a major diversification and a mass extinction event.

BSJ: What are rhynchonelliform brachiopods, and why did you choose to focus on them in your research?

SF: Fig. 1 shows some Ordovician fossils from our collections at the UC Berkeley Museum of Paleontology. Fig. 2 is a slab of fossils from my own field work in Quebec. All of these little fingernail-shaped things are rhynchonelliform brachiopods. In the Paleozoic period that ended with the Permian-Triassic mass extinction 250 million years ago, they were extremely common and diverse parts of marine ecosystems and the marine fossil record. If you want to study geographic patterns in the fossil record, you need a group with very high preservation potential, meaning every individual has a relatively high likelihood of ending up as a fossil. A lot of the groups we first think of when we hear the word "fossil" have relatively low preservation potential. Dinosaurs are fascinating and have a diverse fossil record, but we don't have fossils of most dinosaur species because it's relatively hard for species that lived on land to become fossilized, and bone is not always as durable as you might think. However, rhynchonelliform brachiopods make their shells out of calcium carbonate minerals which have a very high preservation potential, so they have a rich record. Additionally, the chemistry of the shells of rhynchonelliform brachiopods can tell us a lot about the environmental conditions at the time in which they lived.

BSJ: The Late Ordovician Mass Extinction (LOME) is thought to have been caused by a greenhouse-icehouse transition. What is the greenhouse-icehouse transition?

SF: Greenhouse and icehouse are paleoclimate shorthands for a very warm world and a relatively cold world. Right now we live in a very transitional time. It's an icehouse climate state, since we still have major continental glaciers covering all of Antarctica and Greenland. But, as you are aware, we are busily leveraging ourselves onto the greenhouse climate spectrum. Greenhouse climates are ones where we typically have a high inventory of greenhouse gases—carbon dioxide and methane—and little ice at the poles. The most recent major greenhouse state was about 45 to 55 million years ago in the Eocene. From that time, we have fossils of alligators from Ellesmere island in Canada, which even then was above the Arctic circle! Most of the Ordovician period is a relative greenhouse climate, but towards the end we see rapid climate change and growth of very large glaciers on the supercontinent of Gondwana. This coincides approximately with the extinction events.

BSJ: Prior to your research, why was the Ordovician period regarded as nonselective?

SF: What I mean by selectivity is the pattern of extinction versus survival across different groups of organisms. Understanding the cause of extinctions is hard because all we have is observations. We can't do controlled experiments to see what drove brachiopods extinct. We have to rely on patterns and correlation. One of our main ways of getting insight into the causes of an extinction event is looking into its selectivity. Which groups and lineages went extinct, which ones survived, and how do they differ from one another? Are there patterns that can tell us about cause? If you think of some of the other major mass extinction events, there are conspicuous diverse groups of animals and plants that go entirely extinct. For example, in the Cretaceous-Paleogene mass extinction, the non-avian dinosaurs became completely extinct. In the LOME, we see very high extinction at low taxonomic levels—species or genera—but it's distributed across most of the major groups of animals that existed at the time, and very few high-level groups of animals become entirely extinct. We don't see a strong selective signature in terms of certain groups being driven to extinction and other groups persisting. Instead, we seem to see almost every group that existed at the time experiencing pretty high, but not total, losses.

BSJ: Your research shows the potential for the LOME to have been selective along certain axes.[1] How did you use predictors to quantify this selectivity?

SF: When we look at the distributions of genera that go extinct, we can see that there is a particular signature with respect to both geographic distribution and depth in the oceans. What we see for the LOME that differs markedly from extinctions that occurred before and after is strong selectivity with respect to the latitudinal distribution of species. Genera that had a wide distribution across latitudes did pretty well, and genera that had narrow latitudinal distributions experienced much higher extinction rates. That pattern is consistent with what we might expect if changing climate is a big part of what's driving them extinct. As the climate cools or warms, the water masses at their habitual temperature range are going to shift—to the equator if it's cooling, and to the poles if

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Figure 1 (left) and 2 (right): *Fossils of Ordovican braciopods in Dr. Finnegan's collection.*

it's warming. And groups that were already widely distributed wouldn't be particularly sensitive to temperature because they have a wide thermal tolerance range. But narrowly distributed genera that have demonstrated a narrow temperature range are going to be in trouble. The other pattern we see is genera found exclusively in relatively deep water go extinct at much higher rates. That's likely because the distribution of dissolved oxygen correlates closely with depth. By looking at the chemistry of rocks during this interval we can determine there were big changes in the amount of dissolved oxygen in the oceans, suggesting this is also a major part of what caused the extinction.

BSJ: Could you go a little further into how the oxygenation affects the extinction of species at greater depths?

