1 · *Introduction*

The Earth has experienced repeated 'ice-ages', when glaciers extended over the continents and sea-levels dropped, changing the configuration of land and sea. The most recent ice-age saw the emergence of our own species, and a host of wonderful animals roamed the land. This ice-age has been an important focus of historical explanation for the origins of our modern landscapes, vegetation, and distribution of flora and fauna.

But there is much more to ice-ages than historical story-telling. Events at any period in Earth history are controlled by processes operating on a variety of time-scales, continuously from those we can see and experience directly up to the age of the Earth itself. But this range of time-scales has become divided by different academic traditions. Ecologists deal with processes operating on human time-scales and work with modern species, Quaternary palaeoecologists work with the fossil record of the same species during the period of the most recent ice-ages, and palaeontologists (mostly) occupy the rest of geological time. That is the theory. In practice, there is some dialogue between ecologists and palaeontologists, perhaps through the continuing influence of *On the Origin of Species* (Darwin 1859), but Quaternary palaeoecology receives barely token attention from either group. For example, a recent prominent symposium volume on *Perspectives in Ecological Theory* includes an 'Ecology and Evolution' section, with papers on population genetics, palaeontology, and a discussion of them (Feldman 1989; Stanley 1989; Travis & Mueller 1989). Why is the record of events on intermediate (Quaternary) time-scales not contributing to ecological and evolutionary theory? Is it because there is nothing of significance happening on those time-scales? Or because no-one is aware of what is happening? Why do Quaternary palaeoecologists keep themselves apart from these other related disciplines?

The ice-ages of the last two million years or so, provide the most accessible portion of the geological time-scale. Deposits are abundant, everywhere. Their temporal proximity means that we can work within them at time-scales measured in thousands of years, and even hundreds of years since the last major ice advance, 15,000 years ago. This temporal resolution is not normally available in the geological column. We are accustomed to the aspect of the ice-ages that treats them as part of our past, a distinctive and interesting portion of Earth history. We have been less comfortable with using the processes operating on time-scales within the ice-ages as data for our understanding of the rest of Earth history on those same time-scales. The fact that an ice-age seems like an unusual episode in Earth history has inhibited incorporation of the record in the hierarchy of time-scales influencing life on Earth.

A key point that needs to be resolved is the extent to which the Quaternary biological and environmental record can be taken as typical of the whole fossil record on the 20–100-kyr time-scale. Without it, we have no data for this time-scale, and would have to assume that processes operating in ecological time (up to hundreds of years) are effective up to geological time-scales (Gould 1985). We do have a record, but is it representative of the 20–100-kyr time-scale over the history of the Earth? What does the record indicate about evolutionary processes? To what extent is evolutionary change driven by changes in the physical environment rather than biological interactions?

This book explores answers to these questions in an attempt to address the fundamental issue of 'the business of life': how it evolves. Explicitly, the aim is to:

(i) Demonstrate that the Earth is and always has been subject to orbital variations that cause climatic changes at the surface of the Earth on Milankovitch time-scales (10^4–10^5 yr).
(ii) Determine the relative frequencies of (a) distribution change, (b) evolutionary change, and (c) extinction, where these can be shown to have occurred in clear temporal relation to climatic changes due to orbital variations.
(iii) Relate the time-scale of orbital variations to biological time-scales (life-spans of organisms, species durations).
(iv) Discuss the significance of the conclusions from aims 1–3 for theories about (a) the way in which life has evolved on Earth; and (b) the approach of ecology to interactions between organisms, and between organisms and environment.

Additionally, the history of attitudes to geological and biological data from the Quaternary will be considered in order to explore the background of the modern failure to include these time-scales in thinking about the processes that brought about the evolution of life on Earth. However, consideration of the genetical aspects of evolution is beyond the scope of this book.

This book, therefore, examines the extent to which the position of Quaternary palaeoecology at a central temporal location between ecology and palaeontology can contribute and illuminate both by extending the range of time-scales each covers. The aim is to achieve a continuum of thinking along a full range of time-scales and show that processes visible in the Quaternary record have a substantial contribution to make to ecological and evolutionary thinking. We now have the means to examine evolutionary theories against a fine geological time-scale: what is the result?

