Birks and Birks

Quaternary Palaeoecology

Arnold

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Preface

The idea for this book originated in a lecture course entitled 'Quaternary Palaeoecology' to final-year undergraduate students at the University of Cambridge. It was evident that no book covered this rapidly developing and interdisciplinary subject. Therefore, we have tried to write a fairly comprehensive introduction, which we hope will be of use to undergraduate and research students with varying backgrounds in botany, zoology, geology, geography, and archaeology. We also hope that it will be of use to research workers in the Quaternary, by drawing their attention to related and perhaps relevant aspects of their subject, and as a general reference book which covers a wide variety of interests.

This book covers a broad spectrum of subjects which can be usefully drawn together in various combinations for the reconstruction of past environments. This broad coverage inevitably leads to superficial treatment of some aspects, particularly those in which we ourselves have not been directly involved during our research. However, we hope that the outline and the references given will stimulate the reader, and will give a useful lead into more detailed accounts.

Because of the interdisciplinary and international nature of Quaternary palaeoecology, the literature is vast and diverse. Therefore, we have listed references at the end of each chapter, and arranged them according to subject. References on a particular topic are thus grouped together for easy use by the student. Inevitably, some references appear more than once. We have also included references to several important and influential publications to which a student should refer, even though they are not mentioned in the chapters. New papers are constantly being published, and therefore this book was out of date as soon as it reached the publisher's hands. This is an unavoidable problem, and we have had to take our cut-off point as 1 March 1979. No papers which have appeared since then are included.

This book does not cover marine Quaternary palaeoecology in any detail. We have restricted ourselves almost entirely to terrestrial and freshwater environments, as they are the ecological settings of our personal research experience. The Quaternary palaeoecology of marine environments is a rapidly developing field, which has great potential, particularly when it can be linked to terrestrial events. It would warrant a separate book to itself.

Palaeoecology, consisting of the reconstruction of past biota, communities, and environments, is the over-riding theme of this book, and we have therefore made little attempt to describe in detail the methods used in palaeoecological investigations or the identification of the various types of fossils. These can be found readily in other reference works mentioned in the text.

We could not have conceived or written this book without the benefit of contact over several years with numerous other Quaternary palaeoecologists. We are grateful to them all for stimulating and inspiring us along various research paths by their friendly discussions and free interchanges of ideas. Our greatest debts are due to Professor Sir Harry Godwin, F.R.S., and Professor R. G. West, F.R.S., who introduced us to the subject, and who have constantly encouraged us. Our research interests and experience have also been particularly influenced by Prof. W. Tutin, F.R.S., Professor H. E. Wright Jr., and Dr. E. J. Cushing, each of whom have added a new dimension to our palaeoecological outlook. Other colleagues and friends have generously discussed their ideas and approaches with us, particularly Dr. S. T. Andersen, Professor B. E. Berglund, Professor M. B. Davis, Dr. B. Huntley, the late Dr. J. Iversen, Dr. C. R. Janssen, Professor R. A. Reyment, Dr. K. Rybniček, Professor W. A. Watts, and Dr. T. Webb III. We owe a great debt to Dr. A. D. Gordon, for his work with H.J.B.B. on the development of numerical methods

applicable to Quaternary palaeoecology. Dr. A. J. Stuart introduced us to the fascinating world of Quaternary vertebrates, and we thank him for reading this section of the manuscript for us. Numerous undergraduates and research students have enthusiastically acted as guinea pigs for ideas and techniques which we would never had the time to try out for ourselves.

We are grateful for assistance in the preparation of this book to Mrs. R. Hockaday, Mrs. A. Bennett, and Mrs. A. Ansell, who typed the manuscript so carefully, and to Mrs. S. Peglar and Mrs. S. Dalton who drafted some of the figures. The conversion of the manuscript into a book was cheerfully and efficiently conducted by the editorial staff of Edward Arnold.

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Cambridge H.J.B.B.
1980 H.H.B.

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Ecology and palaeoecology

Introduction

Palaeoecology is the ecology of the past. It is strongly linked to both biology and geology. It can be studied in any period of earth's history in which there was life. Palaeoecology's main link and relevance to modern or neo-ecology is during the most recent geological interval, the Quaternary. The Quaternary covers the last 1–2 million years and it is unique in earth's history for its oscillating climates, alternating in the latitude of Europe and North America between temperate so-called interglacial phases and cold phases within which glaciation commonly occurred, and also for the fact that man evolved during the Quaternary.

