Faunal turnover patterns in the Pliocene and Pleistocene of southern Africa

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Evolutionary trends among African mammals during the Pliocene have been attributed to climatically induced turnover pulses.[1–5] It has been posited that the origin of the genus Homo *was correlated with and perhaps caused by a putative climatic shift* circa *2.5 Myr (million years ago).[4–6] This notion was tested by a compilation of identified late Pliocene and Pleistocene fossil fauna from the southern African subcontinent. First and last appearances of numerous mammalian species coincide with apparent speciation events among the hominids. However, expectations based on a simulated fossil record modelled under conditions of constant turnover affecting random species and subsequent random sampling correspond closely to the observed evolutionary trends. Thus the southern African data do not support a model of turnover pulses and may contest the hypothesis of climatic causation.*

On the basis of the fossil Bovidae, Vrba[1–3] hypothesized that turnover pulses characterized the evolutionary record of the African Pliocene. The particular pulse that may have resulted in the origin of the genus *Homo* was causally linked to a global cooling event at about 2.5 Myr,[4–7] although many, including Darwin,[8] have doubted the necessity of climatic forcing to explain evolutionary trends.[9–11] If the apparent turnover pulse seen among bovids represents a punctuated evolutionary event induced by a climatic shift, then lineages of other mammalian families of the African ecosystems should be affected as well.[5,12] This can be tested with a recently compiled database of southern African fossil mammals from well-sampled sites of the Pliocene and Pleistocene.[13,14]

Mammalian species identified from fossil site units of southern Africa, mostly cave deposits, were compiled from the literature.[13,14] Dating of the sites has long been problematic among cave sites, so a synthesis of biochronological dates proposed on the basis of bovids,[15] cercopithecids,[16,17] suids,[18] and total combined mammalian fauna[13,14,19,20] was used (Table 1).

Table 1. Fossil site units, approximate ages, and number of species sampled, as used for parameters in the simulation. A total of 205 species is represented at these sites, of which 107 are extinct in southern Africa. The earliest dates from each site's age range were used for the dates of species' first appearances, and the later dates for last appearances.

Site unit	Age (Myr)	Sample size
Makapansgat Member 3	3.00 – 3.20	51
Makapansgat Member 4	2.80 – 3.00	34
Taung Dart Deposits	2.60 – 2.80	7
Sterkfontein Member 4	2.50 – 2.60	45
Taung Hrdlic&&ka Deposits	2.40 – 2.60	33
Sterkfontein Member 5	2.00 – 2.20	31
Kromdraai B	1.90 – 2.00	33
Kromdraai A	1.70 – 1.80	48
Swartkrans Member 1	1.60 – 1.70	46
Swartkrans Member 2	1.30 – 1.40	25
Swartkrans Member 3	1.20 – 1.30	34
Plovers Lake	1.00 – 1.20	24
Cornelia	0.80 – 0.90	18
Elandsfontein Main	0.40 – 0.70	40
Cave of Hearths (Acheulian)	0.60 – 0.70	29
Florisbad Springs	0.10 – 0.20	22
Klasies River Mouth	0.08 – 0.10	34
Equus Cave (MSA levels)	0.03 – 0.10	46

The total mammalian perspective presents a picture initially suggestive of a pulse with 27 species first appearing at sites spanning the time range of 2.4 to 2.6 Myr, and 21 species making their last appearance during the same time period (Fig. 1). Counts of first and last appearances also swell during the time period of 1.6 to 2.0 Myr, corresponding with the southern African emergence of the genus *Homo* and *Australopithecus robustus*.[12] Vrba[1,2] noted further that the dominant fauna at fossil sites had changed.

