FORTY YEARS OF PALEOECOLOGY IN THE GALAPAGOS

By: M.B. Bush[1,2], P.A. Colinvaux[3], M. Steinitz-Kannan[4], J.T. Overpeck[5], J. Sachs[6], J. Cole[5], A. Collins[1], J. Conroy[5], A. Restrepo[1] & Z. Zhang[6]

[1]Department of Biological Sciences, Florida Institute of Technology, 150 W. University Blvd, Melbourne, FL, U.S.A.
[2]Correspondence: <mbush@fit.edu>
[3]Marine Biological Laboratory, Woods Hole, MA, U.S.A.
[4]Department of Biology, Northern Kentucky University, Highland Heights, KY, U.S.A.
[5]Department of Geosciences, University of Arizona, Tucson, AZ, U.S.A.
[6]School of Oceanography, University of Washington, Seattle, WA, U.S.A.

SUMMARY

The Galapagos Islands provided one of the first lowland paleoecological records from the Neotropics. Since the first cores were raised from the islands in 1966, there has been a substantial increase in knowledge of past systems, and development of the science of paleoclimatology. The study of fossil pollen, diatoms, corals and compound-specific isotopes on the Galapagos has contributed to the maturation of this discipline. As research has moved from questions about ice-age conditions and mean states of the Holocene to past frequency of El Niño Southern Oscillation, the resolution of fossil records has shifted from millennial to sub-decadal. Understanding the vulnerability of the Galapagos to climate change will be enhanced by knowledge of past climate change and responses in the islands.

RESUMEN

Cuarenta años de paleoecología en las Galápagos. Las Islas Galápagos proporcionaron uno de los primeros registros paleoecológicos de tierras bajas en los Neotrópicos. Desde que las primeras muestras sedimentarias fueron levantadas en las islas en 1966, ha habido un incremento sustancial en el conocimiento de los sistemas del pasado, y en el desarrollo de la ciencia de paleoclimatología. El estudio en las Galápagos de los fósiles de polen, diatomeas y corales, y de los isótopos de componentes específicos ha contribuido a la maduración de esta disciplina. A medida que la investigación ha trascendido desde las preguntas sobre condiciones en la era glacial y estados promedio del Holoceno, hacia la frecuencia pasada de El Niño Oscilación del Sur, la resolución de los registros fósiles se ha refinado desde milenial a sub-decadal. La comprensión de la vulnerabilidad de las Galápagos al cambio climático mejorará con el conocimiento de pasados cambios y respuestas climáticos en las islas.

INTRODUCTION

The Galapagos Islands are iconic for their isolation and their place in the development of evolutionary theory. As understanding of evolutionary processes on the islands has grown, so too has the realization that both long- and short-term habitat changes may influence niche (Grant & Grant 1985). For such small islands, the breadth of terrestrial habitats on the Galapagos is impressive, from lowland semi-desert to humid montane. Each of these habitats offers challenges and opportunities for invading species, be they natural invasions over millions of years, or those induced by the human activity of the last 200 years. For each habitat, climate change can alter the balance of which species can establish a population or win in competition: dry times may relatively favor the invasion of the uplands, whereas wet times allow access to the lowlands. Consequently, understanding the scope of habitat change induced by past climate change is an important part of understanding the evolutionary history of these islands and predicting what may lie ahead.

The islands lie in the heart of the warm tongue of water that characterizes many El Niño events in the eastern equatorial Pacific and, as such, are highly sensitive to changes in ocean and atmospheric circulation. Much of the modern paleoclimatic interest in the islands relates to testing predictive models of climate, but this was not what drove the first paleoecological research on the islands. In this retrospective, we provide a historical context for the maturation of ideas relating to the paleoecology and paleoclimatology of the islands and also how the islands have played a role in the development of these disciplines. We conclude by considering how that role will continue as we seek to predict the impact of future climate changes.

THE EXPLORATORY PHASE

In 1966, Colinvaux (1968) conducted the first paleoecological reconnaissance of the Galapagos Islands. He reported on fourteen lakes, most of which were saline or hypersaline lagoons. The only permanent freshwater lake on the islands was El Junco crater lake, San Cristóbal. Colinvaux's expedition came at a time when the first reports of ice-age tropical cooling were emerging. A long palynological record from the high plains of Colombia depicted multiple glacial-interglacial cycles manifested by the replacement of Andean forest (interglacial) with paramo (glacial) (Van der Hammen & González 1960). Meanwhile, research was also taking place in the highlands of Costa Rica (Martin 1964). In both settings, cooling appeared to be the dominant signal of the ice age, but effects on the lowland Neotropics were virtually unknown. That the tropics became much drier as they cooled was a logical extension for European researchers familiar with transitions from boreal to steppe environments (Godwin 1956). But although Colinvaux's intent was to answer the fundamental ecological question of why there are so many species in the tropics compared with high latitudes, climate history was to be important in his quest. That Colinvaux started this research in the Galapagos rather than in the Amazon, was part serendipity and part pragmatism: surely a simple flora would be easier to learn than a complex one.