Outline

Chapter 2 covers the theoretical background of evolutionary and ecological processes. This is done through an historical approach to show the way that ideas have developed, and the state of scientific understanding about Quaternary climatic events at the time that ideas were developed. Chapter 3 describes the astronomical background for the Earth's orbital variations, how climatic change is forced by these, and then Chapter 4 presents the geological evidence for astronomically-forced climatic change throughout Earth history. In principle, the biological response to these climatic oscillations might take in any of three modes: distribution change, evolutionary change, or extinction. It is likely that all three occur, so the principal concern is with establishing the relative frequency of each mode rather than whether it exists. Response by distribution change is discussed in Chapter 5, by evolution in Chapter 6, and by extinction in Chapter 7. A post-modern synthesis of evolution and ecology across a full range of time-scales, from ecological moments to geological time, is presented in Chapter 8.

Terms and Definitions

The names and ages of stratigraphic units used follow Harland *et al.* (1990), except where there is indication to the contrary. The units 'Ga', 'Ma' and 'ka' are used to refer to dates before present in billions (10^9), millions, and thousands of years, respectively, and 'Gyr', 'Myr' and 'kyr' are used to refer to duration of time in billions, millions, and thousands of years, respectively. The term 'BP' is restricted to mean radiocarbon

Table 1.1. *Simplified geological time-scale*

Eon	Era	Period	Epoch	Age at base (Ma)
Phanerozoic	Cenozoic	Quaternary	Holocene	0.01
			Pleistocene	1.64
		Tertiary	Pliocene	5.2
			Miocene	23.3
			Oligocene	35.4
			Eocene	56.5
			Paleocene	65
	Mesozoic	Cretaceous		146
		Jurassic		208
		Triassic		245
	Paleozoic	Permian		290
		Carboniferous		363
		Devonian		409
		Silurian		439
		Ordovician		510
		Cambrian		570
Proterozoic				2500
Archaean				4000
Priscoan				4500

Source: From Harland *et al.* (1990).

years before present, where 'present' means 1950 AD. The measurement of time in radiocarbon years is not quite the same as calendar years, and calibrations have been proposed (Stuiver & Reimer 1993). Here, radiocarbon years are maintained because many of the ages concerned have entered common usage, and calibration makes little difference for the points being made.

A summary geological time-scale is given in Table 1.1 to place the geological terms used in a temporal framework. The term 'Milankovitch time-scales' is used to refer to time-scales of 10^4–10^5 yr. Throughout, the period name 'Quaternary' is used in preference to the epoch name 'Pleistocene', except in quotations, because, by covering 'Pleistocene' plus 'Holocene', it gives some coherence to a period of time that has a unity by virtue of repeated expansion and contraction of continental ice-sheets that we have every reason to believe is continuing. The term 'Holocene' is used for the most recent 10 kyr as an available name for that period of time. As yet, there are no other formally recognized subdivisions of the Pleistocene (Harland *et al.* 1990), although the deep-sea sediment stage numbers (Shackleton & Opdyke 1973), based on analyses of oxygen isotopic ratios ($\delta^{18}O$), are frequently used informally. The term 'last interglacial' is used to refer to the phase near 125 ka when the Earth's climate was last similar to the present (probably slightly warmer), and the term 'last glacial' is used to refer to the latest Quaternary cold oscillation (about 115 ka until 10 ka). Viewing the Holocene as a period of time in Earth history equivalent in status to the Pleistocene (as in 'the end of the Pleistocene') has had a stultifying effect on consideration of Quaternary events: the acceptance of the Holocene as just another phase in (so far) 1.6 Myr of Quaternary climatic oscillations cannot come soon enough (Gould 1991).

Taxonomic nomenclature of organisms should be assumed to follow the usage of the author(s) of works cited. Each scientific name used is included in the Index, together with a brief description derived from the sources used, and additional information from Honacki *et al.* (1982), Mabberley (1987), Carroll (1988), and Vaught (1989).

I avoid the term 'cycle' when referring to anything operating through time, because time does not 'cycle'. Instead, I use terms such as 'period' or 'oscillation' to mean quantities that vary more or less rhythmically with time.

2 · *Development of ideas*

This chapter presents the current status of thinking on evolutionary processes in ecological and geological time. Subsequent chapters examine actual data from the fossil record, but, since the way we see data is shaped by the ideas available for interpretation, the development of evolutionary and ecological theory will be presented first. Evolutionary theory has, unfortunately, become replete with claim and counter-claim about evolutionary processes, and the degree to which they can or cannot be resolved with the ideas of Darwin (1859). It is now impossible to obtain a balanced view by summarizing the literature, because too high a proportion of it is already secondary. Some of the primary sources went through several editions and the author's ideas shifted fundamentally, so it can make a difference which edition is being cited (Peckham 1959). If ever an area of scientific literature had an excessive ratio of words to ideas, this is it. Much of the debate has become confused by the similarity in language and terminology of various aspects of evolution, and the scientific environment at the time of writing has not received corresponding attention.

