

costs during periods of food scarcity? Do males reduce these costs by foraging in maternal core areas? How does territory use change as males grow up and gain independence from their mothers?

Finally, the inherent conservatism shown by male chimpanzees in the study of Murray *et al.* [5] differs dramatically in one important respect from our own behavior. Humans began to disperse from the African continent around two million years ago. What factors led our early human ancestors to shed the shackles of their natal homes and to roam more widely [16]? Seeking answers to these questions promise to furnish new insights into the behavior of chimpanzees as well as our own. Time is running out, though, as chimpanzees are highly endangered, with the Gombe chimpanzees severely threatened and particularly vulnerable [17]. As we approach the completion of 50 years of research at Gombe, chimpanzees there and elsewhere face an uncertain future. Effective action is required now to ensure that wild chimpanzees continue to have homes.

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C₄ Photosynthesis: Differentiating Causation and Coincidence

Determination of the historical causes of organismal adaptations is difficult, but a recent study has suggested that at least one of the transitions to C₄ photosynthesis was directly facilitated by changes in atmospheric CO₂ levels. But what about the other 50+ origins of C₄?

Eric H. Roalson

In terms of understanding mechanisms of organismal diversification, making a link between ecological, geographical, and genetic changes and the adaptive advantages those changes confer is one of the most important and interesting questions biologists are studying — and it is also one of the most difficult to solve. In order to demonstrate cause and effect between external factors affecting individuals and changes to populations of those individuals through time, two things are necessary: firstly, statistical tests that can show a correlation of the change in the influencing factors and the associated changes in the organisms; and secondly, the

demonstration of a functional advantage of the derived trait under the new conditions. While considerable effort has been expended on this second point by physiologists, less focus has been placed on statistically testing the correlations between the 'causative' agents and the derived traits. Nonetheless, various statistical tests have been employed in an attempt to show these cause-and-effect relationships, most recently in studies of C₄ photosynthesis origins in grasses [1], but also in studies of net venation and fleshy fruits in monocots [2], directionality of evolution in crustaceans [3], and feeding innovations and parasitism in birds [4], among others.

C₄ photosynthesis is a novel adaptation in plants that allows for higher productivity under warm temperatures and low CO₂ concentrations [5] and has been independently derived numerous times in plants [6]. C₄ photosynthesis is a biochemically and physiologically complex suite of characters and, while C₄ is often associated with hot environments, it is also found in high concentrations in seasonally flooded areas, saline ecologies, and a number of other ecological zones [5]. Further, recent studies have shown that selective pressures have driven parallel origins of the same amino acid residues at multiple positions in the C₄ copies of grass phosphoenolpyruvate carboxylase genes [7] and similar patterns need to be further explored in lineages outside this group [8].

In a recent issue of *Current Biology*, Christin *et al.* [1] used a phylogenetic hypothesis of relationships calibrated by fossils to date the origins of C₄ lineages in the grass family. The earliest grass lineage to develop C₄ photosynthesis was the Chloridoideae

subfamily, with an estimated origin of 32.0–25.0 Mya, a time that correlates well with the known shift in atmospheric CO₂ concentrations. Likelihood modeling of the correlation of these events suggests that the influence of the CO₂ change significantly increased the likelihood of the C₄ origin [1]. This is the clearest demonstration of the influence of CO₂ change on novel adaptations yet and is one of the best examples of historical climatic influence on diversification patterns.

But what about the other 16–17 origins of C₄ in the grass family, or for that matter, the other 30+ origins of C₄ across the rest of the angiosperms? To date, none of the other C₄ origins appears to correlate as closely with historical atmospheric CO₂ change, although the grass lineages *Aristida* and *Arundinelleae* overlap with the CO₂ change dates (28.8–14.4 and 26.4–7.9 Mya, respectively). The CO₂ threshold for selective advantage of C₄ occurred between 32 and 25 Mya and C₄ lineages (other than the three discussed above) are dated anywhere from 22 to 3 Mya [1,9].

While likelihood modeling of the influence of CO₂ change on origins of the other C₄ grass lineages suggests that this change might have influenced the likelihood of C₄ origins [1], why was there a significant lag between the CO₂ change and the origin of C₄ in those lineages? CO₂ change might have created a general physiological selective advantage, but what was the cumulative suite of conditions that led to the necessary selective advantage to drive these later origins of C₄? It has previously been suggested that heat, drought, salinity, disturbance, fire frequency, competition, seasonal rainfall patterns, and/or some combination of these factors might have played a role in selection for C₄ photosynthesis [5, 10–12]. How can we test the potential influence of these other factors?

The answer to these questions is to attempt to integrate statistically rigorous phylogenetic hypotheses, inferences of historical climatic conditions (e.g., modeling continental and regional climate change), historical biogeography, and ancestral character states in a new way. Each of these fields has made major advances in recent years that include advancements in statistical

phylogenetics [13], ancestral character state reconstructions and correlated character evolution [14,15], inferences of historical biogeographic patterns [16], and climate-change modeling [17]. What is necessary now is to build models that can be used in a statistical phylogenetic framework to test hypotheses of the influence of geography and climate on character evolution. In this case, these models would allow us to test the potential influence of historical increases in fire frequency, salinization of soils, changes in seasonal rainfall patterns, etc. on the lineages of C₄ plants that originated in a particular region.

Some progress towards the integration of these fields has occurred in the last few years, examples of which include the reconstruction of ancestral ecologies in African Cape genera [18], the testing of hypotheses of ecological specialization in insects [19], and studies that demonstrate the influence of environmental variability on cooperative breeding in birds [20], among others. However, these studies have only modeled historical ecologies on regional scales and have generally used geographically restricted lineages.

The ability to integrate the fields of statistical phylogenetics with climate modeling, historical biogeography, and ancestral character reconstruction will move us from using correlative evidence to create ‘just so’ stories on the influence of climate change on biological innovation to providing actual statistical tests of the influence of climatic factors on diversification patterns. This should be a major goal of evolutionary biologists. Christin *et al.*'s [1] study of the influence of CO₂ changes on the origins of C₄ photosynthesis in grasses is a good first step to understanding the selective pressures that led to C₄ photosynthesis adaptations, but further studies on the influence of other ecological factors on C₄ lineages that are much younger than the historical changes in atmospheric CO₂ are needed to really understand the origins of this important biological innovation.

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