SF: It's a very active area of research and there has been a lot of back and forth in the literature over what's happening through this interval. Partly, it's because this happened almost half a billion years ago and it's very hard to reconstruct changes in local oxygen conditions. For a long time, our expectation was that when the climate cools, oxygenation of deeper waters will increase because cooler water holds more dissolved oxygen. The water at the poles, for example, has more dissolved oxygen than the water at the equator. One of the things we worry about now is that as the oceans warm they will also lose oxygen, adding an additional stress to organisms living there. For a long time, the thought was that as the climate cooled during the late Ordovician, deep water was oxygenated. Under most conditions, we wouldn't expect oxygenation to cause extinction, but if we have ecosystems that are adapted to low oxygen conditions, it may not be great for them. As we get better at reading the chemistry of the rocks, we are beginning to see that, at least in some places, the opposite happened and you got deoxygenation of relatively shallow waters. So, the whole community is in the process of working out how to combine the observations we are getting from geochemistry and extinction patterns with climate models to understand how this could all be happening at once.

BSJ: Could you explain what cratonic seaways are and how the LOME specifically affected the fauna there?

SF: A craton is a geological term for the stable, interior part of a continent. Cratonic seaways occur when you have extensive ocean flooding onto the continents. Because the LOME was a greenhouse climate state with very little continental ice and warm oceans, the continents were very extensively flooded. Most of the places where we now have good records, like North America, Northern Europe, Northern Africa, China, and Argentina were largely flooded by oceans at this time. But where we are now worried about flooding the continents as a consequence of global warming, in the Late Ordovician period flooded continents were great ecosystems for marine animals to live in. For example, these fossils (Fig. 2) come from a cratonic seaway that was in what is now Ohio and Kentucky—which in the Ordovician would have been a great place to go snorkeling. But as the ice sheets grew on Gondwana, sea levels dropped and cratonic seaways drained away, so some of the animals that lived in those seaways may not have been able to establish themselves in open marine ecosystems with very different environmental conditions, leading to greater extinction of fauna inhabiting cratonic seaways.

BSJ: You used similar predictors to the ones we talked about earlier to create a model identifying the most surprising victims in mass extinctions.[2] How were you able to determine unexpected victims by applying this model to the LOME?

SF: The idea here is pretty simple. Whenever we have a big extinction, certain groups of species that go extinct are going to help us understand the causes of extinction, and others not so much. Extinction is a fact of life. Any period of time we look at, there's always groups that go extinct and new groups that appear in the fossil record. So if we want to try and look at the pattern of extinction and figure out what causes mass extinction, we want to filter the surprising extinctions from the ones that are less surprising. The analogy I always use here is to epidemiology, where we try to understand a major epidemic that occurred in the past. For example, most of the time epidemic influenza has a pretty distinct mortality pattern—mortality rates are higher in very young and very old people. In 1918, the "Spanish Flu" swept all over the planet and killed somewhere between 20 and 100 million people worldwide. And if you look at the distribution of mortality in the Spanish Flu compared to other flu epidemics, like other epidemics there was high mortality among the very young and the very old, but there was also a peak in mortality among healthy, young adults—people we normally consider to be least vulnerable to flu. That's what you would refer to as an unexpected victim. This paper tried to do something analogous using extinction patterns in the 10 to 15 million years preceding the LOME to determine predictors for extinction.[2] And as with the flu example, they are not very surprising. If you are very narrowly distributed, you are usually pretty likely to go extinct at a given time. But there are also genera, such as the *Foliomena* Fauna, a distinctive group of brachiopods that lived in deep tropical oceans, where it's very surprising to us that they go extinct. This is a major departure from the normal extinction regime.

BSJ: One factor that may have influenced your results was sampling bias. Can you explain the concept of sampling bias?

SF: An issue with the fossil record is that it's incomplete in many different ways. So what we call sampling bias collapses a whole set of processes and events that multiply together to determine the likelihood of having a fossil record of any particular individual or species that existed at some point in the past. Brachiopods have nice mineralized hard parts that hang around after they die, but jellyfish, for example, will get fossilized only under exceptional circumstances. So, our sampling of brachiopods is much better than our sampling of jellyfish. Additionally, there are many places where I can't see the Late Ordovician rocks because they are buried under younger rocks and the only way to look at them is by coring down. So another sampling bias is found anywhere the record of the organisms might exist but can't be accessed. On top of that there is true sampling bias, which occurs when we haven't sampled even the parts of the rock record that we can get to. Unsurprisingly, the most intensively sampled parts of the fossil record tend to be the ones located in wealthy industrialized countries where people have the luxury of spending their time studying fossils. There's a strong bias towards North America, Northern Europe, and increasingly China, but there are still big parts of the world where we don't know as much as we would like about the fossil record for socioeconomic or practical reasons. I'd like to know much more about the fossil record of Brazil, but I'm not going to advocate clearcutting the Amazonian rainforest just to study the fossil record better.

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BSJ: You've used past extinction risk predictors to predict "intrinsic risk" in modern marine fauna.[3] Could you explain the concept of intrinsic risk?