Colinvaux recovered a 16-m sediment core from El Junco with a basal age beyond the limit of bulk radiocarbon dating (effectively 35,000–38,000 years). Fossil pollen and spores were well preserved in the Holocene (defined as the last 11,000 years) sediments (the upper 3.3 m of the core), and revealed a largely constant floral history for the past 12,000 years (Colinvaux 1972, Colinvaux & Schofield 1976a, b). Given the isolation of the islands, it is implausible that large-scale migration from the mainland occurred, even with glacial cycles. Furthermore, given that almost all species on the islands did not evolve *de novo* in the last 36,000 years, all floral responses to climate change would have comprised a reshuffling (or loss) of existing species. Beneath the organic Holocene sediments lay 12 m of red clays. No pollen or spores survived in those clays and their low organic content pointed to severe oxidation. In other words, during the last glacial maximum (*c.* 26,000–22,000 years ago) and the subsequent de-glacial period (*c.* 22,000–13,000 years ago) the lake was dry. The inference was clear, less precipitation would cause the lake level to drop, allowing the sediments to oxidize (we will return to this idea later). However, within that thick clay band lay a lens of organic-rich lake mud that yielded radio-carbon ages >36,000 years. In that mud, the pollen assemblage was similar to that of the Holocene section, but this earlier lake had supported a different species of *Azolla* than that in the Holocene, as well as *Myriophyllum*, a genus no longer found on the islands (Schofield & Colinvaux 1969). The period of low lake level appeared to have caused the local extinction of these aquatic species.

Colinvaux (1972) hypothesized that the cause of the drying was the northward migration of the annual range of the ITCZ, such that its southern boundary lay permanently to the north of the Galapagos. The ITCZ is a region of strong convection where the trade winds converge. During a year, the ITCZ migrates, tracking the warmest ocean water across the Atlantic and Pacific Oceans. The arrival of the ITCZ heralds the onset of the wet season, and should it fail to reach a given location, rainfall for the year may be greatly reduced. Newell (1973), a climatologist, responded to Colinvaux's suggestion by observing that steepened temperature gradients between the vast Laurentide ice-mass and the equator would have made a northward ITCZ migration far less likely than a southerly one, and subsequent research provides overwhelming support for the ITCZ migrating southward of its modern position during cold episodes (Haug *et al.* 2001, Chiang *et al.* 2003, Sachs *et al.* 2009). Thus the discussion of the placement of the ITCZ in the Eastern Equatorial Pacific during glacial-interglacial cycles began in the Galapagos.

Johnson & Raven (1973) highlighted the potential importance of the drying of the Galapagos highlands in explaining the unusual relationship of endemic species to elevation on the islands. On most oceanic islands endemicity increases with elevation, but the opposite is true on the Galapagos. If the islands lost their cloud cover, arid zone species would have moved upslope and displaced the montane elements, so the montane flora may be essentially a product of the Holocene (Johnson & Raven 1973).

Another target of the exploratory research phase was the hypersaline landlocked crater Lago Guerrero of Genovesa. The lake is about 29 m deep, and is apparently connected to the ocean by subterranean systems. The low rainfall of Galapagos precludes the maintenance of lowland lakes without hydrological subsidy from the ocean. Because of strong evaporation, these lakes become hypersaline. L. Guerrero even has a tidal cycle, but because of the complex phreatic pipes and sumps connecting it to the ocean, that cycle is a few hours out of phase with adjacent Darwin Bay. The 6-m core raised from the deepest part of the lake was beautifully banded, with hundreds of fine laminations separated by plates of white carbonate. A crucial question was: how can a lake in what appears to be a very stable setting develop banded sediment?

At high latitudes, annual bands in lakes often occur as a couplet, or pair of bands, formed by spring thaw and summer algal blooms. When such annual structure is found, it guarantees that there has been no post-depositional bioturbation, and allows researchers to reconstruct records at annual, even seasonal, scales. In the tropics, banded sediments usually reflect storm events, or the onset of rainy season conditions that erode weathered clays to form a reddish layer, followed by an algal bloom that forms a green or black layer (Bush *et al.* 1992). These banding events are seldom truly annual. Another means of forming laminated sediments is if the lake is fluctuating between supersaturated and fresher states. Each time that evaporation drives lake level down, salts precipitate to form a layer of gypsum or calcium carbonate, which appears as a thin white band. As the lake becomes fresher, algal material is deposited as a contrasting layer. Again, these laminations are unlikely to be truly annual. In his original sedimentary description of the islands, Colinvaux (1968) alluded to such mechanisms to explain the changes in sediment color in the mid-Holocene core section from El Junco, but the exact origin of the laminations remained obscure.

