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Bush, M.B.; Gosling, W.D.

DOI

[10.1017/qua.2017.109](https://doi.org/10.1017/qua.2017.109)

Publication date

2018

Document Version

Final published version

Published in

Quaternary Research

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Citation for published version (APA):

Bush, M. B., & Gosling, W. D. (2018). In search of the ice age tropics, a tribute to Prof. Daniel Livingstone and Prof. Paul Colinvaux. *Quaternary Research*, 89(1), 1-6.
<https://doi.org/10.1017/qua.2017.109>

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In search of the ice age tropics, a tribute to Prof. Daniel Livingstone and Prof. Paul Colinvaux

Mark B. Bush^{a,*}, William D. Gosling^{b,c}

^aDepartment of Biological Sciences, Florida Institute of Technology, Melbourne, Florida 32901, USA

^bInstitute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, 1090 GE Amsterdam, the Netherlands

^cSchool of Environmental, Earth and Ecosystem Sciences, The Open University, Milton Keynes MK7 6AA, United Kingdom

(RECEIVED November 20, 2017; ACCEPTED December 2, 2017)

PIONEERS OF TROPICAL PALEOECOLOGY

Daniel Livingstone and Paul Colinvaux (Fig. 1a and b) were intellectual pioneers who helped to shape modern tropical paleoecology. Linked in life by bonds of friendship, they shared a common philosophy of challenging conventional wisdom and exploring remote areas to seek answers. Dan and Paul both had common starts to their research careers with PhD's focused on the arctic (Livingstone, 1955a) and strong early influence and guidance from Prof. Ed Deevey at Yale; he was Dan's PhD advisor and Paul's postdoctoral mentor. At Deevey's urging, both men turned their attention to the tropics. In his 2007 book, Paul summed up their division of labor: "Dan was already doing Africa; I chose the Amazon" (Colinvaux, 2007, p. 11). Both Livingstone and Colinvaux were first and foremost ecologists, who used paleoecology to answer ecological questions. Dan and Paul both died in the spring of 2016, and this special issue is a tribute to the inspiring enthusiasm and energy they brought to research and education.

Members of every generation can argue that they live in interesting times, but for budding ecologists, the late 1950s and 1960s, when Dan and Paul were in graduate school, were especially formative. Geology, climatology, and ecology were being revolutionized by new ideas and technologies. In this period, plate tectonics went from being a fringe idea to being widely accepted (Dietz, 1961). Gone was the insistence that organisms must have dispersed across oceans or migrated across lost land bridges. Vicariance was now a far more plausible means of speciation than previously thought (Wilson, 1963). A welter of new information based on isotopic chemistry was reshaping paleoecology and paleoclimatology. Radiocarbon dating, first developed by Libby (1960), allowed fist-sized sections of organic-rich material

to be dated. This development transformed the study of lake sedimentary sequences, allowing real chronologies to be developed and to set aside assumptions that similar looking vegetation changes were coeval. Emiliani's (1955) isotopic record of marine sediment provided the first strong record of the changes of global temperature within the Quaternary.

That Quaternary ice ages were relatively slow to develop, stair-stepping down toward a maximum cooling, before rapidly bouncing out into interglacial conditions, was of tremendous significance to anyone contemplating species migrations. For decades ecologists had been debating whether communities were relatively fixed or fluid in composition (Clements, 1916; Gleason, 1926), and a pivotal moment was reached in that discussion in the early 1960s. Plant phytosociologists whose views had held sway since the 1920s tended to see the world as tightly coevolved communities that would migrate as a unit. When viewed through time, vegetation zones of temperate forest, boreal forest, and tundra were depicted being driven north and south (Braun, 1955) or up- and downslope (Gonzalez et al., 1966). Whittaker's demonstration that species did not turn over in unison along ecological gradients in the Smoky and Siskyou Mountains (Whittaker, 1956, 1960) signaled a paradigm shift in how ecologists viewed species occurrence in communities. As paleoecologists started to champion the individuality of species' responses to past climate change, Livingstone in Africa and Colinvaux in South America became advocates of this new view.

