How to sample the carbon isotopes of tropical ecosystems without leaving your armchair

Linda K. Ayliffe[1]

Research School of Earth Sciences, The Australian National University, Canberra, ACT 0200, Australia

Well-dated records of terrestrial environmental change in Southeast Asia spanning the past 50 kyr (kyr = 1,000 y) are few and far between. The problem is often one of preservation. Organic-based paleoenvironmental proxies in warm and wet tropical environments are often subject to severe microbial degradation processes rendering them unsuitable for radiocarbon (^{14}C) dating. Notable exceptions to this problem include tropical speleothems, which can be dated using the ^{230}Th method (1) and can provide information on the relative intensities of isotopically depleted Asian monsoonal rainfall back to ~400 kyr ago (2). Speleothem records tell us little about the specific ecosystem responses to past rainfall and temperature changes, however. How can we tell how much rain is needed to maintain dense tropical rain forest as opposed to more open grasslands? Pollen and charcoal records go some way toward filling this knowledge gap in tropical settings (e.g., refs. 3–5), but they can be affected by biases in the representation of local plant species and are sometimes difficult to date accurately. In PNAS, a relatively innovative technique is explored in insular Southeast Asia that uses the vegetation-derived carbon isotope ($\delta^{13}C$) records preserved in cave guano deposits (6).

In tropical regions with monsoonal climates, plants can be divided into two main categories according to the photosynthetic pathways they use. C3 plants include most trees, shrubs, and other dicots, whereas C4 plants largely comprise grasses. Because each of these has distinctly different carbon isotope compositions, it should be possible to reconstruct the changing proportions of forested vs. grassy habitats in the past by $\delta^{13}C$ analysis of preserved organic matter. In lower rainfall temperate and arid areas, soil carbonate can be used as an integrator of vegetation $\delta^{13}C$ values, but soil carbonates rarely form where precipitation exceeds 100 cm/y (e.g., ref. 7), thus ruling out the tropics. So what other means are available to obtain representative samples of vegetation in tropical settings? This is where the study of Wurster et al. (6) displays a high level of "out of the box" thinking.

Guano deposits are ubiquitous features in thousands of caves throughout Southeast Asia and accumulate from the labors of bats and cave-dwelling swiftlets (echolocating birds) (Fig. 1), which act as "random samplers" of the local insect populations. The insects, in turn, feed on the prevailing vegetation, fixing the average carbon isotope composition into their tissues in the process (8). Therefore, guano deposits represent a promising archive for preserving the average $\delta^{13}C$ of vegetation in the feeding catchment area of cave-dwelling insectivorous bats and birds. They can also be composed of well-stratified and continuous sequences and are amenable to ^{14}C dating; thus, they represent rich pickings indeed for the isotope paleoecologists among us.

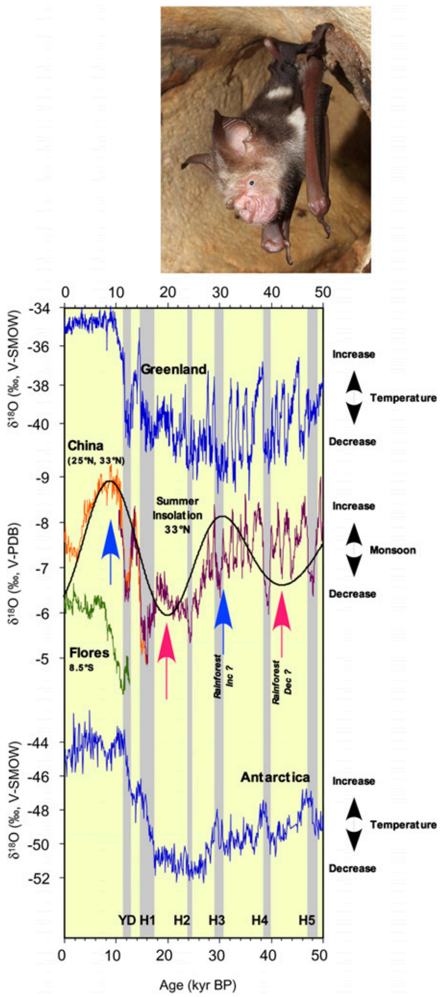

Fig. 1. Speleothem $\delta^{18}O$ records from China (11, 12) indicate dominant insolation control on monsoon strength during the past 50 kyr B.P., with greater monsoon strength occurring at times of higher summer insolation. Superimposed on this insolation signature in the Chinese speleothem record are millennial-scale events associated with the Younger Dryas and Heinrich stadials (gray shading). Coincidental millennial-scale variability is also observed in ice core $\delta^{18}O$ records from Greenland and Antarctic (13, 14) and speleothem records from Flores, Indonesia (10). Note the antiphased Northern vs. Southern Hemisphere proxy responses. Likely vegetation changes from insular Southeast Asia arising from insolation-driven changes in monsoon rainfall are marked by blue (increases in rain forest extent) and pink (decreases in rain forest extent) arrows. V-PDB (Vienna-Pee Dee belemnite); V-SMOW (Vienna-standard mean ocean water). Also shown is a cave-dwelling bat from Mulu Caves, Sarawak, Malayasia. Bats similar to this one would have contributed to the formation of the guano deposits investigated by Wurster et al. (6).