Both the Genovesa record and the El Junco record contain sections of core that are finely laminated. In the case of El Junco, the banding probably reflects changes in the precipitation:evaporation balance, leading to deep conditions with hypoxic bottom water and very little bioturbation. The laminations of the lowland lakes, however, cannot be explained so simply. These lakes do not have catchments of weathered clay, and so long as sea-level is stable their level is basically invariant with respect to climate because of direct connection with the ocean. Consequently, the sediments should be monotonous in color, chemistry and texture; but they are not. The Genovesa sediments are very complex, but a strong discontinuity in the core is evident at about 2 m depth. Deep rust-reds alternate with ochre-colored sediments in the upper 2 m section, whereas blue-green layers alternate with dull emerald green layers and black sections lower in the core. In this case, the white bands do not appear to have been derived under evaporitic conditions; at least some of them are composed of almost pure layers of coccolithophores (single-celled marine algae with platy exteriors of $CaCO_3$). Other white bands are comprised of calcium carbonate crystals, and one grayish-white band appears to be a tephra. Textures of the bands vary from being almost gelatinous to being as brittle as thin china. How can such an apparently constant sedimentary context produce such complex patterns?

An early hypothesis was that some of the pattern may have been biologically induced through variations in the size of sea-bird colonies (Goodman 1972). Genovesa supports about 250,000 boobies *Sula* spp., which can move substantial amounts of marine-derived nutrients, particularly phosphate, onto the island. If variations in booby colony size changed through time, so too would the phosphate loading of the lake, and the algal biomass of the sediments. The Genovesa core proved undatable with conventional large-sample radiocarbon techniques, as sections of the upper 2 m of the column had ^{14}C ages older than those below. The unruly dates, which all ranged between 4400 and 6400 years in age, prevented a full analysis being published (see Goodman 1972).

In 1969, a novel hypothesis of climate change that projected vast Amazonian droughts during the ice ages, grabbed the attention of paleoecological researchers (Haffer 1969). The Galapagos were taken as a prime example of this aridity, as proponents and detractors of the "refuge hypothesis" sought to test the antiquity of Amazonia as a primarily forested biome. Perhaps because the paleoecological answer for the Galapagos was "known", and the obvious coring sites had been exploited, the islands were largely ignored for several decades.

TRANSITION TO HIGH-RESOLUTION SAMPLING

Paleoecological data from the Amazon and adjacent regions pummeled the refugial hypothesis (Colinvaux 1987, Bush & Colinvaux 1990, Colinvaux *et al*. 2001) and demonstrated that there had been no such widespread long-lasting aridity. There had been drought-prone episodes in the last 2 million years, but not ones that lasted for the 100,000 years of recent ice ages. Rather they seemed generally to last < 10,000 years, and to be too weak to disrupt the Amazon forest landscape (Bush *et al.* 2002). The explanation was that tropical lowland climates were influenced by the precession of the equinoxes, which causes the Earth's axis of tilt to point closer to or further from the sun at midsummer's day. This either enhances seasonality (pole points towards the sun in hot, wet season) or depresses it (pole points away from the sun in hot, wet season). An entire precession cycle takes 19,000–23,000 years to complete and results in dry events that last less than half a cycle. Based on precession, a mid-Holocene drought would be predicted for the southern Neotropics.

In South America, such a dry event was first documented in the Andes, by Servant *et al*. (1981), but was largely ignored because researchers were still focused on the glacial period. However, as records from Amazonia and the Andes accumulated, it became clear that a low lake stand between *c.* 9000 and 4000 yr BP in the southern hemisphere coincided with a time of high lake level in Central America and the Caribbean (Hodell *et al*. 1991, Bush *et al*. 1992, Baker *et al*. 2001, Bush *et al*. 2007). The Galapagos, sitting on the equator, showed evidence of moderate drying at this time, but not the extreme conditions of the Altiplano. The data from the initial investigation of El Junco had revealed a dry basin throughout the last glacial maximum and into the Holocene, but the dry event that Colinvaux & Schofield (1976a, b) documented between 9000 and 5000 BP did not repeat the full loss of the lake, and so was evidently not as severe.

Until the 1990s, most paleoclimatologists had thought of the glacial and the various climatic convulsions associated with de-glaciation in the North Atlantic region to be more interesting and dynamic than the Holocene. Arguably, we had tried to understand the past without fully understanding the variability of the present. Although wreaking havoc in the marine fauna of the Galapagos (Robinson 1985) and inducing exceptional productivity in terrestrial systems (Grant & Grant 1985), the importance of the El Niño event of 1982–3 was not immediately recognized by most paleoecologists. As the global significance of these events became apparent, attention was turned on the eastern equatorial Pacific, but this time the resolution of the studies had to be at the scale of the El Niño Southern Oscillation (ENSO) rather than the millennial oscillations of glaciation.

Historical records provided some basis for evaluating changes in El Niño frequency since the 1500s (Quinn *et al*. 1987). However, as Ortlieb (2000) pointed out, some of those records could easily be misinterpreted. Ecuador's Quelccaya ice-cap provided one of the first longer records of El Niño activity (Thompson *et al*. 1986), but this only extended the record back to about AD 500.

