RESEARCH UPDATE

Species stability

Darwin's *On the Origin of Species* linked processes observable in the present to patterns in the fossil record and formulated a coherent theory of evolution by natural selection. That link has been challenged by paleontologists on the grounds that the fossil record actually demonstrates long periods of little change in lineages interspersed with brief periods of relatively rapid change (punctuational equilibria). Stephen Jay Gould has proposed that evolutionary theory should include processes at three separable tiers of time: ecological moments, geological time (millions of years), and mass extinctions. Whatever progress is made at the first tier can be undone by the processes at the second tier (by punctuational equilibria) or third tier.

However, this hierarchy overlooks the significance of global climatic changes on the time scale of 20,000–100,000 years resulting from astronomical forcing of variations in the Earth's orbit, known as Milankovitch oscillations. These variations have profound impacts on the abundance and distribution of organisms, best seen in the fossil record of the Quaternary Period (the last 1.6 million years). Such climatic changes must have been present throughout Earth history, and thus phenomena seen in the Quaternary fossil record may illuminate processes in the history of life more generally on time scales intermediate between those of ecology and paleontology.

Milankovitch oscillations

The Earth is subject to perpetual quasi-cyclical changes over a wide range of frequencies because of its position and movement relative to other bodies in the solar system. Diurnal and annual cycles derive from the Earth's rotation about its own axis, the tilt of that axis, and an elliptical orbit around the Sun. Tidal cycles result from weak gravitational attractions between the Earth, Sun, and Moon. More generally, the Earth's orbit is influenced by gravitational attractions between the Earth and all the other bodies of the solar system, compounded by the Earth's own slightly irregular shape. The gravitational attractions are strong enough to affect the eccentricity of the orbit, the angle of tilt of the Earth's rotational axis, and the precession of the equinoxes (changing position in the elliptical orbit of the equinoxes, when the Sun crosses the Equator). These variables fluctuate with frequencies of 20,000–100,000 years. They are known as Milankovitch oscillations, after the mathematician who made the first modern calculations of these changes. They were probably established, with minor subsequent change, by the initial orbit of the Earth.

It has now been shown that Milankovitch oscillations control the pace of Quaternary ice ages. They produce variation in the amount of solar radiation received by the Earth and the latitudinal and seasonal variation of this radiation. This variation produces climatic changes, affecting temperatures, precipitation, and other aspects of the atmospheric environment. Computer models of these effects indicate that at the time of the last glacial maximum (around 20,000 years ago), continental surface temperatures were 2.5–40°C (4.5–72° F) colder than today, depending upon location and proximity to subcontinental scale glaciers. Rainfall was also affected, with important changes in the strength and location of subtropical monsoons.

Milankovitch oscillations are a consequence of gravitational attractions between celestial bodies and have, therefore, been a permanent feature of Earth history. Sedimentary rocks with regularly repeating sequences that have periodicities corresponding to orbital variations have been reported throughout the geological record, from the Precambrian to the present.

Biological time scales

The two relevant time scales here are the generation times of organisms and the duration of species, relative to the time scales of astronomical forcing of environmental change. Generation times may be from a few minutes for bacteria up to a hundred years for some trees. For most organisms, diurnal changes take place on a shorter time scale than their lives and can be considered as part of their environmental background. For those organisms that live longer than one year, the annual cycle of the seasons is a recurrent, predictable event. No organism, however, lives for periods of time exceeding the periodicity of Milankovitch oscillations, and so for no organism do these oscillations form part of its predictable environmental background. An ordinary winter kills off most of the populations of insects that have life-spans shorter than one year, and mass extinctions remove a high proportion of taxa (at any level) at approximately 26-million-year intervals. In the same manner, orbital variations have a profound influence on individuals and populations that persist within shorter time scales.

The other relevant time scale is the duration of species. Species typically persist for periods of 1–30 million years, depending on taxonomic group. They thus persist much longer than the period of Milankovitch oscillations. Insofar as the duration of species is concerned, these oscillations might just as well not be happening. This is true even for the current (Quaternary) series of oscillations with climatic changes enhanced to yield massive, subcontinental-scale glaciation across much of the Northern Hemisphere.