Livingstone and Colinvaux combined developments in geology, climatology, and ecology and used these advances to tackle great questions of species distributions, endemism, and richness. When they started their careers in the 1960s, fossil pollen records existed for Europe and much of North America, but areas of more extreme climate were virtually unknown. At the time of their deaths, in 2016, hundreds of records of past ecological change existed from the tropics (Flantua et al., 2015). Today, the pursuit of the origins of tropical diversity goes on, but this is now guided by a

*Corresponding author at: Department of Biological Sciences, Florida Institute of Technology, 150 W. University Blvd., Melbourne, Florida 32901, USA. E-mail address: mbush@fit.edu (M.B. Bush).



Figure 1. (color online) (a) Dan Livingstone (photo courtesy of Duke University). (b) Paul Colinvaux at El Junco Crater Lake, Galapagos Islands (photo courtesy of Miriam Steinitz-Kannan).

framework of knowledge that both Dan and Paul helped establish. In their search for the ice age tropics, both Dan and Paul came to realize the rarity of ancient lakes in the tropical lowlands and the potential importance of any such archive. Consequently, they were at the forefront of multiproxy analysis, actively seeking collaborators to maximize data extraction from sediments using X-radiography, geochemistry, diatoms, charcoal, wood, phytoliths, and cuticles (e.g., Livingstone and Fleischer, 1963; Steinitz-Kannan et al., 1986; Maley et al., 1990; Bush et al., 1992).

Dan Livingstone will be remembered for his seminal studies of the paleoecology of African lake systems that revealed the history of African glaciations (Livingstone, 1962, 1965, 1967, 1971a, 1975; Talbot et al., 1984), the history of the African rift lakes (Livingstone, 1965), and the invention of the Livingstone piston corer (Livingstone, 1955b). Dan's first publication had been on fish populations in four lakes in northern Alaska (Livingstone, 1950/1951). Although his career moved away from fish biology, he maintained a deep connection to limnology, and his graduate students were often engaged in studying the limnology of tropical systems (Stager et al., 1986; Haberyan and Hecky, 1987; Kling, 1988). Dan built an extensive pollen collection, describing the pollen of many African species for the first time. The pollen collection supported analysis of fossil pollen from African lake sediments. Although obtaining long histories of African climate and vegetation change was a passion, his laboratory at Duke University was an incubator of ideas where ecological questions, not geography, drove inquiry. Indeed, Dan's first doctoral student, Paul Colinvaux, never worked in Africa, but undertook a study of Alaskan systems, and Dan's last student, Eric Kjellmark, worked on blue holes in the Bahamas (Kjellmark, 1995). It was this breadth of knowledge that made Dan such an engaging colleague and effective mentor. In today's world of *H*-indexes and academic metrics, Dan stood out by not claiming authorship on papers resulting from his PhD students' endeavors. He contributed

to those papers but believed the body of work was that of the students and that they deserved full, sole-author recognition.

Paul Colinvaux loved the challenge of big ideas. Unlike Livingstone, who was naturally retiring, Colinvaux was energized by a crowd and thrived at Ohio State University where he taught ecology classes to as many as a thousand students. He advanced newly burgeoning ideas in ecology and attempted to popularize the discipline through textbooks (Colinvaux, 1973), social commentary (Colinvaux, 1980), and short essays (Colinvaux, 1979). As a researcher, the driving question behind much of his work was, why are there so many tropical species? Haffer (1969) revolutionized the discussion over the origin of Amazonian diversity by hypothesizing that during glacial periods, arid conditions forced a contraction of rain forests into isolated islands separated by seas of savanna, with forests expanding to their present limits during the interglacial periods. He argued that such glacial-interglacial changes in rainfall served as a pumping mechanism creating the isolation necessary for allopatric speciation. After at first accepting this idea, Colinvaux went on to challenge it. Indeed, the quest to refute the refugial hypothesis propelled him to search for ancient lakes across Central and tropical South America.