Because the Galapagos lay in the heart of the eastern equatorial Pacific it became an obvious place to look for the long-term history of El Niño. Almost certainly, the banded sediments from Genovesa held a clue to ENSO history, but the problems associated with dating them forced researchers to look elsewhere. A new 4-m core was raised from the crater lake on Bainbridge Rocks, which was dated using ^{14}C accelerator mass spectrometry (Steinitz-Kannan *et al*. 1998, Riedinger *et al*. 2002). Why this core yielded suitable sediments to form a chronology, but Genovesa did not, may indicate a lack of volcanic activity at Bainbridge, contrasting with regular out-gassing at Genovesa in the last 6000 years. Bainbridge is another hypersaline lake, fed from beneath by seawater. Its sediments are banded and inferred to reflect changes in lake chemistry driven by excess freshwater input during El Niño events. In addition to suggesting that extreme rainfall events resulted in the in-wash of clays to form siliciclastic laminae, Riedinger *et al*. (2002) suggested that weaker events may have resulted in carbonate deposition. They hypothesized that stratification of the lake by rainwater or wave-driven seawater forming a fresher floating lens of water could have led to meromixis and developed strong reducing conditions in the hypolimnion. Under such conditions carbonate would precipitate out. Thus, the frequent carbonate bands probably represent moderate El Niño events, while the siliciclastic bands represent extreme events. By looking at the composition and frequency of the bands, Riedinger *et al*. (2002) inferred the relative activity of El Niño for the last 6000 years.

A recently published lake sediment record from El Junco adds to the emerging picture of how ENSO changed through the Holocene (Conroy *et al*. 2008). Changes in grain size in this sediment core reflect changes in lake level and precipitation events, with larger-diameter particles (sand, relative to clay and silt), deposited from high intensity precipitation events. Today, intense rainfall in Galapagos is exclusively associated with El Niño events. Thus Conroy *et al*. (2008) inferred that past periods of increased grain size in the El Junco core reflect El Niño event frequency or intensity. The record of percent sand from El Junco indicates a shift toward more frequent El Niño events 4200 years ago (Conroy *et al*. 2008). A period of unusually frequent, perhaps also intense, El Niño events also occurred between 2000 and 1000 years ago.

Research in the Ecuadorian Andes at Lake Pallcacocha (4120 m altitude) (Rodbell *et al*. 1999, Moy *et al*. 2002) corroborated much of the observed pattern detected in Bainbridge and El Junco, though differing in some of the detail. Times of very active ENSO appeared to have more events (positive or negative) than in the past century, while events in other periods seemed relatively sporadic. Very active phases were documented in both records between *c*. 2200 BP and 1000 BP, with a marked burst of activity 800–700 BP. The mid-Holocene, from 9000 to 4000 BP, was a time of low lake levels and weakened ENSO. Strong El Niño events still occurred, but were relatively rare. However, neither the Bainbridge record nor the Andean record is a perfect measure of past El Niño activity. Bainbridge is only separated from the Pacific by a 3 m high, 10 m wide berm that bears obvious signs of regular overwash. If laminations are partly caused by overwash influencing chemistry, storms unrelated to El Niño events could contribute to the observed banding. In contrast, the Andean record lies so far from the ocean and the center of upwelling that other factors could influence its history of precipitation and laminations.

Interest in ENSO activity quickly changed into a broader concern with overall climate change and the role of anthropogenic forcing. Dunbar *et al*. (1996) investigated the isotopic signature of uplifted corals in Urvina Bay, which provided a 400-year history, suggesting that the 1600s and early 1800s were cool, and that the 1700s were warm. An unusual observation was that the period 1880–1940 appeared to experience lower sea-surface temperatures. These data were not replicated in an analysis of corals from Palmyra Island, which showed a warming trend beginning around 1880, accelerating markedly after 1950 (Cobb *et al*. 2003). This trend has been found in a recent calibrated proxy record from El Junco (Conroy *et al*. 2009, 2010), and agrees with a general pattern in Pacific reef systems (Cole 2003). Such apparent disparities suggest that the Pacific Ocean is less homogeneous than we might assume. Local changes in upwelling, gyres, and surface currents can all induce local changes, without necessarily being representative of the regional picture.

Some of the latest research on El Junco draws on new proxies for past precipitation, such as hydrogen isotope ratios in fossils of the alga *Botryococcus braunii* (Zhang *et al*. 2007, Zhang & Sachs 2007). These new tools suggest relatively wet conditions during the Little Ice Age (*c*. 1400–1800), terminating with a dry event that peaked around 1870, before a trend toward wetter conditions through the 20th century (Sachs *et al*. 2009). Traditional methods are also being used, such as fossil pollen and diatoms, but these are being analyzed at much higher temporal resolution than before (*e.g*. Conroy *et al*. 2008, Restrepo *et al*. 2008, Conroy *et al*. 2009). Rather than sampling at intervals representing centuries to millennia, we are now taking samples at 3–7 year intervals. The pollen data indicate increasing transport of lowland pollen types, such as *Bursera*, up to El Junco in the last 40 years. This is interpreted as being dut to increasing convection lifting pollen grains to cloud height prior to upslope deposition by rain. We hypothesize that this trend is connected to a strengthening of El Niño. Unfortunately, the local signal of vegetative response in the fossil pollen record from El Junco after 1930 is one of human-induced alteration rather than of climatic influence. Grazing animals profoundly altered the vegetation of the cone and crater, eliminating the two most abundant elements of the pollen flora of the last 2000 years, *Acalypha* and *Alternanthera* (Restrepo-Correa 2007). The diatom record, which to date is the only Galapagos proxy that correlates with instrumental climate variables, suggests a warming trend in Galapagos SST beginning in the 19th century, with modern SST exceeding those of the last 1200 years. Gridded datasets of SST, air temperature and sea level pressure also point toward warming of the eastern equatorial Pacific and weakened Walker Circulation during the 20th century (Deser *et al*. 2010).

