Quaternary palaeoecology and ecological theory

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Abstract. A review showing the potential contribution of Quaternary palaeoecology to the ecological theory, focused on the ecosystem evolutionary processes, is presented. By analyzing oceanic and continental Pleistocene and Holocene records, some reflections about ecological succession, diversity, rhythms, predictability, stability, and modelling are made, and compared with theoretical statements derived from neoecology.

As a general conclusion, the necessity of considering palaeoecological findings in ecological theory is emphasized. In addition, it seems essential to place palaeoecology in a more ecological framework.

Resum. *Paleoecologia del quaternari i teoria ecològica.* Aquest article revisa la possible contribució que la paleoecologia del quaternari pot tenir, envers la teoria ecològica, especialment en els processos que estan relacionats amb l'evol·lució dels ecosistemes. L'anàlisi de seqüències pleistocenes i holocenes, tant continentals com oceàniques, permeten fer una sèrie de reflexions sobre conceptes com: successió ecològica, diversitat, estabilitat, ritmes, predictibilitat i modelatge, tot contrastant-les amb aquelles sorgides de l'estudi neoecològic.

S'arriba a la conclusió general que els resultats paleoecològics són necessaris en Teoria Ecològica. També es proposa la necessitat de situar la Paleoecologia en un marc més ecològic.

Introduction

The etymological definition of palaeoecology is the shortest one –«palaeoecology is the ecology of the past»– (Birks & Birks 1980). It is, however, sufficient since it contains the essential concepts involved: ecology and time. The temporal study of ecosystems needs past evidences for strictness, becoming speculative when predictive models are pursued. In the middle lies the study of the present living communities (neoecology), whose temporal domain is scarcely representative of the ecosystem evolution. Ideally, ecology should be concerned with all these views: past, present, and future.

The search for regularities in the ecosystems, which allow derive explanatory and predictive models, that is, the theorization of ecology (Margalef 1977), arises generally from neoecologial studies. Thus, models in which time is an essential component are derived from short periods of observation. The

evidence is insufficient, and analogies with more deterministic sciences, like mathematics or physical thermodynamics, become necessary. This is a reasonable procedure, because living systems and beings are no less than complex physico-chemical entities, but, undoubtely, the possibility of obtaining a more extended time-depth is better than extrapolation. Therefore, the interaction between palaeoecology and neoecology is a more appropiate approach for a temporal understanding of ecosystems.

Up to very recently, palaeoecology was not capable of providing much suitable data for generalization and modelling purposes (Valentine 1972). Therefore, theoretical ecology grew, to a great extent, on the basis of neoecology. At present, although generalization of palaeoecological results, with trends toward the development of theoretical bases are increasing, most studies depend upon data derived from neoecology with the resultant limitations in the independence and uniqueness of interpretations (Olson 1985). The book «Models in Paleobiology» (Schopf 1972) is a good example of this approach. Furthermore, some writers do not agree with the possibility of theorization in palaeoecological (Hoffman 1979, Olson 1985). Their opinion is largely supported by the use of the so-called «community reconstruction approach», which is, according to these workers, the only valid way to study community evolution and, therefore, to make generalizations in time. Since good reconstructions of past ecosystems are difficult and scarce, due to inherent problems of the fossil record, detailed knowledge at the intra-community level seems not guaranteed by palaeoecology.

The present work is an attempt to analyze the contribution of palaeoecology to ecological theory, based on very different premises. First, detailed knowledge of a community is not the only way to understand its evolution. There are indicator parameters which are associated to the trends in variation and tendences of the ecosystem (Pielou 1974). Second, the palaeoecological study is concerned with extra-ecosystem variations, acting as important forcing mechanisms, whose study contributes to elucidate causal relationships of the observed phenomena. Concepts such as succession, stability, climax rhytmicity, predictability, and modelling in time will be the main object of the present review.

In this article, evolutionary processes are not considered. Undoubtely, evolution occured in the Quaternary, just like in former times, intermingled with ecological succession. However, only such processes operating and developing on unchanged species will be considered. The relations between succession and evolution are of great ecological significance (Margalef 1986), and need special treatment.

Time scales: the Quaternary

The ecological phenomena recorded are a function of the time interval considered. Several classifications of time scales are available, but since coinciden-

ces are clear, that of Delcourt et al. (1983) may be used as example. According to these workers, three temporal domains can be distinguished in the study of vegetational dynamics:

1. Microscale: characteristic phenomena at this level are physiological events (0-10 years), colonization, mortality, and growth rates (10-100 years), interespecific relationships (50-500 years), such as competence, predation, and others affecting the ecological succession.