Colinvaux's first foray into South American ecology was to investigate the paleoecology of the Galapagos Islands (Colinvaux, 1968, 1972). His efforts spread to mainland Ecuador, Peru, Panama, and Brazil (Steinitz-Kannan et al., 1983; Colinvaux et al., 1985, 1988; Liu and Colinvaux, 1985; De Oliveira et al., 1986; Bush and Colinvaux, 1990; Piperno et al., 1990) and still pursued long records in the Arctic (Eisner and Colinvaux, 1990; Lozhkin et al., 1993). To facilitate his exploration of remote areas, Paul developed the lake sediment corer invented by Dan into a lightweight "backpackable" design (Fig. 2) that has become the standard kit for many tropical paleoecologists (Colinvaux et al., 1999). Both Paul and Dan recruited and trained graduate students from the countries where they worked, creating an international legacy of ecologists and paleoecologists.



Figure 2. (color online) A core being raised using a Colinvaux-Vohnout piston sampler from a raft of inflatable boats at Lake Llaviucu (also called Surucucho) in June 2010. This lake had previously been cored by Colinvaux's team in 1988 (Colinvaux et al., 1997).

CLIMATE, VEGETATION, AND BIODIVERSITY

In this issue, we present 10 articles that build on the legacy of Livingstone and Colinvaux, contributing to the key themes of climate, vegetation, and biodiversity within the tropics that can be found throughout their work. Inferences about the magnitude of past human influence and climatic change in the tropics have been based on inferences drawn from the fossil record, including seminal work by Livingstone in Africa (Livingstone, 1971b, 1975, 1982, 1984) and Colinvaux in South America (Colinvaux, 1989, 1996; Colinvaux et al., 2001). In the 10 articles in this issue, 9 new tropical fossil records are presented to provide new insights into past climate change and help to expand our knowledge of spatial variation in tropical vegetation change.

From Africa, new data from three sites, Lakes Edward, Ejagham, and Ishiba Ngandu, are presented (Haberyan, 2018; Ivory and Russell, 2018; Stager et al., 2018). Ivory and Russell present new fossil pollen and charcoal data from Lake Edward (Democratic Republic of Congo and Uganda) that indicate an expansion of forests during the early Holocene under warm, wet climates. Subsequent oscillations in forest cover reflect a combination of change in precipitation and human land-use practices. Stager et al. (2018) report a ^{14}C -dated paleoecological record from Lake Ejagham in Cameroon. Originally cored by Dan Livingstone, the sediments from this lake define the age of the lake and constrain the evolutionary window that allowed five cichlid fish to speciate. Haberyan provides fossil diatom data from Lake Ishiba Ngandu, Zambia; Livingstone raised the sediments in the early 1960s and described the fossil pollen (Livingstone, 1971a). The diatom data provide a limnological history of the site and suggest unusually stable conditions for the last 30,000 yr compared with systems such as the Okavango to the west and the great rift lakes to the east.

Vegetation reconstructions from five previously unstudied South American lakes (one in Peru and four in Brazil) are presented here and give new insights into past climate. The data presented by Schiferl et al. (2018) provide a 3800 yr paleoclimatic history from midelevation forests in the Peruvian Andes. The fossil pollen data relate changes in forest composition to changes in North Atlantic sea-surface temperature. The record from Lake Acarabixi (Rodríguez-Zorro et al., 2018) lends weight to inferences that Amazonia was already forested at the onset of the Holocene (following Colinvaux et al., 1996), although the composition of the fossil pollen shows marked differences between the early Holocene and modern times. The Serra do Tabuleiro peat bog record, presented by Behling and de Oliveira (2018) is from the Atlantic rain forest and captures the transition from open woodland to Atlantic rain forest at the onset of the Holocene. Raczka et al. (2018) present the first study from the lowland Neotropics on fossil pollen and *Sporormiella* to reconstruct the history of megafaunal loss from two sites in southeastern Brazil. The 25,000 yr sequences provide new insights about the timing of nonanalog plant communities relative to megafaunal population collapse.