An uncertainty inherent in subdecadally-resolved lake sediment records is assessing season-specific variability. Wolff (2010) concludes from 44 years of Santa Cruz SST data that Galapagos SST warming is confined to the warm season. Thus, the diatom-inferred SST record might be recording a warming trend during the warm season only. Precipitation, which controls the El Junco lake level, is also most strongly correlated with SST during the warm season, while during the cool season many months have zero precipitation, leading to a non-normal distribution and weaker correlation with SST (Wolff 2010). Regardless, lakes are data reservoirs, integrating precipitation on longer than monthly time-scales, so it is more meaningful to evaluate the relationship between SST and precipitation on longer timescales when considering the relationship between SST and lake level. Our observation that lake levels have been relatively high in the last half century, and that convection has been strengthened, is consistent with Wolff's (2010) observation of increased seasonality.

The last 50 years have included some exceptionally strong El Niño events (Rein 2007), but the cumulative effects of strong ENSO variability have yet to be fully understood in the context of evaporation:precipitation balance in the El Junco system. More research is needed to reconcile the data from diatoms, pollen and the lipid deuterium:hydrogen ratio biomarker, as they were all derived from the same core.

A proverbial elephant in the room is cloud cover. All of our proxies for past climate are derived from photosynthetic organisms and all will be influenced by growing conditions, which is why they are a climate proxy. In this system where soils, temperatures at the scale of tolerance of organisms, and daylength are constant, the strongest variables are the inter-related cloud, temperature (at the scale of shaded versus brightly lit), precipitation and light.

The presence of the *garúa*, misty rain caused by stratiform cloud that hangs at *c.* 400 m on the islands, influences all climatic factors down to sea-level. *Garúa* is strongest in the cool season and during La Niña events. The highlands are frequently so cloud-shrouded that visibility is just a few meters. Under these conditions, photosynthetic organisms will be starved of light, soils will be saturated and evaporation from the lake will stall. Conversely, the warm season brings evaporation, bright light, and soil moisture deficit. We have yet to unravel the impact that changing cloud cover has on paleoecological proxies, but note that lake hydrological modeling can be useful (Conroy *et al*. 2008).

This observation begs the question of evidence of past changes in *garúa*. We do not know for sure, but *garúa* intensity and cover have probably varied through time. That El Junco dried out during the last glacial maximum, and to some extent during the mid-Holocene dry event, could be explained by the traditional suggestion that precipitation was reduced, or that the *garúa* lifted.

Colinvaux (1972) and Newell (1973) discussed the ITCZ moving north or south to induce aridity in the islands, but the range of that movement would have to be considerable, certainly more than the *c.* 5° suggested by Sachs *et al*. (2009) for the Little Ice Age. The northward limb of the Pacific ITCZ reaches the coast of Panama at 10°N, and so a very substantial southward shift would be required to have it stay to the south of the islands. Furthermore, Glacial SSTs in the Galapagos region were probably 1–2°C cooler than modern (Lea *et al*. 2006, Otto-Bliesner *et al*. 2009), but no conclusive evidence exists regarding the possible influence of altered ENSO on the eastern tropical Pacific during the last glacial period. If the delivery mechanism of rain was still present, another possibility is that *garúa* formed less often, lasted for fewer months or for fewer hours each day. Under such conditions, rainfall coming from the ITCZ may have been largely unchanged, but the reduction in *garúa* at other times of the year may have increased evaporative loss from lakes, vegetation and soils.

A past weakening of the *garúa* is conjectural, but is a potentially testable hypothesis, and it would help to accommodate the existing data. Developing an independent measure for past *garúa* activity is one of the most important tasks ahead of us. Projections of "permanent El Niño conditions" forming in the Pacific by mid-century as a result of climate change (Cox *et al*. 2004) may be overstated (Cochrane & Barber 2009), partly because ENSO is more complex than originally thought. Indeed there is a movement towards referring to "enhanced equatorial warming", rather than a "permanent El Niño", because these two phenomena are not uniquely coupled (DiNezio *et al*. 2009). As we learn more of the complexity of ENSO, especially the possible shifts as Pacific temperatures warm between typical El Niño events and Modoki El Niños, where there is strong warming in the central Pacific but the warm pool of water does not extend to the Ecuadorian coast (Ashok *et al*. 2007), predicting what will or will not happen on the Galapagos Islands becomes increasingly difficult, since warming of the central Pacific is not automatically linked to decreased upwelling at the Galapagos. If the warming of the central Pacific is not accompanied by a switch toward classic El Niño conditions, the Galapagos will enter a climatic state without geologically recent analog. In terms of the long-term conservation of the island ecosystems, understanding what happens when the *garúa* lifts may be crucial for management.