2. Macrosale: the most important phenomena are climatic changes, migration, extinction, and speciation processes, afecting the ecosystem evolution.

3. Megascale, events which lie in this category produce biological revolutions exceeding the ecosystem frame. Examples are plate tectonics and biological evolution.

Neoecological studies produce microscale data, with the longer processes being effectively observed for no more than decades or, at most, a few centuries. Furthermore, a relatively complete understanding of the present biosphere may be considered as a cross section of a complex of ecosystems in different evolutionary stages. This instantaneous picture may be compared to a derivate, at the time t_a, of a hypothetical function $F(t)$, describing the history of the ecosystems. For a real understanding of the biosphere, as was recognized long time ago by Donnan (1936), the integration of $F(t)$ between t_o and t_a is the most suitable procedure. However, where does one locate point t_o? Since we are interested in the present living communities, the point t_o represents the «moment» in which the originated and, therefore, it is a mathematical artifact. But a reasonable, although not concrete, departure point is possible. The fossil record shows that present living species are generally no older than the Quaternary or Late Tertiary, whereas former organisms have become extinct. As a consequence, the Quaternary period and, therefore, the macroscale level, will be the time frame for the present issue.

Quaternary evolutionary rates have been low, and extinction, as well as some degree of speciation were the most significant processes. Migration, displacement, mixing, isolation, and other spatial reorganizations, correlated with climatic variations, are characteristic of this period (Dunbar 1952, Flint 1971, Bowen 1978). As a consequence, inter –and intra– ecosystem interplay has been intense, producing complex evolutionary processes as the community level, and resulting in the present, still dynamic, situation. The future is no less tha the continuation of $F(t)$, so any prediction must be based on it.

Succession and substitution

The classical concept of ecological succession refers to a community development process which is characterized by structural and functional, time-ordered, changes (Odum 1971). This process results from the modification of the physical environment by the community, which is the controlling agent, while time and speed of change are determined by the environment. The

hypothetical culmination of succession is a stabilized and equilibrated ecosystem, called climax. Some general criteria have been proposed to recognize different successional stages. Among them, the tendence to a biomass, complexity, and diversity increase in time deserve mention (Margalef 1977). It has also been stated that stability and independence from external condition augment with succession (Margalef 1968). These principles are derived from neoecological studies, mainly from experimental, cyclic (frequenly annual), and secondary successions. Hypothetical reconstructions, based on the simultaneous observation of several communities, which are interpreted as different successional stages of the same process, are also used. As a consequence, these records are time-limited, and the long-therm influence of environmental changes is implicitly rejected. Between the longer primary successions recorded, those developed on recently deglaciated areas are especially interesting. For instance, Reiners *et al.* (1971) studied the colonization of Glacter Bay (Alaska) by the vegetation, during the last 250 years. After deglaciation, about 100 km of bare soil were rapidly exposed, and some herbaceous communities were the pioneers. The following stages were characterized by *Picea*, and later by *Tsuga*, forests. The final community is herbaceous again. Relatively stable environmental conditions prevailed during this succession. Diversity showed a rapid initial increase, followed by a progressive attenuation, and a later asymptotic stabilization, which is maintained at present. The rate of increase of diversity was controlled by the addition of new species in the earlier stages, and the equitability of their abundances, near the stabilization. The assumed climatic community showed maximum diversity, associated with a complex microhabitat pattern, supporting the view that stability favours diversification by progressive niche-subdivision (Margalef 1963, Connell & Orias 1964, Sanders 1968). Similar coincident diversity trends have been found in other studies (Birks 1980). A longer successional record, covering the entire Holocene (the last 10 000 years), and developed in a stable environment, was found in the Galapagos islands (Colinvaux & Schoffield 1976 a and b). The transition from the last glacial period to the Holocene was characterized by increase in humidity, and the establishment of tropical rain forests. The recolonization process about 1000 years. From about 9000 years before present (BP), both climate and vegetation remained unchanged, until today. This surprisingly long period of stability seems to be an exception among palaeoecological records; recent findings reveal temporal changes in the community composition. During the Holocene, climatic fluctuation have been recorded, including mean temperature charges of about 3°C (Denton & Karlén 1973). The living communities were undoubtely affected by these variations, as shown, for example, by diatom communities of some Finish lakes (Koivo 1970). The postglacial colonization, as well as diversity trends of these Holocene communities, are very illustrative concerning this point. The general rule of a rapid, richness-dependent, initial diversity increase was also recorded here. Asymptotic stabilization, however, was not reached. On the contrary,

diversity variations, correlated with climate and trophic status were observed. The maximum diversity coincided with phases of oligotrophy and higher temperature, whereas distrophy and temperature decreases were associated with low diversity values. Thus, not only the internal community organization, but also external forcing factors affect the successional process.