We must define the terms ecology and palaeoecology, in order to see the differences and similarities between them, to delimit the sphere of the subject of this book, and to establish the close interaction between ecology and palaeoecology. ***Ecology*** can be defined as the study and understanding of the complex relationships between living organisms and their present environment. Ideally, ***Palaeoecology*** could be defined as the study and understanding of the relationships between past organisms and the environment in which they lived. In practice, however, palaeoecology is largely concerned with the reconstruction of past ecosystems. To do this, all the available evidence, both biological and geological, is used to reconstruct the past environment. Therefore, it is difficult to deduce the relationships between organisms and their environment in the past if the evidence of the organisms had already been used to reconstruct the environment. Independent lines of evidence for environmental reconstruction are required before organism–environment relationships can be assessed.

Although, in theory, ecology and palaeoecology have similar aims and invoke many of the same biological principles, in practice they have different concepts and working methods. These differences arise for two main reasons. Firstly, past ecosystems cannot be observed directly. The biotic and abiotic components of the ecosystem must be inferred from the fossils and the sediments in which the fossils are found. Palaeoecology is thus limited to the study of past organisms whose fossils are preserved. Secondly, the fossil record on which all palaeoecology depends can be seriously distorted due to the processes of transportation, diagenesis, and redeposition. Due to transportation, evidence from one area may be mixed with and indistinguishable from that from other systems. Therefore the organisms which are preserved as fossils cannot necessarily be assumed to have lived in the system within which the fossils are found today. Due to diagenesis, fossils and other environmental evidence may be modified or even destroyed by geological processes operating in the ecosystem surrounding the fossils at contemporary or subsequent time intervals. Due to redeposition, evidence that originated at one point in time and space may be deposited and preserved with evidence derived from different points in time (either earlier or later) and space. There is thus little control in palaeoecology over what can be observed and over the range in time and space that the palaeoecological evidence occupies. Fortunately, in many instances, the limitations imposed on palaeoecology by this lack of spatial and temporal control are not insurmountable, as the processes of transportation, diagenesis, and redeposition can often be identified and their effects evaluated and allowed for.

There are six major differences in approach to the study of ecology and palaeoecology. These important differences influence the working methods used in palaeoecology.

1. An ecologist can select the organisms and the physical and chemical variables to be studied. A palaeoecologist is restricted to studying those organisms preserved as fossils, and he must use evidence from them and from the associated sediments to reconstruct the past environment.

2. An ecologist must establish and operate within defined boundaries of space and time. These boundaries, defined implicitly or explicitly, delimit the ecosystem of study. A palaeoecologist has little control over the limits in space and time represented by his fossils, due to the processes of transportation, diagenesis, and redeposition. A palaeoecologist must accept the evidence where it can be found, and attempt to decide what it represents and from where it originated.

3. An ecologist can usually plan a series of observations and/or experiments, and with care, he can make repeatable observations. A palaeoecologist can usually never repeat an observation, except perhaps for taxonomic revisions or re-examination of his samples. A palaeoecologist makes a once-only investigation of his material. Any anomalies or unusual features that are found can usually only be checked by comparison with other samples from a different part of the system of interest or from other systems nearby. Such a set of new observations is not an analogy of a repeatable experiment or recording in ecology.

4. An ecologist generally makes his observations at one or a few points in time; more rarely observations may be made over a short period (20–50 years) of time. A palaeoecologist makes observations that cover long periods of time (100–10 000 years or more). Each sample studied may represent many years (often 10–200 years), and a set of samples collected in stratigraphical order may cover many thousands of years. The time dimension, although often measured with less precision than in ecology, is much more important in palaeoecology than in ecology.

5. An ecologist is usually not directly concerned with evolutionary, migrational, and other biogeographical processes. A palaeoecologist is usually very concerned about such processes, and in some cases evolution and/or migration may be the main purpose of the study.

6. An ecologist has a wide range of strategies available for sampling ecosystems. A palaeoecologist is restricted in his sampling strategy, because the palaeoecosystem of interest is dead, partially or wholly decayed, and mixed and changed by processes of diagenesis and transportation operative up to the time of sampling.

What is the fascination, relevance, and value of studying palaeoecology at the present day?

Despite many of the limitations imposed by the nature of the fossil record, palaeoecology can provide reconstructions of past ecosystems which appear, in many instances, to be valid and useful. Inevitably such reconstructions are rather gross and frequently unsophisticated. The reconstructions do, however, enable comparison to be made with ecosystems from other periods of time, including the present, so that possible causes and mechanisms of biological change with time can be sought (Deevey, 1965, 1969). Many processes which are important in understanding modern ecosystem composition, structure, and dynamics operate over long periods of time, and thus cannot be studied within a single human lifetime. Modern ecology and biogeography can benefit directly from the results of palaeoecology and from the historical and evolutionary perspectives that palaeoecology can uniquely provide. For example, in considering the succession of organisms through time, Gould (1976) emphasized the importance of palaeoecology to modern ecological theory by saying, 'Palaeoecology can provide the only record of complete *in situ* successions. The framework of classical succession theory (probably the most well known and widely discussed notion of ecology) rests largely upon the inferences from separated areas in different stages of a single, hypothetical process (much like inferring phylogeny from the comparative anatomy of modern forms). Palaeoecology can provide direct evidence to supplement ecological theory.'