Taphonomic processes,[10,21] regional ecological variations,[13,14,22] differential faunal representation and sampling in site units (Table 1) and temporal gaps in the fossil record (Fig. 1) may obscure the correlation between real species' durations (origins and extinctions) and that apparent in the fossil record (first and last appearances). In order to test the effects that these factors could have had in relation to the apparent turnover pulses, the fossil data were compared with simulated samples derived under a gradualistic model. The turnover pulses should be distinct from the simultaneous first and last species' appearances that would be expected under a regime of continuous turnovers.[1,5]

A computer model was constructed to simulate constant turnover through the past 3.2 Myr and subsequent sampling of the fossil record. Origin and extinction dates were simulated by randomly assigning beginning and ending ages to an array of 300 possible species (some of which never 'evolved') at 100-kyr (thousand year) intervals, using a deterministic turnover rate. The population size available for deposition and preservation during any 100-kyr period was placed at a base level of 105 species, the greatest number of coeval species known from southern African fossil sites. A turnover rate can be determined from the fossil data, but as some of the simulated species do not get sampled at any fossil site, the actual evolutionary rate must be higher. Thus the simulation results reported here used a turnover rate that yielded an average extinction rate corresponding to that of the fossil data (Fig. 1).

In order to model the complex nature of taphonomic processes and subsequent sampling by excavation under local conditions, species for each site were chosen randomly from the simulated community existing within the time range of the site units. The number of species currently identified from the site unit (Table 1) was used as the sample size for the simulation. This produced, for each species sampled in the array, an apparent first and last appearance based on the respective maximum and minimum ages of the units at which they were sampled (with extant species having no last appearance). These dates usually differed from the simulated true times of origin and extinction.

The results of 1000 runs of the simulation were compared with the data from the southern African fossil record (Fig. 1). In all cases, the real data fell within the range of simulated frequencies. The patterns of mean simulated first and last appearances corresponded closely to the observed sequence of high and low turnover

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frequencies. A chi-square test of a contingency table of corresponding points demonstrated that there was no statistically significant difference between the mean expected frequencies and observed data points (first appearances: $\chi^2 = 9.62$, 13 d.f., $P > 0.1$; last appearances: $\chi^2 = 13.31$, 16 d.f., $P > 0.1$).[*] The model is robust, yielding a similar correspondence of patterns even when the parameters, including turnover rates and site ages (with the same sequence), were varied, or when microfauna were excluded. This can be attributed to the relative timing and proportions of samples from the fossil sites. Thus the observed synchronous frequencies of first and last appearances are what could be expected under conditions of constant, stochastically regular turnover and subsequent sampling. It is not necessary to postulate periodic pulses to account for the observed trends of turnover.

Although the simulation shows that southern African fossil data cannot be used as evidence for turnover pulses, it is not necessarily true that no pulses occurred. The randomizing factors of taphonomic agencies and site sampling, as well as our relative ability to recognize fossil species and establish accurate dates, could have concealed a small punctuated event that may otherwise be detected as being beyond the realm of chance within a constant turnover regime. On the other hand, these same factors, inherent to the fossil record, may have created the appearance of pulses even if they never occurred.

As over half of the fossil species of the past 3.2 Myr are extinct, it is conceivable that the entire period represents an increase or pulse of turnovers within the greater context of geological time. However, important caveats emerge from the simulation, as the perceived turnover rate can vary tremendously from the rate of evolution. With the total mammalian sample evolving at a constant turnover rate of 4.4 species per 100 kyr, simulated first appearances showed an apparent speciation rate of 4.0 to 5.3 species per 100 kyr. Simulated last appearances yielded apparent extinction rates of 2.9 to 3.9 species per 100 kyr. Thus observed long-term turnover rates, like the apparent pulses, must be treated with due regard for an incomplete fossil record.