Upland areas of the inhabited Galapagos islands have become flooded by introduced invasives such as Hill Blackberry *Rubus niveus*, Quinine *Cinchona pubescens*, and Guava *Psidium guayava*. Van Leeuwen *et al*. (2008) provided a novel use for paleoecological results on the islands in their assessment of the native or exotic status of several plant species. Using pollen and macrofossils they were able to show that some presumed invasive weeds, *e.g*. *Hibiscus tiliaceus*, occurred in sediments pre-dating human.

Another unknown is the impact of the native large herbivore, the Galapagos giant tortoise *Geochelone* spp. Tortoise populations collapsed in the mid 1800s. Ships' logs show a doubling of effort needed to secure tortoises in the 1860s compared with the 1830s (Townsend 1925). Although the natural population of tortoises is unknown, their habit of visiting highland swamps is well documented. Tortoises have been shown to have an impact on island floras through both grazing and seed dispersal (Gibbs *et al*. 2008), though more research is needed to evaluate their full role in the natural ecology of the islands. These animals thermoregulate by moving in and out of water, and all shallow pools must be regarded as potential tortoise wallows. Wallowing tortoises cause tremendous bioturbation (pers. obs. on Santa Cruz). Whether tortoises ever used the high elevation bogs, which are important core sources, as wallows remains uncertain. Under modern conditions, the tortoises do not travel so high. However, if during periods of reduced precipitation, heightened evaporation or reduced cloud cover, the tortoises used these bogs, their value as paleoecological archives would be compromised. A hopeful sign is that the bogs yield sequences of ^{14}C dates that do not exhibit reversals (van Leeuwen *et al*. 2008).

Forty years of research on the Galapagos have taught us many things about the islands, and contributed to a larger debate over the importance of the Pacific to global climates. A further insight is that a bioclimatic system as simple as a low-diversity, equatorial, desert island, surrounded by a warm sea, produces paleoecological records that are easy to interpret — unless you are trying to get the answer right.

ACKNOWLEDGMENTS

We are indebted to the people and government of Ecuador who have allowed us to work on the Galapagos Islands, especially to the Galapagos National Park Service. The logistic support of the Charles Darwin Research Station is gratefully acknowledged. This work has been supported by grants from the National Science Foundation and the National Oceanic and Atmospheric Administration of the U.S. Government. This publication is number 39 of the Florida Institute for Technology's Institute for Research on Global Climate Change.

LITERATURE CITED

Ashok, K., Behera, S.K., Rao, S.A., Weng, H. & Yamagata, T. 2007. El Niño Modoki and its possible teleconnection. *Journal of Geophysical Research* C 112(11): 7–13.

Baker, P.A., Seltzer, G.O., Fritz, S.C., Dunbar, R.B., Grove, M.J., Tapia, P.M., Cross, S.L., Rowe, H.D. & Broda, J.P. 2001. The history of South American tropical precipitation for the past 25,000 years. *Science* 291: 640–643.

Bush, M.B. & Colinvaux, P.A. 1990. A long record of climatic and vegetation change in lowland Panama. *Journal of Vegetation Science* 1: 105–119.

Bush, M.B., Miller, M.C., de Oliveira, P.E. & Colinvaux, P.A. 2002. Orbital forcing signal in sediments of two Amazonian lakes. *Journal of Paleolimnology* 27: 341–352.

Bush, M.B., Piperno, D.R., Colinvaux, P.A., Krissek, L., De Oliveira, P.E., Miller, M.C. & Rowe, W. 1992. A 14,300 year paleoecological profile of a lowland tropical lake in Panama. *Ecological Monographs* 62: 251–276.

Bush, M.B., Listopad, M.C.S. & Silman, M.R. 2007. A regional study of Holocene climate change and human occupation in Peruvian Amazonia. *Journal of Biogeography* 34: 1342–1356.

Chiang, J.C.H., Biasutti, M. & Battisti, D.S. 2003. Sensitivity of the Atlantic Intertropical Convergence Zone to last glacial maximum boundary conditions. *Paleoceanography* 18: 1094–1112.

Cobb, K.M., Charles, C.D., Cheng, H. & Edwards, R.L. 2003. El Niño/Southern Oscillation and tropical Pacific climate during the last millennium. *Nature* 424: 271–276.

Cochrane, M.A. & Barber, C.P. 2009. Climate change, human land use and future fires in the Amazon. *Global Change Biology* 15: 601–612.

Cole, J.E. 2003. Holocene coral records: windows on tropical climate variability. Pp. 168–184 *in* Mackay, A., Battarbee, R., Birks, J. & Oldfield, F. (ed) *Global Change in the Holocene*. Arnold, London.