A historical, palaeoecological perspective on the development and structure of modern ecosystems and on ecological processes acting through the geological past, can provide a basis for the formulation of ecosystem models in which predictions about the future effects of environmental change can be made.

Classification of ecology and palaeoecology

There are several broad approaches to the study of modern ecology, depending on the aims and interest of the investigator. Similarly, palaeoecology can also be approached in several ways, depending upon the questions asked by the palaeoecologist.

Ecology

1. Descriptive ecology, in which the ecologist aims to describe the features of an ecosystem. He seeks simplifications of the real world by classifying and generalizing observations on specific ecosystems. Hypotheses can be tested against new, independent observations.

2. Deductive ecology. In this approach the ecologist constructs generalized dynamic models of an ecosystem that simulate the relationships between organisms and their environment. This approach of 'systems analysis' tests the value and relevance of generalized models with real observations from descriptive ecology (see Clymo, 1978, for a model of peat growth).

3. Experimental ecology. This approach attempts to simplify nature by controlling as many environmental and biotic factors as possible and by varying one or a few factors at a time in order to study their influence on an ecosystem under controlled conditions.

These three approaches are complementary and essential. Ideally an ecologist should use all three in his study of an ecosystem. In practice, ecologists tend, however, to concentrate on one approach only.

Palaeoecology

Palaeoecology can similarly be subdivided into descriptive, deductive, and experimental approaches.

1. *Descriptive palaeoecology.* This is the dominant approach in much of palaeoecology, because the reconstruction and description of past ecosystems is usually difficult and time consuming, as well as being of such intrinsic interest. In such an approach, the palaeoecologist faces sampling problems that the modern ecologist can largely avoid. Besides selecting where and how to sample and finding the relevant evidence, the palaeoecologist must decide what the evidence represents and where the fossils came from. These difficulties have inevitably led to simplifications, and the palaeoecologist uses the present to model the past by extending observations about processes within present ecosystems backwards in time. There is thus a close interaction between descriptive ecology and descriptive palaeoecology.

2. *Deductive palaeoecology.* A few attempts have been made recently to develop mathematical models to simulate palaeoecological systems (see Reyment, 1968; Harborough and Bonham-Carter, 1970). For example, Craig and Oertel (1966) presented deterministic models (i.e. models in which the random variation factor is ignored) of living and fossil populations of animals involving growth rates and death rates.

One of the few examples of the deductive approach in Quaternary palaeoecology is that of Martin (1973) and Mosimann and Martin (1975). They considered the problem of the possible cause for the sudden and dramatic extinction of many species of large mammals in North America at the end of the Pleistocene about 10–12 000 years ago. One hypothesis to account for this extinction involved the arrival and expansion of man into the previously uninhabited North American continent; man was directly responsible for overkill and extinction. It has been suggested that the early North American men were highly skilled predators with thousands of years of Palaeolithic experience in Asia. The mammalian prey was, it is proposed, unable to develop suitable defensive mechanisms within the relatively short time available.

Mosimann and Martin (1975) constructed a mathematical model to simulate how an initially small human population could increase sufficiently rapidly to cause the extinction of the large fauna. They represented the arrival of man across the Bering Land Bridge at about 12 000 years ago by starting the model with 100 men and women at Edmonton, Alberta. If this population doubled every 30 years, the model predicts that a wave of 300 000 humans would have reached the Gulf of Mexico in about 300 years, having populated an area of 780×10^6 ha (3 million square miles). Such an advancing front of humans would have been large enough to kill a biomass of large mammals comparable to 42×10^9 kg (93×10^9 pounds), which would have reflected an animal density similar to a modern African gamepark. Such a human population explosion could have resulted in massive predation, or overkill of the native mammal fauna, leading to its rapid extinction in about 300 years. As the food supply dwindled behind the advancing front, the model predicts a decline in the human population to a level in equilibrium with the environment. The model proposes a mechanism to explain the observations of a rapid extinction of large mammals in North America, and the paucity of archaeological sites of this age where both human artifacts and animal remains have been found together.

Mosimann and Martin inserted different values for population growth, animal density and biomass, etc. into their model. Even with figures well below the theoretical maximum, the result was always an extinction of the fauna in a relatively short time (see Fig. 1.1).

The deductive approach shows considerable promise, and although the numerical and computer techniques can be rather complex, there is already a wealth of experience in this type of approach in ecology.

3. *Experimental palaeoecology*. This approach involves controlled experiments using either living organisms or scale models of fossils to investigate the effect of processes and factors that are recognizable at the present day and that were almost certainly operative in the past.

