MATTERS ARISING

A pitfall in random sampling

MANY statistical tests depend on random samples. A random sample can be defined[1] as a sample from a distribution (for a univariate distribution this is an area) in which each point or neighbourhood has the same probability of being chosen. It is therefore necessary to pay close attention not merely to the process of sampling, but also to the nature of the distribution itself. It is sometimes easy to misinterpret a distribution and thereby invalidate the resulting test. For example, one can treat as stationary a distribution which may change over time. So stated the trap is obvious, but it can be subtle and occasionally catches excellent biologists. The question is totally different from estimating the shape or position of an average distribution determined *post facto* from a non-stationary process. Such an average distribution exists statistically but may have no causal meaning; an obvious example is the joint distribution of annual income of all residents of London since 1800.

Cole[2] criticizes the work of Evans and Murdoch[3], who showed that herbivorous insect species in a community are a roughly constant proportion of all insect species over a season, despite much turnover. They therefore showed that the distribution is stationary, an important result. Cole not surprisingly found that Evans and Murdoch's data are not significantly different from what they would be if they were random samples of the same size from the total species pool. He then concluded that the data are irrelevant to ecological processes.

The fallacy is in assuming that there is a uniform pre-existing population from which samples are drawn (commonly without replacement, which affects the statistics in a subsidiary way). However, the very existence of such a stationary population is the interesting question, because it implicitly assumes that the relevant properties (here, diet) of the species sampled at different times are the same. Otherwise there would be no overall distribution which could be sampled randomly, and no reason to expect approximate constancy over time in the proportion of herbivores.

Thus, the results of Evans and Murdoch[3] do add support for the idea of a dynamically maintained balance in trophic structure. This balance also has other aspects, notably in energy flow, and its control remains a central problem in ecology[4].

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Anomalous ^{13}C depletion in Precambrian organic carbon

SOME isotopic analyses of Precambrian reduced carbon which is strongly depleted in the heavier ^{13}C isotope have been reported by Schoell and Wellmer[1]. They have argued that these anomalous graphitic carbons might be isotopically light as the result of a fractionation related to methane bacterial action in the Precambrian. This argument is quite reasonable insofar as it assumes that the organic carbon in most Precambrian and early Phanerozoic sediments is itself normal. However, the average isotopic value of such reduced carbon is normal only from the experimental standpoint. When placed in context with the algal biota presumed to have been responsible for its origin and overall composition, it is also anomalously depleted of ^{13}C.

In Fig. 1 of ref. 1, and in other similar compilations[2–5], the mean values for δ^{13}C(PDB) cluster around −24 to −28‰. Such values appear quite normal when compared with the reduced carbon of modern C_3 terrestrial plants[3,4,6,7]. However, a substantial land plant community did not develop until the Silurian, so that when compared with the reduced carbon from modern marine algae and algal mats, these 'normal' Precambrian isotopic ratios become disturbingly anomalous, and are especially so for the carbonate stromatolites[5,8]. Present-day marine algal organic carbon is significantly heavier isotopically, with mean values ranging from −18 to −20‰ (refs 3, 4). Modern marine algal mats are even heavier[8–12], with values ranging from −8 to −19‰. This difference between the average terrestrial isotopic values and the average marine values of reduced carbon is so striking that it has been used to evaluate the impact of land-derived organic matter in modern marine sediments[13,14].

In the absence of a significant terrestrial biota in the Precambrian, how can average values ranging from −24 to −28‰ be explained? Those who have discussed this problem (see refs 3, 8, 10, 12, 15) have variously concluded that the depletion might be the results of: preferential diagenetic enrichment of isotopically light (lipid) fractions; a higher CO_2 partial pressure in the Precambrian environment; or perhaps different primitive metabolic fractionations.

When compared with data on ancient organic matter having both carbon isotopic and H/C atomic ratios[2,16,17], recent laboratory-simulated thermal maturation experiments on algal mat kerogen[11] do not support the diagenetic argument. In these experiments only the most immature algal mat kerogens showed any tendency towards ^{13}C depletion; all mature kerogens (H/C atomic ratios <1.0) were enriched in ^{13}C.

Some laboratory experiments with marine algae grown under elevated CO_2 (1.5 to 3.5%) have produced carbon isotope ratios consistent with the idea of an increased level of CO_2 in the Precambrian[10,15]. But the low cell densities involved and the absence of a potential for bicarbonate-derived CO_2 in these experiments makes them doubtfully applicable to the conditions in which the carbonate stromatolite mats of the Precambrian thrived.

While the very depleted values reported by Schoell and Wellmer[1] and others[2] are certainly anomalous in their own right, and may be the result of Precambrian biogenic methane, a more important anomaly remains. Until the average isotopic composition of organic carbon in a variety of Precambrian and Phanerozoic marine deposits can be explained in a consistent fashion, interpretations of the data to infer the physiology of the organisms involved, or the environments in which they were living, must be considered as tentative. This is especially important to timing the onset of oxygenic photosynthesis in the early history of life[18].

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