Colinvaux, P.A. 1968. Reconaissance and chemistry of the lakes and bogs of the Galapagos islands. *Nature* 219: 590–594.

Colinvaux, P.A. 1972. Climate and the Galapagos Islands. *Nature* 240: 17–20.

Colinvaux, P.A. 1987. Amazon diversity in the light of the paleoecological record. *Quaternary Science Reviews* 6: 93–114.

Colinvaux, P. A. & Schofield, E.K. 1976a. Historical ecology in the Galapagos Islands. I. A Holocene pollen record from El Junco Lake, Isla San Cristobal. *Journal of Ecology* 64: 986–1012.

Colinvaux, P.A. & Schofield, E.K. 1976b. Historical ecology in the Galapagos Islands. II. A Holocene spore record from El Junco Lake, Isla San Cristobal. *Journal of Ecology* 64: 1013–1026.

Colinvaux, P.A., Irion, G., Räsänen, M.E., Bush, M.B. & Nunes de Mello, J.A.S. 2001. A paradigm to be discarded: geological and paleoecological data falsify the Haffer and Prance refuge hypothesis of Amazonian speciation. *Amazoniana* 16: 609–646.

Conroy, J.L., Overpeck, J.T., Cole, J.E., Shanahan, T.M. & Steinitz-Kannan, M. 2008. Holocene changes in eastern tropical Pacific climate inferred from a Galápagos lake sediment record. *Quaternary Science Reviews* 27: 1166–1180.

Conroy, J.L., Overpeck, J.T. & Cole, J.E. 2010. El Niño/Southern Oscillation and changes in the zonal gradient of tropical Pacific sea surface temperature over the last 1.2 ka. PAGES News 18: 32–34.

Conroy, J.L., Restrepo, A., Overpeck, J.T., Steinitz-Kannan, M., Cole, J.E., Bush, M.B. & Colinvaux, P.A. 2009. Unprecedented recent warming of surface temperatures in the eastern tropical Pacific Ocean. *Nature Geoscience* 2: 46–50.

Cox, P.M., Betts, R.A., Collins, M.B., Harris, J.P., Huntingford, C. & Jones, C.D. 2004. Amazonian forest dieback under climate carbon cycle projections for the 21st Century. *Theoretical and Applied Climatology* 78: 137–156.

Deser, C., Phillips, A.S. & Alexander, M.A.. 2010. Twentieth century tropical sea surface temperature trends revisited. *Geophysical Research Letters* 37 (L10701): 1–6.

DiNezio, P.N., Clement, A.C., Vecchi, G.A., Soden, B.J., Kirtman, B.P. & Lee, S.-K. 2009. Climate response of the equatorial Pacific to global warming. *Journal of Climate* 22: 4873–4892.

Dunbar, R.B., Linsley, B.K. & Wellington, G.J. 1996. Eastern Pacific corals monitor El Niño/Southern Oscillation, precipitation, and sea-surface temperature variability over the past three centuries. Pp. 375–407 *in* Jones, P.D., Bradley, R.S. & Jouzel, J. (eds) *Climatic Varations and Forcing Mechanisms over the Last 2000 Years.* Springer, Berlin.

Gibbs, J.P., Marquez, C. & Sterling, E.J. 2008. The role of endangered species reintroduction in ecosystem restoration: tortoise–cactus interactions on Española Island, Galápagos. *Restoration Ecology* 16: 88–93.

Godwin, H. 1956. *The History of the British Flora*. The University Press, London.

Goodman, D. 1972. *The Paleoecology of the Tower Island Bird Colony: A critical examination of complexity-stability theory.* Ph.D. dissertation, Ohio State University, Columbus.

Grant, P.R. & Grant, B.R. 1985. Responses of Darwin's finches to unusual rainfall. Pp. 417–447 *in* Robinson, G. & del Pino, E.M. (eds) *El Niño en las Islas Galápagos: el Evento de 1982–1983*. Charles Darwin Foundation for the Galápagos Islands, Quito.

Haffer, J. 1969. Speciation in Amazonian forest birds. *Science* 165: 131–137.

Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C. & Rohl, U. 2001. Southward migration of the Intertropical Convergence Zone through the Holocene. *Science* 293: 1304–1308.

Hodell, D.A., Curtis, J.H., Jones, G.A., Higuera-Gundy, A., Brenner, M., Binford, M.W. & Dorsey, K.T. 1991. Reconstruction of Caribbean climate change over the past 10,500 years. *Nature* 352: 790–793.

Johnson, M.P. & Raven, P.H.. 1973. Species number and endemism: the Galapagos Archipelago revisited. *Science* 179: 893–895.

Lea, D.W., Pak, D.K., Belanger, C.L., Spero, H.J., Hall, M.A. & Shackleton, N.J. 2006. Paleoclimate history of Galápagos surface waters over the last 135,000 yr. *Quaternary Science Reviews* 25: 1152–1167.

