



RESOLUTIONS OF RESPECT

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Paul Colinvaux 1930–2016



Paul Colinvaux on the rim of El Junco Crater Lake, San Cristobal Island, The Galapagos, Ecuador 2004. Photo credit: Miriam Steinitz-Kannan.

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Paul shipped the oars and grounded the inflatable. A first row around a lake was his ritual. It did not matter if we had driven to the site or walked for a couple of days to reach it, Paul's first act at a new lake was to pump up one of his cherished Avon Redstart inflatable boats and take off for a solitary tour. In many ways, this act was a metaphor for him as a scientist: he was adventurous, intensely curious, eager to be at the forefront of new ideas, and willing to be a lone voice. On February 28th, 2016, Paul died on Cape Cod, and ecology lost another from the generation that raised our science from obscurity to a household word.

Paul Alfred Colinvaux was born in London, England, in 1930 (September 22) where he went on to attend the University College School. At an early age, he was bit by the rowing bug, taking part in the

Henley Regatta as a schoolboy. Rowing remained a passion and years later Paul was the first faculty advisor to the Ohio State University rowing team. In post-WWII Britain, he entered the army and served in Germany. This experience with the military was formative, both in honing logistic skills that would be essential for running expeditions, but also arousing his interest in military history. Paul left the army and attended Jesus College Cambridge where he studied zoology. He was a keen outdoorsman and took a position with the Canadian soil survey. Working in New Brunswick, he met his wife Llewellya Hillis. Paul spent 2 years working for the survey before becoming Dan Livingstone's first doctoral student. Dan's paleoecology laboratory at Duke University was becoming focused on long records from the African Rift lakes, but Paul, showing his independence, jumped at the opportunity to core Lake Imuruk in Alaska. The reality of raising that core introduced Paul to work in almost impossibly remote locations, to bush pilots, to overcoming a sunken boat and flooded outboard motor, and to obtaining the longest possible sedimentary record by pounding and pounding on a coring rig.

Paul's next stop was a post-doctoral appointment at Yale University with Evelyn Hutchinson and Ed Deevey (1963–1964). Having produced the first Alaskan fossil pollen record that spanned a glacial cycle, Ed Deevey cut him down to size with "So Paul, I believe you showed that Alaska was cold during an Ice Age." While this jibe may have caused Paul to look to the tropics for his next research, it was not entirely fair, as there is still considerable disagreement over the existence of a "mammoth steppe" vs. a tundra during the time of the Beringian corridor. Paul's impersonations of the plummy British accent of "Hutch" confounded mid-western students for the next 30 years. In 1964, Paul and Llewellya, respectively, took up faculty positions in the Zoology and Botany departments of The Ohio State University. Paul would teach ecology to larger and larger classes, even attracting the revered football coach Woody Hayes to sit in on sessions. He was a dynamic teacher, winning every teaching award that Ohio State had to offer. Paul's impersonations of the behavior of elephants and wolf spiders became etched in the minds of his students, as he imparted a sophisticated understanding of ecology. Even great communicators can be misunderstood. One day while lecturing on predation, Paul went into a colorful digression about hunting to hounds (one of his passions). As the students packed their books, Melanie Riedinger-Whitmore, who was his teaching assistant at the time, overheard one shocked sophomore as he muttered to another, "The man shoots dawgs!" Paul roared with laughter when he heard this, but decided not to correct that impression.

Influenced by his academic mentors, Paul wanted to answer big questions. Using paleoecology to attempt to answer the riddle of why there were so many tropical species had strong appeal, and was central to his academic life for the next 50 years. If climate change was a significant part of that story, Paul realized that the exquisitely sensitive setting of the Galapagos Islands could provide telling data. The paleoecological work on the Galapagos was novel, did not answer the fundamental diversity question, but did introduce Paul to penguins, diatoms, and limnology. Dee Boersma had joined the Galapagos project and her doctoral dissertation dealing with the effects of climate change on penguin populations on the islands paved the way to creating a very real link between paleoecology and conservation.