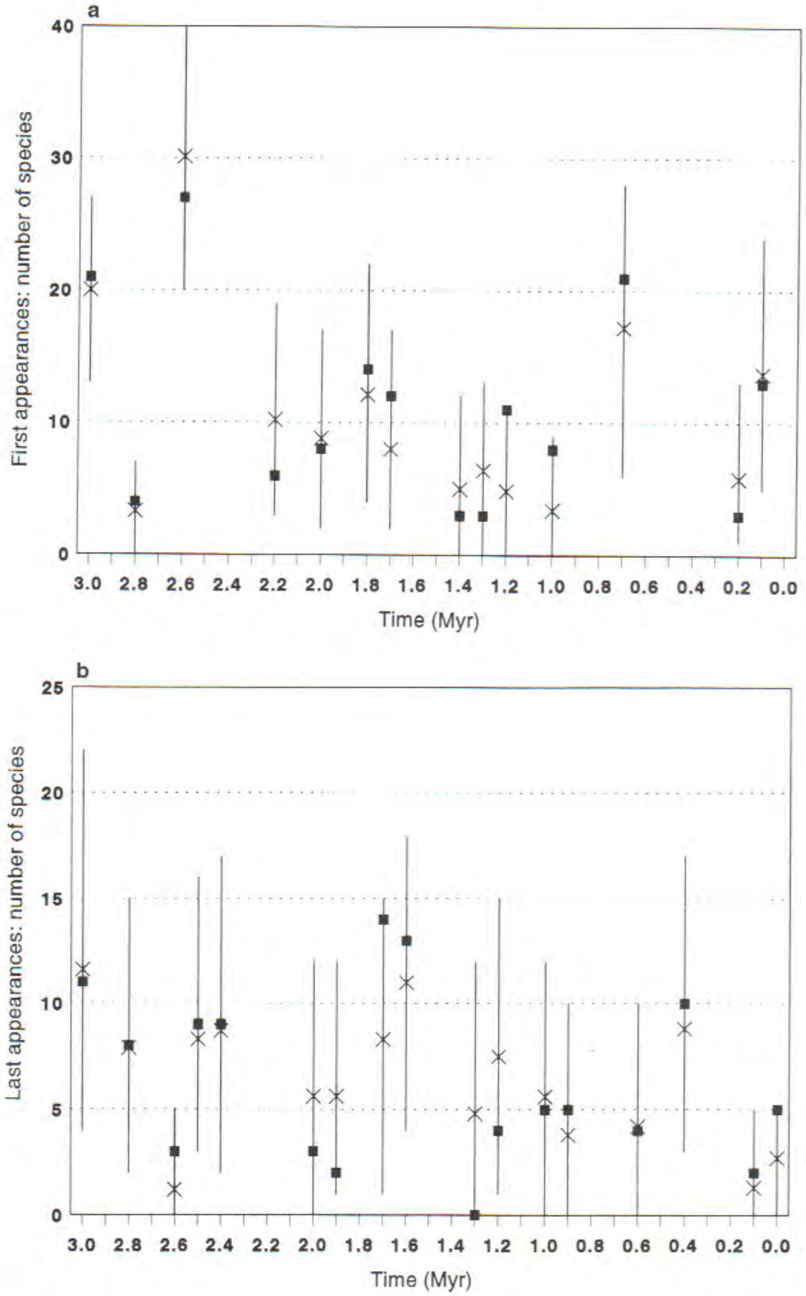

Fig. 1. Number of first appearances (*a*) and last appearances (*b*) of mammalian species in the southern African fossil record are represented by solid squares. The range of simulated frequencies is indicated by the vertical lines, with the mean simulated frequencies marked by an X. The simulation assumed a constant turnover rate of 4.4 species per 100 kyr (the figure was stochastically rounded to a whole number for each time interval). It began with 105 species of which 51 were sampled as first appearances at 3.2 Myr (representing Makapansgat Member 3 — not shown). The number of species thus sampled ranged from 180 to 221, with an average of 200 (compared with 205 species in the southern African fossil record). Last appearances ranged from 92 to 126 species, with an average of 107 as in the southern African fossil record.

The lack of evidence for turnover pulses among southern African mammals may challenge the notion that climatic cooling events in the Pliocene and Pleistocene caused speciation events among early hominids and other animals. A gradualistic evolutionary model involving complex ecological interactions within the biotic community, without abiotic forcing, is equally tenable.