In the former examples, it was assumed that diversity measures, in some way, the complexity and organization of the ecosystem. However, these point-diversity values may be biased by sampling limitations. In palaeoecology, additional sources of error must be considered, mainly those derived from differential sedimentation (Smol 1981), and preservation of fossils (Lasker 1976). Margalef (1968) proposed a spectral approach, which considers the cumulative diversity from a sequential sampling of an ecosystem, with progressively langer sample size. These diversity spectra, like other measures of the pattern-diversity (Pielou 1966), are better measures of the structural features of the ecosystem, permitting a more clear relation between diversity and properties such as organization, energy fluxes, maturity, and others. A simple community, that is, one that has few, homogeneously distributed components, some of them dominant, has a diversity spectrum with an early saturation point. On the contrary, an ecosystem composed by many species, none dominant, and with complex spatial patterns (like most tropical forest), provides diversity spectra difficult to saturate. If the spatial dimension is substituted by a temporal one, the spectrum may be used to study structural variations in a successional process.

To test this method, a pollen record from the tropical Venezuelan Andes is used. Glaciers retreated from 3 000 to 4 700 m altitude, between the last glacial maximum (probably 18 000 years BP; Schubert 1974, 1984) and the present. In a locality situated at about 4 000 m, the colonization by vegetation started around 12 000 BP (Rull 1985).

The pollen diversity spectrum (whose values did not coincide with those of vegetation represented, but their trends are necessarily correlated) shows that different pollen types arrived by waves (Fig. 1). To a great extent, equitability determines the diversity tendences. This implies that addition or disappearance of types are not responsible for the compositional changes. The reorganization of relative frequencies is the determining factor. Independent evidence, such as tree line position, indicator taxa, and others, were the basis for the climatic history of the site, showing that about 9 000 years BP the glacier was located near the boring site locality, and no more than scattered herbaceous stands lived there. Poor and fluctuacting communities are suggested by the spectrum, for this phase. A typical succesional trend, with a saturation point, can be observed later; however, a further increase, coinciding with a mean temperature rise of about 1.2° C, occured, around 2 500 BP. Since all the types were already present, equitability was the responsible for the compositional charge. Although charges in pollen abundances as a consequence of variations in pollen productivity of the species involved cannot be discarded, the
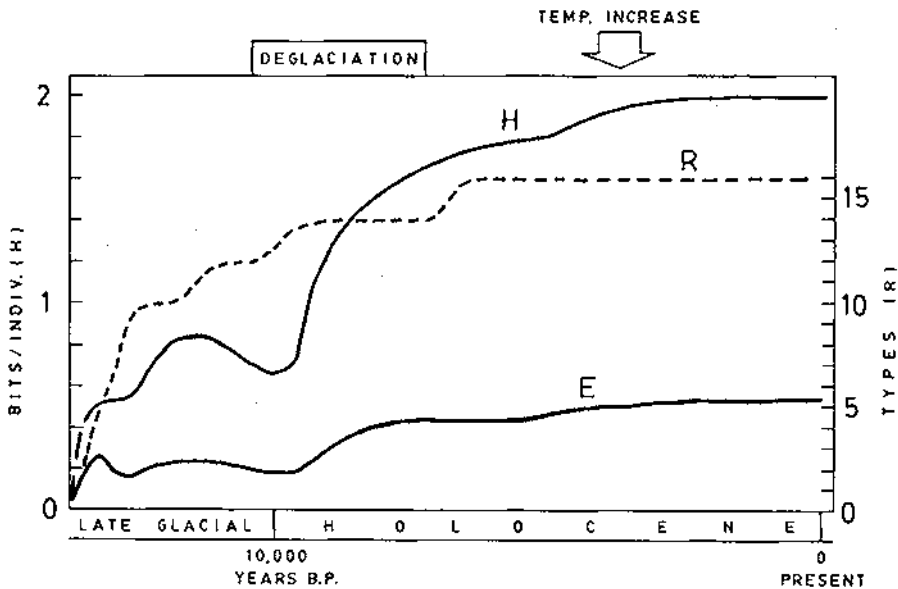
Figure 1. Variations of the Shannon-Weaver index of diversity (Pielou 1966), equitability (E=H/Hmax), and type richness (R), from pollen assemblages found in the stratigraphical analysis of a postglacial peat bog, from the Venezuelan Andes. Data in Rull (1985).

succession was modified, but maintained. The term «modulated succession» seems appropiate for this situation.