SF: In this paper, a couple of colleagues and I brought together both paleontologists and modern biologists who were interested in extinction in marine environments, and tried to think about how we can bridge the time gap between the fossil record and the modern day.[3] The fossil record shows us that not all groups that exist in the oceans today are equally vulnerable to extinction under normal conditions. If we look through the last 23 million years of Earth history—the period of time of during which the major groups that dominate marine ecosystems today were already in place—we can identify a set of relatively diverse groups of animals that have pretty good fossil records. We looked at molluscs, sea urchins and their relatives, corals, marine mammals, and sharks, and made a model for each of them determining the relationship between their ecology and aspects of their geographic distribution and extinction risk. Then we projected that on to the modern world (Fig. 3). The underlying idea is pretty simple: as we begin to worry about which genera will be most affected by the modern era of anthropogenic change, it is useful to identify genera that might be at intrinsically high risk of extinction anyway. You could argue that we don't need to worry about groups that already have a high intrinsic risk, or you might say these are the ones we really want to focus conservation efforts on. That's a policy and planning question. But the hope is that this model can serve as a kind of baseline to compare to our growing body of information about modern population response to climate change, ocean acidification, overfishing, deoxygenation, plastics, and all of the myriad awful things that we worry about in modern marine ecosystems.

BSJ: You found a high intrinsic risk for tropical genera. Was this more reflective of environmental characteristics or characteristics of the actual genera?

SF: We don't really know. There are some periods of time where tropical genera seem to exhibit higher extinction risk, but not uniformly. In some cases, that's associated with episodes of cooling, which may affect the tropics more strongly. But what we actually found is that simply being narrowly distributed is a big determinant of extinction risk, and that on average there are more narrowly distributed genera in the tropics than there are in extratropical regions. It also may be related to thermal tolerance range. Species that live at high latitudes experience a much larger range of temperature conditions in a given year than do those that live

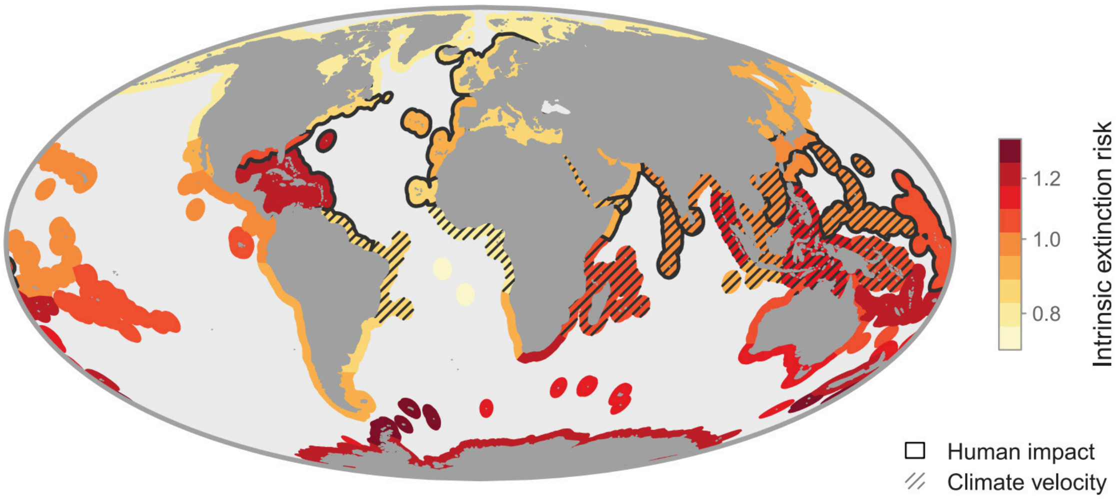

Figure 3: *Overlap of global areas with high extinction intrinsic risk with global areas of high human impact.*[3]

in the tropics. As the climate begins to shift, groups that have very narrow thermal tolerance ranges may be at much higher risk of extinction, depending on their adaptability. Also, because the solubility of oxygen is a function of temperature, some species in the tropics are already barely getting enough oxygen to function. For marine ectotherms (cold-blooded animals), warmer temperatures mean higher metabolic rates but at the same time less oxygen. So that's a bad combination. Naively, we think that cooling should be bad for tropical ecosystems, but warming might also be bad for them.

BSJ: How can the overlap of this intrinsic risk and our human impact help predict which coastal regions may face high extinctions in the future?

SF: This is absolutely the toughest question. This paper was part of a big working group involving both paleobiologists and marine biologists, and we wrestled with this question a lot.[3] We're looking at very long time spans, and the question is: what's the time frame which we're actually planning for? Are we crafting policy for ecosystems a million years in the future or are we crafting policy for more immediate concerns? For example, if we look at the kinds of corals that exhibit high intrinsic risk in the record versus the kinds of corals that are currently thought to be at greatest risk, they're not generally the same groups. That tells us we might need to be thinking about processes that play out on longer time spans than we can observe directly, or alternatively that the current anthropogenic impacts change the fitness landscape so much that the old rules no longer apply. This is one of the major challenges we face in studying evolution and ecology: we know that relevant time spans extend out to thousands and millions of years, but in most cases we only have direct observations of populations for maybe a few decades. There are important processes happening over longer timescales that we're missing when we only think about vulnerability in the short term.

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IMAGE REFERENCES

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