Loughlin et al. (2018) studied an area that had yielded one of Colinvaux's most important paleoecological records, that of Mera Ecuador (Liu and Colinvaux, 1985; Bush et al., 1990). Loughlin et al.'s work explores an understudied source of potential paleoecological data by analyzing non-pollen palynomorphs. Habitat fidelity is revealed among spores that had never previously been described.

With the ever-increasing number of studies from the tropics, collating and synthesizing information is an ongoing challenge. This special issue includes two synthetic analyses of fossil pollen data—one from Africa, led by Jean Maley, a longtime collaborator of Livingstone (Maley et al., 2018), and one from South America by Smith and Mayle (2018). The manuscript by Maley et al. centers on the equatorial east African region and provides insights on regional vegetation prior to widespread agricultural expansion. Smith and Mayle provide a synthesis of vegetation change for the last 6000 yr, drawn from 153 Southern Hemisphere Neotropical sites. The 83 citations that underpin this study reflect how rapidly this field is changing, insofar as just 13 of those citations predate the year 2000.

LEGACY AND FUTURE PERSPECTIVES

Dan Livingstone and Paul Colinvaux advanced their science and provided a platform of knowledge from which the current generation of paleoecological researchers is able to delve deeper into tropical ecological and biogeographic questions. They would have been the first to recognize that, although making significant discoveries, some of those big questions that they strove to address remain as topics for future research. Such an admission lies at the heart of science, for as we gain knowledge of a system, the questions become more sharply focused. When Livingstone and Colinvaux started their research, the lowland tropics were seen as climatically

stable over the long term or, in the case of refugial hypothesis, a very simple dichotomy between wet and dry (with constant temperature). It was their efforts that revealed ice age cooling in the tropical lowlands and indicated that there was also considerable variation in precipitation.

Throughout the tropics, paleoecology is a lake-limited science. Livingstone and Colinvaux knew the disappointment of coring many promising sites only to find pollen was not preserved, the coring was stopped by ash, or the site was simply too young to provide a glacial-aged record. However, they were motivated to keep searching by the sheer delight of the rare find, an ancient lake with a story to tell. Over the coming years, paleoecologists working in the tropics must continue the quest for further records to improve our understanding of spatial variance within these complex systems. The heterogeneity of the tropics to climatic forcing is becoming ever more apparent from modern studies (Marengo et al., 2012), so it is unlikely that vast tropical regions, such as Amazonia, responded in a spatially uniform fashion to past global climate changes.

The sheer diversity of lowland tropical systems is both a curse and a boon. Nowhere else is there the potential sensitivity to investigate ecosystem responses to human or natural forcing. The challenge, however, is in recognizing the host of rare taxa that form the long distributional tail of tropical pollen data. Again, Livingstone and Colinvaux led the way in establishing significant modern pollen reference collections, some of which were captured in pollen atlases (Colinvaux et al., 1999; Bush and Weng, 2007; Gosling et al., 2013), but there is a huge potential for improvement in this aspect of our discipline.

Ancient lakes suitable for paleoecological reconstruction are treasures, especially in the lowland tropics where they are so rare. Extracting the maximum amount of information from those records is an obligation for all tropical paleoecologists and should foster new collaborations to broaden the range of analytical techniques applied to each record. As truly multi-proxy records emerge from the tropics, we can move from linking vegetation change and climate to understanding the function of ecosystems and landscapes. Such understandings improve our ability to relate ecosystem resilience and sensitivity to habitat and species complexity and, ultimately, to conserving biodiversity. This observation brings us back to that most fundamental question inherent to, but not answered by, Livingstone's and Colinvaux's research: Why are there so many tropical species?

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