Reyment (1971, 1973) has devised ingenious experiments with scale models of shells of ammonites and nautiloids in tanks of water. The experiments were designed to estimate their necroplanktonic dispersal properties, for example what shell sizes and shapes floated or sank after death. The results obtained help to explain the composition of some fossil assemblages which, due to processes of transportation, do not reflect the life assemblages of the different cephalopod shells. Other types of palaeoecological experiments involve observations in the laboratory on palaeoecologically important living organisms. For example, Reyment and Bränn-

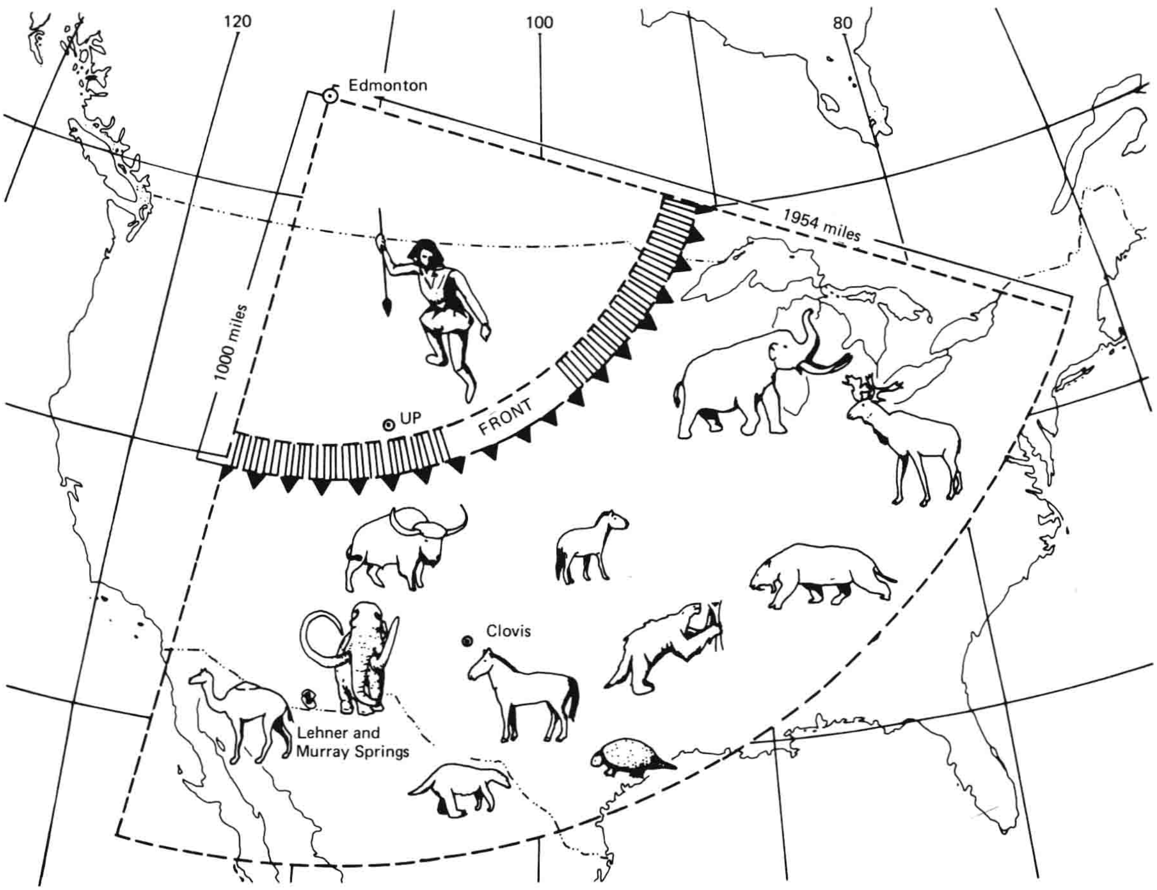

Fig. 1.1 A hypothetical model for the spread of man and the overkill of large mammals in North America. Upon arrival the population of hunters reached a critical density, and then moved southwards in a quarter-circle front. One thousand miles south of Edmonton, the front is beginning to sweep past radiocarbon-dated Palaeoindian mammoth kill sites, which will be overrun in less than 200 years. By the time the front has moved nearly 2000 miles to the Gulf of Mexico, the herds of North America will have been hunted to extinction. For further explanation, see text. (After Mosimann and Martin, 1975.)

ström (1962) studied the growth reaction of the carapace of the ostracod *Cypridopsis vidua* to various environmental factors such as calcium carbonate and water aeration.

Examples of the experimental approach in Quaternary palaeoecology will be described in various parts of this book, for example the study of the dispersal, deposition, and preservation of pollen, spores, and seeds in different sedimentary environments. For example, laboratory studies under controlled experimental conditions have been made on the differential preservation of pollen with high sporopollenin content, and on the mixing of pollen and sediment in a lake by burrowing worms.