During the Galapagos project, parallel work by a German geologist, Jurgen Haffer, introduced a new hypothesis to explain Amazonian diversity. The so-called Refugial Hypothesis suggested that ice-age aridity caused Amazonian rainforests to contract into pockets surrounded by seas of isolating savannas. At first Paul thought this was an elegant explanation, but Paul spent much of his subsequent academic energy demonstrating that this hypothesis was deeply flawed.

Paul's core field team emerged with the arrival of Miriam Steinitz-Kannan from Quito and Mike Miller from the University of Cincinnati. The Ecuadorean Andes and Amazonia became the focus of expeditions that added a wealth of knowledge about lakes, pollen, and diatoms, but none were old enough to shed light on Paul's driving concern—the ice-age Amazon. Science is full of tales of serendipity and here, too, chance played a role. Paul's team had been looking for ancient lakes in Ecuador for a decade. The field season of 1982 was just starting, with the team packed into a beaten up old truck negotiating the precarious mud roads at the foot of the Andes. A landslide stopped them in their tracks. As all sediment-obsessed scientists are wont to do, Paul and the team started scratching around at the cliff exposure beside the road. Excitement rose as it became apparent that the cliff was a cross section through an old marsh complete with ancient logs. Sampling bags were quickly produced. Paul's post-doc Kam-biu Liu analyzed the deposits, finding evidence of vertical tree migrations of about 1,000 m during the ice age. That cliff exposure changed the dialog about ice-age Amazonia, as the data indicated a climate that was about 5°C, cooler than today and, moreover, that this section of lowland Amazonia was wet. This was the first real evidence against the Refugial Hypothesis, which relied on low precipitation, not temperature, as the driver of Amazonian evolution. The debate over refugia became lively and would not be settled by a single site.

Although Paul was driven to find lakes that would provide ice-age sediments, the many younger lakes that his team cored provided important new insights. The first description of the history of permanent lakes in Amazonia identified a time of flooding that we now associate with the Medieval Climate Anomaly. This finding was the first suggestion that large changes in precipitation could influence Amazonian ecology during the modern interglacial. A discovery that resulted in being listed in the 1989 Guinness Book of Records was the identification of the oldest maize pollen (6,000 years old) yet described from Amazonia. Pollen grains and phytoliths (silica bodies) from maize were found throughout the sediments of Lake Ayauchi¹, Ecuador, along with charcoal, indicating that people had been burning the forest around the lake for much of the last 7,000 years. This finding was contested by archaeologists, as it forced a revision of the estimated adoption of agriculture in Amazonia to be at least 2,000 years before the earliest cobs recovered from digs.

Paul itched to get back to his foundational research in Alaska, but more than this, Siberia beckoned. The Cold War was not an impediment to Paul. With colleagues at the University of Washington, Paul entered into negotiations with a very senior Soviet researcher, Academician Shilo. Paul needed an unprecedented level of détente, at least within ecology, to be allowed to mount an expedition to core lakes in Siberia. Paul persuaded the President of Ohio State University to fly Academician Shilo into Columbus, Ohio and award him an honorary Ph.D. With Shilo's help, the Siberian field season took place in the summer of 1989. The Russians were able to provide large Soviet Army troop-carrying helicopters to ferry scientists and equipment to Jack London Lake, Siberia. Despite such spectacular support, the only meat available to the party was the cans of tuna and corned beef brought by the Americans. The following year the Russian team joined their U.S. partners to core Wonder Lake in Denali. The collaboration continued after the Berlin Wall had fallen with another field season in Siberia's Kola Peninsula.