This chapter discusses the development of ideas in evolution and ecology relative to advancing knowledge of the details of Earth history, especially with respect to the Earth's orbital variations and Quaternary ice-ages. The aim is to show how the present state of affairs came about.

Evolutionary processes

Scientific beginnings

There is a long history of evolutionary and ecological thought over many centuries (Mayr 1982). But it is during the last century that those ideas that came to shape modern thinking were expressed scientifically, especially following Charles Darwin and his contemporaries, notably Charles Lyell and Alfred Wallace.

Geology and the nature of species

Charles Lyell (1797–1875) was a British geologist who dominated geology through most of the nineteenth century. His classic text *Principles of Geology* (Lyell 1830, 1832, 1833) described the geological record in terms of modern processes, and is one of the foundations of modern geology. Lyell's philosophy on the nature of species through time was covered in the second volume of the work (Lyell 1832). He began his argument by inquiring:

> first, whether species have a real and permanent existence in nature; or whether they are capable, as some naturalists pretend, of being indefinitely modified in the course of a long series of generations? Secondly, whether, if species have a real existence, the individuals composing them have been derived originally from many similar stocks, or each from one only, the descendants of which have spread themselves gradually from a particular point over the habitable lands and waters? Thirdly, how far the duration of each species of animal and plant is limited by its dependance [*sic*] on certain fluctuating and temporary conditions in the state of the animate and inanimate world? Fourthly, whether there be proofs of the successive extermination of species in the ordinary course of nature, and whether there be any reason for conjecturing that new animals and plants are created from time to time, to supply their place? *(Lyell 1832, pp. 1–2).*

These are thoroughly modern and reasonable questions. Lyell concluded that species do have a real existence in nature, and when each first appeared, it had the attributes and organization that it does now. He thought that each species originated as a single pair (or individual, for species where that was sufficient), and that species might have been created in such a way as to multiply and spread for a particular period of time and space. He saw no evidence for the transmutation of one species into another, because there were other processes in operation that were so much more active in their nature, that they would intervene and prevent the accomplishment of any transmutation. Thus, to Lyell, the question of transmutation of species was a side issue, because it would never be likely to happen in practice even if it was, theoretically, a possibility. In answer to his own fourth question, Lyell argued that animal and plant species are dependent on certain physical conditions and on the numbers and characteristics of other species in the same region. However, all these conditions fluctuate, as a result of changing physical environments and as a result of changing distributions of species. It follows that species existing at any one period must become successively extinct. Local changes restrict the range of some species, and enable the enlargement of the ranges of others. Since new species originate in a single spot, each needs time to spread over a wide area. So there must be, simultaneously, species of recent origin and species of 'high antiquity'. He suggested, as a speculative figure, that there might be one new species and one extinction, globally, per year, which is low enough that neither extinction nor origin is likely to be observed in any one area on human time-scales (Lyell 1832).

Lyell's view on species and their origin was thus that they are created at a single spot, multiply, and spread, surviving certain environmental and biotic fluctuations, but without being transformed, and they eventually become extinct. Species, he believed, were stable units that came into existence at ecologically-appropriate points in space and time, survived for a longer or shorter period of time in dynamic ecological equilibrium with other organisms and spread to some degree, but were eventually eliminated by the pressures of the ever-changing physical and biotic environment (Rudwick 1990). Lyell was not specific about how species came into being, but his studies of contemporary geological processes showed him that the surface of the Earth is in a state of constant change, so associations of plants and animals could not always have been maintained in exactly the same spots, but shifted continually over land and sea (Worster 1985). He saw that the process of shifting distributions was likely to be a more rapid response to environmental change than *in situ* transformation, because there would always be species around better suited to new conditions than the species on the spot originally. He pointed out that, following climatic change, some species would be preserved by shifting their distributions, but the same change would be 'fatal to many which can find no place of retreat, when their original habitations become unfit for them' (Lyell 1832, p. 170). He noted that:

> if a tract of salt-water becomes fresh by passing through every intermediate degree of brackishness, still the marine molluscs will never be permitted to be gradually metamorphosed into fluviatile species; because long before any such transformation can take place by slow and insensible degrees, other tribes, which delight in brackish or fresh-water, will avail themselves of the change in the fluid, and will, each in their turn, monopolize the space *(Lyell 1832, p. 174)*.