The results of the study by Wurster et al. (6) reveal spatially varying responses in the $\delta^{13}C$ of vegetation across the northern sector of insular Southeast Asia during the Last Glacial Period. The guano $\delta^{13}C$ records indicate considerable reduction of rain forests at certain times in the past 50 kyr in Peninsular Malaysia and the southern Philippines but more persistent forest cover in northern Borneo. The results suggest that ecosystem responses to past changes in climate were quite site-specific. This highlights the utility of the guano isotope technique in providing a realistic and complete picture of ecosystem responses to climate and a deeper understanding of ecosystem resiliences to climate change. The potential detail available from the guano technique is astounding. Imagine how useful another 20 such guano-based vegetation reconstructions spread throughout Southeast Asia would be to the climate modeling community wishing to incorporate vegetation structures into its model simulations (e.g., ref. 9). From the collective knowledge gained by our Flores research team (ref. 10 and accompanying background story) as a result of extensive fieldwork and caving exploration in Indonesia and Southeast Asia, it would not be unrealistic to surmise that at least one long guano record could be obtained from at least one cave in every river valley in a karst terrain.

Author contributions: L.K.A. wrote the paper.

The author declares no conflict of interest.

See companion article on page 15508 in issue 35 of volume 107.

[1]E-mail: linda.ayliffe@gmail.com.

 www.pnas.org/cgi/doi/10.1073/pnas.1010665107

The guano isotope records of Wurster et al. (6) also show that vegetation in this tropical region has responded dynamically to climate forcings observed in other parts of the Southeast Asian monsoon system during the Last Glacial Period (e.g., refs. 11 and 12). For instance, the close correspondence between guano records from the Philippines and speleothem $\delta^{18}O$ records from China (at non-Heinrich event times) between 30 and 15 kyr B.P. is suggestive of insolation forcing as the common driver. The maxima in summer insolation at ~30 and ~10 kyr B.P. (Fig. 1) correspond to periods of increased monsoon strength and rain forest expansion at this site, whereas the insolation minimum at ~20 kyr B.P. correlates with rain forest contraction. Although the resolution of the guano records of this study limits more precise comparisons, the guano records do indicate that the millennial-scale variations seen in speleothem $\delta^{18}O$ records from China and Flores (10–12) (Fig. 1) could also be shaping the response of the guano isotopes in insular Southeast Asia.

Further work on guano records such as that by Wurster et al. (6) is needed to confirm a link between vegetation changes throughout the tropics and the millennial-scale perturbations observed in Chinese speleothems and high-latitude climate records (e.g., refs. 13 and 14) during the Last Glacial Period. After all, it would be a shame to see all that diligent aerial fieldwork go to waste.

ACKNOWLEDGMENTS. I thank G. K. Smith for providing the photograph in the figure.

1. Edwards R, Chen JH, Wasserburg GJ (1987) ^{238}U-^{234}U-^{230}Th-^{232}Th systematics and the precise measurement of time over the past 500,000 years. *Earth Planet Sci Lett* 81:175–192.
2. Cheng H, et al. (2009) Ice age terminations. *Science* 326:248–252.
3. Hope G (2001) Environmental change in the Late Pleistocene and later Holocene at Wanda site, Soroako, South Suluwesa, Indonesia. *Palaeogeogr Palaeoclimatol Palaeoecol* 171:129–145.
4. Haberle SG, Ledru M-P (2001) Correlations among charcoal records of fire from the past 16,000 years in Indonesia, Papua New Guinea, and Central and South America. *Quat Res* 55:97–104.
5. Turney CSM, et al. (2006) Integration of ice-core, marine and terrestrial records for the Australian last glacial maximum and termination: A contribution from the OZ INTIMATE group. *J Quat Sci* 21:751–761.
6. Wurster CM, et al. (2010) Forest contraction in north equatorial Southeast Asia during the Last Glacial Period. *Proc Natl Acad Sci USA* 107:15508–15511.
7. Cerling TE (1984) The stable isotopic composition of modern soil carbonate and its relationship to climate. *Earth Planet Sci Lett* 71:229–240.
8. DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–406.
9. Crowley TJ, Baum SK (1997) Effects of vegetation on an ice-age climate model simulation. *J Geophys Res* 102: 16463–16480.
10. Griffiths ML, et al. (2009) Increasing Australian-Indonesian monsoon rainfall linked to early Holocene sea-level rise. *Nat Geosci* 2:636–639.
11. Wang YJ, et al. (2001) A high-resolution absolute-dated late Pleistocene Monsoon record from Hulu Cave, China. *Science* 294:2345–2348.
12. Yuan D, et al. (2004) Timing, duration, and transitions of the last interglacial Asian monsoon. *Science* 304: 575–578.
13. Stuiver M, Grootes PM (2000) GISP2 oxygen isotope ratios. *Quat Res* 53:277–283.
14. EPICA Community Members (2006) One-to-one coupling of glacial climate variability in Greenland and Antarctica. *Nature* 444:195–198.