Experimental palaeoecology is an extremely important approach and one which merits a great deal more attention than it has received up to now. It differs from experimental ecology in that the experiments are generally designed to explain particular features of the fossil assemblage relevant to the reconstruction of the past ecosystem. Ecologists can experiment directly on living organisms, to study and quantify the organism's response to environmental factors.

Palaeoautecology and palaeosynecology

The bulk of palaeoecology falls within the general framework of descriptive palaeoecology. This in turn can usefully be subdivided into palaeoautecology and palaeosynecology, just as modern ecology is conveniently divided into autecology and synecology.

Palaeoautecology

Autecology considers the ecology of the individual organism or species, and it is primarily concerned with life histories, behaviour, adaptive morphology, and ecological tolerance. Palaeoautecology is the palaeoecological study of individual fossils or species of fossils, and, as in autecology, the emphasis is on behaviour, adaptive morphology, and life histories. A good example of a palaeoautecological study is that by Gould (1974) on the Giant Irish Elk (*Megaloceros giganteus*). This huge deer was common in Ireland at the end of the last glaciation, and its enormous antlers, weighing about 40 kg (90 pounds), have frequently been found in lake and bog sediments of this age in Ireland. Gould studied the morphology and structure of the antlers, and suggested that their function was in display and courtship rather than in fighting. The Giant Irish Elk became extinct at the beginning of the Holocene, possibly because the antlers were very cumbersome, and because they could not be seen in a wooded environment.

Palaeosynecology

Synecology considers the ecology of groups of organisms which are associated with each other as a functional unit, either as a population, a community, or an ecosystem. Palaeosynecology is the study of groups of fossils, so-called fossil assemblages, and the reconstruction of past environments. Such studies are also concerned with populations, communities, or ecosystems. It is more informative to talk of community palaeoecology, population palaeoecology, etc. rather than the broad term palaeosynecology.

Descriptive palaeoecology

Just as descriptive ecology is often subdivided on the basis of habitat type (marine, freshwater, terrestrial) or a taxonomic basis (vascular plants, birds, mammals, insects), descriptive palaeoecology can usefully be subdivided in various ways, according to habitat, taxonomy or geological age.

a) *Habitat.* Fossils can be studied in sediments formed in marine, freshwater, or terrestrial habitats.
b) *Taxonomy.* Different groups of organisms can be studied as fossils, such as diatoms, vascular plants, vertebrates, foraminifera, mollusca, etc.
c) *Geological age.* Fossils can be studied from sediments of different geological age; Palaeozoic, Mesozoic, Tertiary, Quaternary. In this book we shall restrict ourselves to the study of Quaternary fossils, preserved in continental rather than marine environments.

These subdivisions are often sharp within descriptive palaeoecology, because of the nature of the evidence and because of the uneven distribution of the fossil record. For example, the bulk of the fossiliferous rocks of the Palaeozoic and Mesozoic now preserved were sedimented in the sea. Hence their palaeoecology is concerned mainly with the marine environment and with those marine organisms with readily preservable hard parts, such as shells of brachiopods, molluscs, and echinoderms. In contrast, the vast majority of fossiliferous sediments of Quaternary age that are accessible and easily studied were formed in terrestrial or freshwater habitats. Their palaeoecology is thus largely concerned with terrestrial or freshwater organisms with readily preservable hard parts, such as vertebrates (including man), insects, vascular plants (pollen, spores, seeds), and diatoms. Quaternary marine sediments are beginning to be studied in detail (see, for example, Imbrie and Kipp, 1971), but compared with terrestrial and freshwater Quaternary palaeoecology, marine Quaternary palaeoecology is in its infancy.

Approaches to palaeoecology

Despite the numerous subdivisions of palaeoecology, the approach to the subject is the same in all branches of palaeoecology. The topic of primary concern to the palaeoecologist is the palaeoecosystem (Fig. 1.2). In contrast to the modern ecosystem studied by an ecologist, a palaeoecologist has

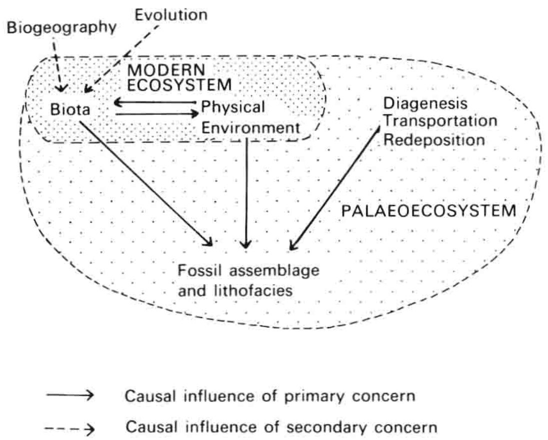

Fig. 1.2 Representation of a palaeoecologist's approach to the study of the fossil record.

to consider not only the ecosystem, but also the processes of diagenesis, transportation, and redeposition, along with the influences of biogeography and evolution. This palaeoecological viewpoint can be contrasted with the approach of a historical biogeographer and of a palaeontologist (Fig. 1.3). Both gather their primary evidence from the fossil record. Their main interests are the biota and the resulting fossil record, whereas the influence of the physical environment on the fossil record and the effects of diagenesis and transportation are usually of less interest (see Imbrie and Newell, 1964).