Effects of Quaternary oscillations

The Quaternary has long been recognized as a period of fluctuating climates. There have been several continental glaciations within the last 425,000 years and many during the last 2.3 million years. The distinctive Quaternary feature of major glaciation may be due to the present configuration of the continents or to the relatively recent uplift of the mountains of western North America and the Tibetan plateau. Apart from the direct effects of ice sheets, the major environmental aspect of the Quaternary ice ages was repeated sea-level changes on the order of 100 m (about 300 ft), as water from the oceans became locked up on land as ice.

There is an excellent fossil record of the response of terrestrial plants to Quaternary climatic oscillations, in the form of pollen and macrofossils in sequences of peat and lake sediments. In eastern North America and western Europe, the present natural deciduous forests did not exist 20,000 years ago but developed during the period from about 15,000 to 5000 years ago by the spread of the individual species concerned from full-glacial refugia. These species appear to have spread as much as 1000 km (about 600 mi) at rates of 100–2000 m (about 300–7000 ft) per year. Each species appears to have responded individually to climatic change. During this period of change, some communities persisted for only 1000–2000 years and then broke up. The forest communities of eastern North America and western Europe have no history longer than 10,000 years. Forest communities formed and broke up repeatedly during the intervals between successive glacial periods.

Eastern North America and western Europe were subjected to extreme temperature changes during the Quaternary because of their proximity to continental ice sheets. However, substantial changes in flora and vegetation have been identified in nonglaciated regions that experienced much smaller temperature changes. These regions were probably more representative of the likely effects of preQuaternary Milankovitch oscillations on flora and vegetation. There is no doubt that tropical forests, even in lowlands, experienced substantial changes during the climatic shifts of the Quaternary.

The late Quaternary fossil record for animals is less complete than for plants, but it has led to the same conclusions. Communities of mammals and beetles, for example, formed and broke up as the climates changed, because each species responded individually. Similarly, marine organisms were also highly mobile, on spatial scales of whole oceans, in response to Quaternary climatic changes. Such change happened repeatedly and regularly on time scales of only a few thousand years, much less than typical species durations.

Evolutionary consequences

The environmental history of the Quaternary is undoubtedly of great interest for the history of modern communities. This history assumes a greater significance, however, if it can be read as a model for the way that species have responded to climatic changes of the frequency of Milankovitch oscillations.

Over periods of ecological time, climates may be constant enough for stable communities to develop. In such circumstances, adaptation and evolution by Darwinian natural selection takes place. As climate changes in response to Milankovitch oscillations, these communities break up and new communities develop under the new conditions of climate and other aspects of the environment. Many species will have shifted their distributions on a subcontinental or suboceanic or even larger scale. Adaptations accumulated under the previous relatively stable conditions are likely to be lost unless they prove workable. It is unlikely that adaptation could proceed in the same direction as before: the climate has changed, the species may be living in a different environment, and its competitors have changed. Thus, orbital forcing of climatic and environmental change on time scales of 20,000–100,000 years may undo a substantial fraction of any progress accumulated at a microevolutionary level in ecological time, leaving mass extinctions (on time scales of tens of millions of years) to undo any lineage trends resulting from speciation events in the 1–10-million-year time scale. Gould's three-tier hierarchy should thus be expanded to four tiers for a more complete understanding of the processes controlling evolutionary patterns seen in the geological record and for a proper integration of paleontological and ecological evidence (see **table**).

Temporal hierarchy of dominant processes controlling evolutionary patterns seen in the geological record

Tier	Periodicity years	Cause	Evolutionary process
First	—	Natural selection	Microevolutionary change within species
Second	20,000–100,000	Orbital forcing	Disruption of communities, loss of accumulated change
Third	—		Speciation
Fourth	~26 million		Sorrting of species

Most paleontological research takes place at the time scales of the third tier, which is too coarse to delineate what is happening at lower tiers. All ecological research takes place at the first tier, and the problem has been to integrate the two time scales. Until recently, the Quaternary ice ages seemed to form a barrier to this integration, because the one slice of time available for the intermediate time scale seemed to be atypical of Earth history as a whole. Now that it has been accepted that the ice ages are merely accentuated expressions of perpetual variations in the Earth's orbit, it is clear that the data of Quaternary research can be used to illuminate processes in the history of life on time scales between those of ecology and paleontology: the type of change that has taken place in the Quaternary has been operating throughout Earth history. The result reinforces the concept of punctuational equilibria and makes it more difficult to maintain the original thesis of Darwin that processes visible in ecological time build up into the macroevolutionary trends seen in the paleontological record.

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