During this same period, Paul was forging ties to the Smithsonian Tropical Research Institute (STRI) and in the summer of 1991 he and Llewellya left Ohio State to take up appointments at STRI. This was an exciting initiative in which STRI was seeking to establish itself as the pre-eminent tropical paleo-ecological presence. Dolores Piperno, Tony Coates, and Jeremy Jackson were already in place, and the

addition of Colinvaux provided another strong link between their excellence in modern ecology and the burgeoning interest in systems of the past.

The first field season after arriving at STRI provided Paul's best-known paleoecological record from the Amazon. Overcoming huge logistical and political barriers, the Colinvaux team raised cores from three lakes on the Hill of Six Lakes. One of those records, from Lake Pata, reinforced the earlier findings from Mera, but allowed a more nuanced understanding of the complex changes in temperature and precipitation that influenced Amazonia over the last 180,000 years. The debate over the refugial hypothesis was enjoined once more. As the discussion intensified, molecular evidence from the phylogenetic analyses of many organisms began to emerge. These new data indicated that the timeframe of the Refugial Hypothesis was wrong, and that many of the speciation events were pre-Quaternary and had little to do with climate change in the last 2 million years. Paul's often lonely opposition to the prevailing hypothesis of the day was vindicated.

Paul's influence was far greater than someone who investigated mud. Paul mentored young scientists, teaching by example. He delegated effectively, and in the process created successive cohorts of field-trained, laboratory-competent ecologists. Paul's flair for writing and his pursuit of big ideas were imprinted on those who worked with him. He had the ability to distill a complex series of ideas into a few well-turned phrases, and was justly proud of what he termed "wordsmithing" a document. Paul was one of the first to popularize ecology through publishing books for a general audience. Many of us were assigned *Why Big Fierce Animals are Rare* as an undergraduate text, perhaps in Portuguese, Spanish, Chinese or one of the many other languages into which it was translated. In this book, he revealed the ecological mantra "why?"—for the why questions are always the hardest to answer, yet the most satisfying to investigate. Paul's *Fates of Nations* was a grand attempt to synthesize the rise of society through an ecological lens, and received mixed reviews, earning plaudits from biologists and long critiques from social scientists. Paul also wrote the first textbook aimed specifically at undergraduates titled *Ecology*. Together, this body of work formed an important part of ecology becoming a mainstream discipline.

Paul wrote for his own pleasure and also to document events. He wrote a long, weekly letter to his mother, and we all remember the light burning late into the night—probably until 8 pm, for it is dark at 6 pm in the Amazon, and after eating there is nothing to do but to go into your tent—as Paul wrote his diary. These field logs were essential reading for anyone following in Paul's footsteps. The last fieldwork in which Paul took part was in 2004, when he returned to core El Junco Crater Lake on the Galapagos. His notebooks from the 1966 expedition, that provided blow-by-blow accounts of coring the lakes, were invaluable. This lake provided the first of his paleoecological records from the tropics, co-authored by graduate student Eileen Schofield. A symmetry exists in that the second coring of El Junco was the subject of his last publication, with an aspiring female paleoecologist, Alejandra Restrepo, as the lead author.

Everyone who worked with Paul has a trove of "Paul" stories, but we close this remembrance with a quick anecdote. Deep in his DNA was a showman. He loved an audience, whether it was a 1,000+ class of Ecology undergraduates or Shuar warriors in a thatch hut. We had been traveling for several days with Siona Indians working our way down tributaries of the Napo River, when we came to a village of the Shuar nation. Thatch huts raised on stilts that became smoky as cooking fires burned down. When the

embers glowed, the next-day's poison darts were prepared. The Shuar men heated the tips of their darts and told stories and sang songs. There were no translators but the atmosphere was friendly. After some time there was a pause and they were looking at us expectantly. Scarcely missing a beat, Paul stood and provided a very theatrical rendition of Lewis Carroll's *Jabberwocky* "Twas brillig, and the slithy toves did gyre and gimble in the wabe....." I'm not sure who was more surprised by the performance—his colleagues or the Shuar.

Selected Publications

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