Various methodological approaches to palaeoecology are possible (Fig. 1.2), and in this book particular attention is given to (1) biological approaches, ranging from interpretations of individual species to broader studies of entire fossil assemblages, (2) sedimentary approaches involving the study of sediment lithology and chemistry, and (3) statistical approaches.

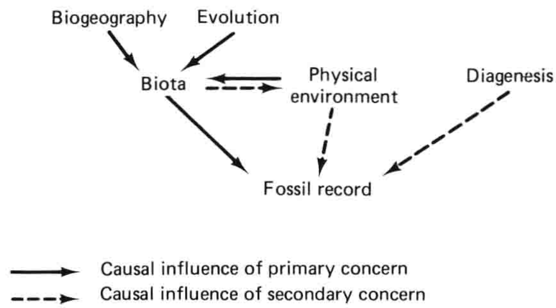

Fig. 1.3 Representation of a historical biogeographer's and a palaeontologist's approach to the study of the fossil record.

Philosophical principles of palaeoecology

Since palaeoecology has a very close relationship with geology, many of the principles and philosophies of geology are applicable to palaeoecology. Watson (1969), Simpson (1970), and Albritton *et al.* (1967) provide useful insights into the philosophy of geology. Because a whole book could be written solely on the philosophy of palaeoecology, we must restrict ourselves to a brief mention of the philosophical principles of the subject. Rudwick (1972) and Albritton (1963, 1975) provide comprehensive accounts of the philosophy of geology and palaeontology, to which the interested reader is referred.

There are seven major features of palaeoecological philosophy.

1. Palaeoecology is a descriptive, historical science, and as such it depends largely on inductive inferences and reasoning. Inductive reasoning is the basic mode of reasoning in empirical science (Hempel, 1966), where one observation leads to another, and where extrapolations are made in an attempt to present generalizations about nature.

2. The method of multiple working hypotheses (see Chamberlin, 1965). This method forces one to consider as many explanations of a phenomenon as possible. Such explanations are likely to be nearer the correct explanation than if only one explanation was considered, which would then become a tentative theory or working hypothesis, and finally a ruling theory into which all subsequent observations are fitted, often without due regard for the evidence. In presenting the method, Chamberlin said 'the effort is to bring up into view every rational explanation of new phenomena and to develop every tenable hypothesis regarding their cause and history'. Multiple hypotheses encourage the seeking of new evidence that will lead to the rejection of, hopefully, all but one working hypothesis. The method thus contributes directly to the planning and design of new investigations.

3. Simplicity. The general scientific principle called Occam's razor, derives from the saying, 'It is vain to do with more what can be done with fewer' (William of Occam, *ca* 1300–49). In other words, let the simplest explanation suffice until more evidence is available which necessitates more complicated explanations (see Anderson in Albritton, 1963, for an analysis of the principle of simplicity in historical geology).

4. Taxonomy and evolution. Palaeoecology deals with fossil organisms. Consequently a sound taxonomy and an appreciation of evolutionary processes is essential in any palaeoecological study. There is thus inevitably some preoccupation with taxonomy, especially at the species and genus levels. It is ecologically more meaningful to consider fossil assemblages as communities of species rather than from the viewpoint of abstract stratigraphic units or constituents of particular lithological units.

5. Language. The terms and vocabulary of palaeoecology are primarily those of biology and geology.

6. Data. Palaeoecological data are frequently quantitative and invariably complex, consisting of many observations and many variables. For example, many different types of fossils may be counted in a sample, which may be one of a whole series of samples related to each other in time or space, or both. Such data are called 'multivariate data' and may be too complex for the palaeoecologist to sort efficiently and to synthesize fully. The use of multivariate mathematical methods for data analysis, such as those described by Reyment (1969, 1972) can be of considerable assistance to the palaeoecologist. Such methods can deal with large amounts of complex data and can process them in precise and repeatable ways. With the primary data simplified and synthesized in this way, the palaeoecologist can then devote himself to the interpretation of the data in as critical and as meaningful a way as possible.