Environmental variations may interrupt the successional process, if some threshold is surpassed. As is well known, sea level changes occured during the Late Glacial-Holocene transition (Flint 1971, Kidson 1982). As a consequence, many temperate coastal lakes experienced successive connections and isolations from the sea. In Norway, mosf of them were saline 10,000 years ago, when sealevel was about 40 m about the present (Mangerud et al. 1974). At this time, diatom communities were dominated by polihalobious species (Stabell 1985). A subsequent sealevel drop produced the isolation and, therefore, desalinization of lakes which became freshwater bodies. As a consequence, the former living communities were replaced by others consisting of halophobus and indifferent species (Stabell 1985). This represents a significant ecological change, similar to the replacement of forest communities by open savannas, recorded in Africa (Bonnefille 1980), and other tropical places, during the last glacial epoch. The term «forced substitution» is more suitable to describe this phenomenon because, not only reorganization, but substitution of a community by another accured. In this case, a diversity spectrum looks like that resulting from a spatial transect, crossing an ecotone, and go into another contiguous ecosystem. Fig. 2 shows the three main situations discussed, which are characterized by the magnitude or environmental variation, as well as

community tolerance. The climatologic terminology may provide some useful terms. Major variations, such as glaciations, are called changes, whereas fluctuation means minor oscillations (Griffiths 1976). Thus, we can relate change with substitution, fluctuation with modulation, and the diversity spectra are useful tools to discriminate between them, and also from non-disturbed successional processes.

Stability and the concept of climax

It is a widespread opinion that the more complex ecosystems, although well adapted to the predictable environment in which the evolved (May 1975), are
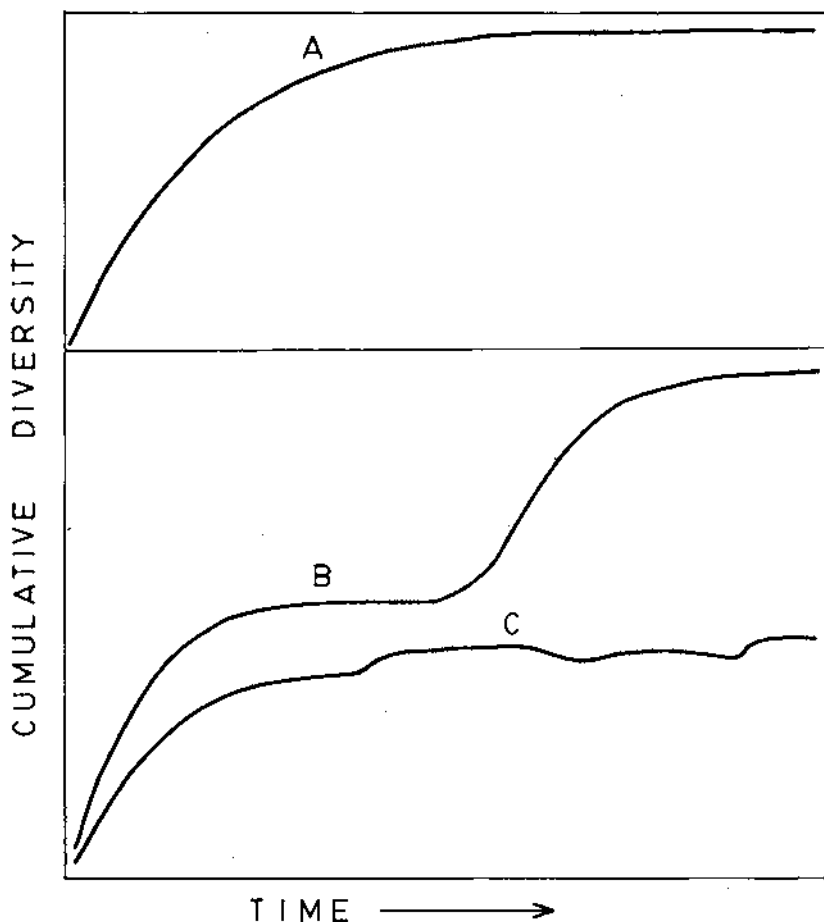