Martin, P.S. 1964. Paleoclimatology and a tropical pollen profile. Pp. 319–323 *in*: *Report on the 6th International Congress on the Quaternary (Warsaw 1961), vol. 2, Palaeo-climatological Section*. Lodz.

Moy, C.M., Seltzer, G.O., Rodbell, D.T. & Anderson, D.M. 2002. Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. *Nature* 420: 162–164.

Newell, R.E. 1973. Climate and the Galapagos Islands. *Nature* 245: 91–92.

Ortlieb, L. 2000. The documented historical record of El Niño events in Peru: an update of the Quinn record (sixteenth through nineteenth centuries). Pp. 207–296 *in* Diaz, H. & Markgraf, V. (eds), *El Niño and the Southern Oscillation: multiscale variability and global and regional impacts.* Cambridge University Press, Cambridge.

Quinn, W.H., Neal, V.T. & Antunez de Mayola, S.E. 1987. El Niño occurrences over the past four and a half centuries. *Journal of Geophysical Research* 92: 449–461.

Rein, B. 2007. How do the 1982/83 and 1997/98 El Niños rank in a geological record from Peru? *Quaternary International* 161: 56–66.

Restrepo, A., Bush, M., Conroy, J. & Overpeck, J. 2008. Vegetation and climate variability in the Galapagos Islands over the last 2000 years: A high-resolution pollen record. *Geochimica et Cosmochimica Acta* 72A: 788.

Restrepo-Correa, A. 2007. *A Late-Holocene History from Vegetation and Climatic Change of El Junco Lake, San Cristobal Galapagos Islands-Ecuador.* M.S. thesis, Florida Institute of Technology, Melbourne, FL.

Riedinger, M.A., Steinitz-Kannan, M., Last, W.M. & Brenner, M. 2002. A 6100 ^{14}C yr record of El Niño activity from the Galapagos Islands. *Journal of Paleolimnology* 27: 1–7.

Robinson, G. 1985. Influence of the 1982–83 El Niño on Galapagos marine life. Pp. 153–190 *in* Robinson, G. & del Pino, E.M. (eds) *El Niño en las Islas Galápagos: el Evento de 1982–1983*. Charles Darwin Foundation for the Galápagos Islands, Quito.

Rodbell, D.T., Seltzer, G.O., Anderson, D.M., Abbott, M.B., Enfield, D.B. & Newman, J.H. 1999. An ~15,000-year record of El Niño-driven alluviation in southwestern Ecuador. *Science* 283: 516–520.

Sachs, J.P., Sachse, D., Smittenberg, R.H., Zhang, Z. & Golubic, S. 2009. Southward migration of the Pacific convergence zone AD 1400–1850. *Nature GeoScience* 2: 519–525.

Schofield, E.K. & Colinvaux, P.A. 1969. Fossil *Azolla* from the Galapagos Islands. *Bulletin of the Torrey Botanical Club* 96: 623–628.

Servant, M., Fontes, J.-C., Rieu, M. & Saliège, X. 1981. Phases climatiques arides holocènes dans le sud-ouest de l'Amazonie (Bolivie). *Comptes rendus de l'Academie des Sciences*, Sér. 2, 292: 1295–1297.

Steinitz-Kannan, M., Riedinger, M., Last, W., Brenner, M. & Miller, M.C. 1998. Un registro de 6000 años de manifestaciones intensas del fenómeno de El Niño en sedimentos de lagunas de las islas Galápagos. *Bulletin de l'Institut français d'Etudes andines* 27: 581–592.

Sugita, S. 1993. A model of pollen source area for an entire lake surface. *Quaternary Research* 39: 239–244.

Thompson, L., Mosley-Thompson, E., Dansgaard, W. & Grootes, P.M. 1986. The Little Ice Age as recorded in the stratigraphy of the tropical Quelccaya ice cap. *Science* 234: 361–364.

Townsend, C.H. 1925. The Galápagos tortoises in their relation to the whaling industry: A study of old logbooks. *Zoologica* 4: 55–135.

van der Hammen, T. & González, E. 1960. Upper Pleistocene and Holocene climate and vegetation of the Sabana de Bogotá (Colombia, South America). *Leidse geologische Mededelingen* 25: 261–315.

van Leeuwen, J.F.N., Froyd, C.A., van der Knaap, W.O., Coffey, E.E., Tye, A. & Willis, K.J. 2008. Fossil pollen as a guide to conservation in the Galapagos. *Science* 322: 1206.

Wolff, M. 2010. Galapagos does not show recent warming but increased seasonality. *Galapagos Research* 67: 38–44 .

Zhang, Z., Metzger, P. & Sachs, J.P. 2007. Biomarker evidence for the co-occurrence of three races (A, B and L) of *Botryococcus braunii* in El Junco Lake, Galápagos. *Organic Geochemistry* 38: 1459–1478.

Zhang, Z. & Sachs, J.P. 2007. Hydrogen isotope fractionation in freshwater algae: I. Variations among lipids and species. *Organic Geochemistry* 38: 582–608.