7. Uniformitarianism. This as a basic assumption and philosophical principle of palaeoecology. It was first formulated by James Hutton in 1788, but more fully defined and discussed by Charles Lyell in 1830 (see Simpson (1970) for a full and penetrating analysis of uniformitarianism). It is the principle of the uniformity of nature, generally regarded as the philosophical foundation upon which historical geology is based. Briefly it can be stated as 'the present is the key to the past'. However, although an attractive cliché, this is an unsatisfactory statement of uniformitarianism in philosophical terms (see Gould, 1965; Scott, 1963).

Uniformitarianism was developed explicitly by Charles Lyell in 1830–33 in his *Principles of Geology*, in response to 'catastrophism' and religious views of divine intervention in the history of the earth. Catastrophism was developed during the eighteenth century, and invoked a series of catastrophies, such as the Great Flood of Biblical times, in order to explain geological features such as the presence of shells on mountain tops, and also to fit in with Bishop Ussher's estimated origin of the earth at 4004 B.C. Lyell, who is commonly regarded as the founder of modern geology, subtitled the first edition of his *Principles of Geology* 'An attempt to explain the former changes of the earth's surface by reference to causes now in operation'. Such uniformitarian ideas were later extended into biology by Charles Darwin. Although there have been arguments about uniformitarianism ever since, Lyell was originally intending to exclude divine intervention in the processes of geology, since all the features of the earth could be explained by processes which still operated at the present day (see Albritton, 1975).

Gould (1965), in a valuable essay, distinguished between 'substantive uniformitarianism', where the rates of geological processes are said to have been constant through the past, and 'methodological uniformitarianism' or 'actualism', which states that the nature of the processes are the same, but that they may occur at different rates at different times. In other words, catastrophies do occur, such as volcanic eruptions, glaciations, floods etc., but they do involve and obey the laws of nature because the properties of matter and energy are invariant with time. Hence these laws can be extended back in time, and are thus applicable to the explanation of past events. Methodological uniformitarianism is basically an extension of the laws of physics, but primarily of those laws relevant to geological processes. It is the basic logic and methodology by which the past can be reconstructed. There is no way to prove methodological uniformitarianism, but alternatively, there is no way to reject it.

Frequently, methodological uniformitarianism merges with, and indeed represents, the simplest approach to reconstructing the past, and thus it is also the geological, and hence palaeoecological, formulation of the logical principles of simplicity (see Albritton *et al.*, 1967; Gould, 1965; Cushing and Wright, 1967) and of induction. Uniformitarianism and its basic postulate that the laws of nature are invariant with time is not unique to geology, but is now a common denominator of all science (Hubbert in Albritton *et al.*, 1967). Hubbert proposes the following definition of history: 'History, human or geological, represents our hypothesis, couched in terms of past events devised to explain our present-day observations.'

The nature of palaeoecological evidence

The observations made by palaeoecologists are of two main types. Fossils are remains of organisms, and can be called ***biotic*** evidence, in contrast to ***abiotic*** evidence, which includes the physical and chemical characteristics of the sediments.

Biotic evidence

Fossils can be defined as the remains or indications of past biota. By indication, we mean such fossils as animal tracks, so-called trace fossils, and leaf impressions. There are five main types of fossils (see Krasilov, 1975).

1. *Original material preserved.* This type would include hard parts of organisms such as shells, plant cuticles, bones, and the exines of pollen grains and spores.

2. *Impressions and films.* Carbonized films found on bedding planes of rocks are the commonest example of this type of fossil. The volatile organic components of plant leaves and of animals with a chitinous exoskeleton such as arthropods have gradually disappeared until only a film of carbon is left. As more and more carbon is lost, the film becomes an impression.

3. *Petrifications and replacements.* Fossils, whether calcareous or carbonaceous, may be altered by the effects of water percolating through the rocks. In the simplest case, pore spaces originally filled by organic matter may be infilled with precipitated mineral matter. In petrification complete replacement takes place, the original hard parts being replaced by silica, by iron compounds, or by phosphate compounds.

4. *Moulds and casts.* Percolating water, instead of replacing the organic material, may dissolve it away. If the walls of the cavity so produced are strong enough, a mould of the original fossil is left.

5. *Trace fossils.* These are markings and structures found in sedimentary rocks resulting from the activities of animals moving on or through the sediment during its deposition. Footprints, tracks, and coprolites are the commonest types of trace fossils.

In Quaternary deposits, the commonest type of fossil is the first, namely preserved organic material. The reasons why some organic compounds are preserved, but others are not, are complex. In general, those compounds with a low free-energy in relation to the depositional environment are stable, and are thus more resistant to decay. There are relatively few such compounds that are sufficiently stable to be preserved, with the result that the fossil record is biased towards those organisms with preservable parts. In the animal kingdom, such compounds include calcium carbonate deposited either as calcite or aragonite in shells, silica, and chitin. In the plant kingdom such compounds include calcium carbonate, silica, cutin, lignin, and sporopollenin.