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[*] Due to the presence in the contingency table of expected cell frequencies less than 5, the chi-square value may be overestimated. This can be corrected by combining the low cells with their nearest temporal neighbour, although some information is lost in the process. This was done for the data, confirming no significant differences between the empirical data and mean frequencies derived from the simulations (first appearances: $\chi^2 = 8.77$, d.f. = 10, $P > 0.1$; last appearances: $\chi^2 = 10.76$, d.f. = 10, $P > 0.1$).

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Errata

In the article 'Competition is tough' by W. Blankley (*S. Afr. J. Sci.* **91**, 499), the following values of gross domestic products should have been cited: for Ireland, US$52.1 billion; for Mexico, US$377.1 billion; the GDPs for Finland, Denmark and Norway range between US$98 billion and $146 billion.

Atmospheric pollution maps to aid policy-making and focus research

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Pollution-related research in this country is fragmented, unfocused and inadequate to meet the needs of policy-makers. To address this problem, the CSIR has devised a draft scheme which aims to address and integrate the three main components of the air pollution problem: assessment and measurement of air quality, evaluation of the effects of poor air quality, and management of air quality.

This scheme, dubbed ADRAS for Atmospheric Deposition Risk Advisory System, is aimed at involving all parties interested in air quality. It provides a framework by which information gathered by means of nation-wide research efforts and monitoring can be integrated and presented to policy-makers in a form that is concise and easy to interpret. The integrating tool of ADRAS is the 'critical loads' approach. This has been developed in Europe, largely through the United Nations Economic Commission for Europe (UN-ECE), which is using critical loads to refine sulphur and nitrogen emission protocols for Europe.[1] The critical load is defined as the maximum quantity of a given pollutant that a receptor can tolerate without suffering any adverse effects.

The critical load approach involves three steps. The first is to map the actual levels of deposition of a given pollutant. The second step is to plot the critical load of the receptor of interest (such as humans, vegetation, soils, waters, buildings) for that pollutant. The third step is to contrast the two maps, and identify the areas where actual loads exceed the critical amounts — resulting in so-called 'exceedance' maps. The areas where critical loads are exceeded are the high risk areas where negative effects are most likely to occur. 'Integrated assessment models' have been developed in Europe which evaluate the costs of different pollution control options in relation to the benefits in terms of reducing areas of exceedance.[2] These cost-benefit analyses, together with the exceedance maps, provide policy-makers with the tools they need to plan an effective air quality management strategy.

The construction and comparison of the maps is done using a geographic information system (GIS). It is the production of the maps that provides the integrating feature — and these maps are of most use to policy-makers, particularly when the com-bined assessment models are incorporated. The actual load maps require the integration of the results from a monitoring network, and atmospheric chemistry and transport models. Such maps are compared annually to establish whether pollution loads are increasing or decreasing. The method used to map the critical load of the chosen receptor depends on the quality of data available. A number of steps have been defined for this process.[3] The key process is to determine the critical chemical limit, which links the observed effect on the receptor to some change in the environment.[4] This is defined as the 'highest value of a critical chemical parameter or combination of parameters that does not cause a significant harmful response in a biological indicator'.[5] For example, acid deposition may increase aluminium in the soil to the point where it is toxic to the roots of a selected indicator tree species. In this case, the critical limit would be the level of aluminium at which root growth is first affected. Once the critical chemical limit is determined, the distribution and areal extent of the receptor needs to be defined. In the example above, the soil is the receptor, the pollutant is acid deposition.

The next step is to select the computation method. This is highly dependent on the quality and quantity of data available. The UN-ECE has defined three levels of approach.[5] The level 0 approach uses existing data to assign critical load classes based on ecosystem sensitivity. The level I approach applies steady-state models to derive critical loads for total acid (sulphur and nitrogen). The level II approach uses dynamic models, which are useful to predict the time before a critical chemical value is reached. Once the level of approach is selected, the input data need to be collected, incorporated into the GIS, and the critical loads calculated. This process identifies where there are gaps in information, and so helps to prioritize and focus research.

The CSIR has conducted a pilot study in Mpumalanga province (formerly the East-

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