His views on the fixity of species, and their occurrence under certain conditions of the physical and biotic environment lead to his notorious declaration that, under the right circumstances:

> the huge iguanadon might reappear in the woods, and the ichthyosaur in the sea, while the pterodactyle might flit again through umbrageous groves of tree-ferns *(Lyell 1830, p. 123).*

This seems a ludicrous statement today, and surprising from such an eminent and respected geologist. But it does follow, with a certain devastating logic, from Lyell's views on the cycling of global environments and the origin of species. This passage and its interpretation in the light of Lyell's views on geological time have been analyzed by Gould (1987). Much of the underlying thinking of Lyell on species, however, remains valid despite the spectacular conclusion, and the end point should not be allowed to obscure the basis of the arguments.

In all, there were 12 editions of *Principles of Geology* and the later editions incorporated, amongst other new material, two ideas not available to Lyell in the 1830s. The first was a discussion of Darwin's ideas about evolution and natural selection, and the second was the notion that global climatic change is forced by variations in the Earth's orbital parameters.

Lyell learned of Darwin's ideas about evolution and natural selection before the publication of *On the Origin of Species* (Darwin 1859), and was not convinced, initially. Lyell worked extensively with Tertiary molluscs, many of which can be identified to living species, and he appreciated that they must have survived changing climates since the Tertiary (Lyell 1830, 1832, 1833), which appeared to conflict with Darwin's ideas. In a letter to Darwin dated 17 June 1856, Lyell wrote:

> And why do the shells which are the same as European or African species remain quite unaltered like the Crag species which returned unchanged to the British seas after being expelled from them by Glacial cold, when 2 millions? of years had elapsed, and after such migration to milder seas. Be so good as to explain all this in your next letter *(Burkhardt & Smith 1990, p. 146).*

This question came at the end of a long letter about uplift of continents, and Darwin commented on that aspect of the letter (in a postscript on 18 June 1856 of a letter to Joseph Hooker, and in reply to Lyell on 25 June 1856 (Burkhardt & Smith 1990, p. 147, pp. 153–155). However, it appears that Darwin did not reply directly to Lyell's closing question, or comment on it anywhere else. Lyell copied the main points of his question into his journal (Wilson 1970, pp. 104–105), which suggests that he thought it was important (Burkhardt & Smith 1990).

Lyell eventually shifted his position on the question of species, accepting the idea of gradual change, but he did notice and comment again on the paradox of little change through 'the Glacial period':

we have yet found evidence that most of the testacea, and not a few of the quadrupeds, which preceded, were of the same species as those which followed the extreme cold. To whatever local disturbances this cold may have given rise in the distribution of species, it seems to have done little in effecting their annihilation. We may conclude therefore, from a survey of the tertiary and modern strata, which constitute a more complete and unbroken series than rocks of older date, that the extinction and creation of species have been, and are, the result of a slow and gradual change in the organic world *(Lyell 1875, vol. 1, pp. 306–307)*.

The idea that global climatic change is forced by varying orbital parameters had been around earlier, but only received serious attention after the mathematics were worked out by the Scottish geologist and philosopher James Croll, and published prominently in the scientific literature (Croll 1864, 1865, 1866, 1867a, b, 1868, 1875). Lyell covered this at length in the final edition of *Principles of Geology*, appreciating that there had been more than one glacial phase since the Tertiary (Lyell 1875). However, he did not realize that there had also been pre-Quaternary glaciations, and he seems to have considered that Quaternary events had little relevance for Earth history in general.

Evolution by means of natural selection

The theory of evolution by means of natural selection was developed independently by two naturalists, Alfred Wallace and Charles Darwin. Darwin was the older of the two, and worked his ideas out first. He discussed them with friends, but did not publish them until receipt of a manuscript from Wallace along similar lines forced the matter into the public domain.

Alfred Wallace (1823–1913) was an English naturalist and explorer, who spent much of his life working in the rain forests of southeast Asia and the Amazon basin. His contribution, initially as an essay sent to Darwin in 1858, was read at a meeting of the Linnean Society, London, together with documents written by Darwin, demonstrating that they had developed similar views independently. The details of how this arrangement came to be set up can be found in a paper by Beddall (1988), and references therein.

Wallace began by establishing two points, via discussion of the tendency of populations to increase geometrically if left unchecked:

1st, that the animal population of a country is generally stationary, being kept down by a periodical deficiency of food, and other checks; and 2nd, that the comparative abundance or scarcity of the individuals of the several species is