The animal groups producing fossils useful in the study of Quaternary palaeoecology are chiefly vertebrates, molluscs, arthropods, testaceous rhizopods, and foraminifers. Plant fossils most commonly studied are pollen and spores, cuticles, wood, leaves, seeds and fruits, phytoliths (siliceous cell thickenings), mosses, fungal hyphae and spores, diatoms, other algae such as *Pediastrum*, and algal cysts from dinoflagellates, chrysophytes, and charophytes.

Fossils may be deposited in the place where the organism died, in which case they are termed ***autochthonous***. If, however, the dead remains are transported to another locality by any agency, they are termed ***allochthonous***. A collection of dead remains ready to be preserved is called a death assemblage, or ***thanatocoenose***, and it is usually different from the life assemblage, or ***biocoenose***, because of the addition of allochthonous material. These processes are summarized in Fig. 1.4.

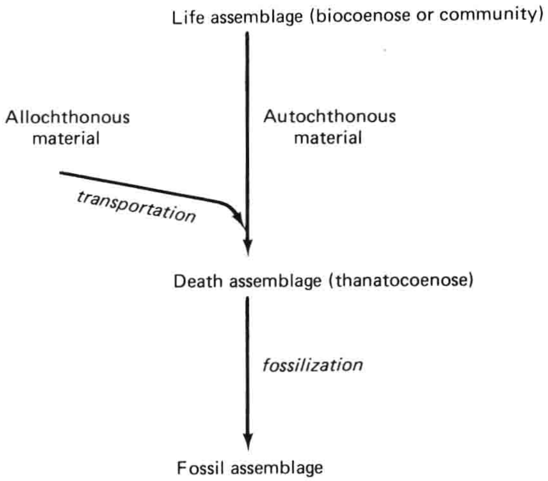

Fig. 1.4 Summary of the processes leading to the formation of the fossil assemblage.

The proportion of autochthonous and allochthonous fossils in a death assemblage varies with the environment of deposition. For example, in a raised bog, the material forming the peat is closely related to the living community of the bog surface, and there is little allochthonous addition, apart from windblown particles. In a lake, however, the material deposited at a certain point may be largely allochthonous, consisting of matter originating in another part of the lake, and transported by water currents, of matter washed in by streams from the catchment area, and matter blown on to the lake surface. Therefore, in reconstructing a past ecosystem, it is important to bear in mind the mode of formation of the death assemblage, or taphonomy (see West, 1973; Lawrence, 1968, 1971).

Abiotic evidence

Abiotic evidence is derived from the physical and chemical characteristics of the sediments. For example, the size of the particles of sediment provides information about the energy of the environment of deposition. In high energy environments, there is much kinetic energy available, and thus only large particles will be deposited, the smaller ones being carried away. For example, shingle beaches are formed at points of strong wave action at the edge of the sea or a lake, whereas sands and muds are deposited in quieter, deeper waters with less movement. In general, deposition occurs in low-energy environments, and erosion in high-energy environments. Thus the situations for fossil preservation tend to be low-energy environments, such as in still water.

Other properties of sediments are also important. For example, chemical characteristics can lead to diagenesis after deposition. Redeposition and mixing of sediments of different origin may also be detected by examination of the physical characteristics of the sediments. For example, the presence of silt or sand particles in sediments of a deep lake suggests that there has been inwashing of this material from the surrounding landscape, and thus the environment at the time of deposition led to erosion of soils. Much of the sediment of a lake with active inflows and outflows may be allochthonous, whereas the organic sediments of peat bogs and swamp forests are mainly autochthonous.

Quaternary sediments may be divided into those which are inorganic in origin, and those which are primarily organic. The main types of inorganic sediments are:

glacial – till, outwash, stratified drift
eolian – wind-blown silt, or loess
alluvial – stream deposits
colluvial – solifluction deposits, hillwash

The main types of organic sediments are:

limnic – lake sediments (mainly allochthonous)
telmatic – deposited at or very near water level (mainly autochthonous)
terrestrial – deposited above water level (mainly autochthonous)

Sediments originating from other environments may be a mixture of organic and inorganic components, for example marine deposits from the sea bottom and estuaries; soils; cave earths; and spring deposits such as tufa. West (1977) gives a detailed account of the full range of Quaternary sediments.

Space and time in palaeoecology

Now that we have discussed the nature of palaeoecological evidence we can construct a conceptual model of a palaeoecological investigation. An ecologist can readily delimit boundaries of space and time in his study of the present day, but a palaeoecologist has great difficulties in defining either, and indeed, the evidence he studies in his fossil assemblage may have originated in several different points in space and time. He can usually define his basin of deposition as a lake, bog, or the sea, but its spatial boundaries may have changed through time,