Figure 2. Hypothetical examples of three possible successional situations: A) Nondisturbed succession. B) Modulated succession. C) Induced substitution.

not able to resist external disturbances. The tropical forest is frequently cited as an example of both biotic and environmental constancy (Fischer 1961, Fedorov 1966, Schawabe 1968). However, recent findings showed that climatic changes also occured in low latitudes. Evidences are found everywhere (Walker & Chen 1987), and are of very different nature, including: pollen analysis, high-mountain moraines, alluvial terraces, former lake basins, diatoms and autogenic minerals in lake sediments, stabilized dunes, and others (Livingstone 1980). The glacial periods of temperate zones coincided with tropical aridity, and forests were replaced by open vegetation and deserts. Thus, the glacial-interglacial alternation was characterized in the tropics, by the alternation of savanna (or desert) and forest (Garner 1975). A refuge hypothesis was proposed to explain the persistence of tropical rain forest, in spite of environmental changes occured; forest refuge areas are assumed to be localities that were not affected by the variations, owing to local conditions, and in which the tropical forest probably survived (Haffer 1982). The successive contractions (glacial) and expansions (interglacial) of the forest contributed to generate more biotic diversity there, as a result of alternative mixing and isolation (Prance 1982). However, the lack of direct evidence of the refuges (Bradbury et al. 1981, Salgado-Labouriau 1980, Schubert & Fritz 1985, Schubert 1988) incited other alternative explanations for the diversity of the tropical rain forest. The most popular are: 1) The occurence of extensive Holocene erosional and depositional events, due to minor climatic fluctuations (Campbell & Frailey 1984); 2) Forest regeneration by lateral migration of rivers and river meanders (Salo et al. 1986); 3) Fluctuations in the intensity and duration of dry seasons (Absy 1986); and 4) Occurence of natural fires during the last 6 000 years (Sandford et al. 1985, Saldarriaga & West 1986). In short, fluctuations were considered more important than changes, in determining the forest composition. Other writers consider that no subtantial changes in the extension, but in the composition of forest occured, as a consequence of glaciation (Connor 1986).

Summarizing the preceding information, the history of tropical lowlands is characterized by both substitutions and modulated successions (see also Flenley 1979, Colinvaux 1987). The formerly presented case of the Galapagos Islands is an exception and, as such, it merits further consideration.

The classical concept of stability considers environmental dynamism to some degree. Ecological stability refers to the tendency of an ecosystem to remain close to some equilibrium point, or to return to it after a disturbance (Odum 1971, Margalef 1977), as a consequence of its internal processes. Several properties, such as constancy, inertia, elasticity, amplitude, and others, may be useful to describe ecosystem behaviour. For example, a high inertia (capacity to assimilate external disturbances) but low elasticity and amplitude (capacity to return, after a modifying disturbance) are assumed for tropical forests, while the contrary would be the rule of temperate forests (Orians 1975). The concepts of resilience and attraction domain were introduced by Holling

(1973). According to him, more than one potential equilibrium point (although no anyone) would be possible for a given community, the sum of them forming their attraction domain. Thus, an ecosystem is more or less resilient, depending on its ability to return to the domain. Although more than twelve meanings of stability exist (Wittaker 1975), resilience is a satisfactory concept in palaeoecology (Delcourt et al. 1983). The Quaternary provides good examples of disturbed ecosystems, and their responses. As shown, plant communities recolonized the new open spaces created by glacier retreat, in a successional way. It is interesting to study the composition of these latter communities, and compare them with those formerly inhabiting the area, that is, before the glacial disturbance. A recurrent cycle in forest vegetation was recorder for the three last interglacials in Great Britain (Godwin 1975, 1977). All of them are characterized by common trends in protocratic (*Betula, Pinus*), mesocratic (*Quercus, Tilia, Ulmus, Alnus*), and telocratic (*Abies, Picea, Fagus*), forest trees. Thus, a standard interglacial may be divided in four substages: 1) pretemperate, dominated by protocratic trees; 2) early-temperate, with mesocratic trees; 3) late-temperate, with telocratic trees; and 4) post-temperate, with protocratic trees again (Turner & West 1968). The most interesting feature in our context, is the fact that relative abundances of these taxa were different during the three interglacials. The same vegetational types, but with different compositions, developed after each glacial period. In other words, these ecosystems adopted three of their potencial compositional sates, as expression of their resilience.

Phenomena of this nature involve different biotic responses to the same forcing influence. The community response is a result of the individual specific behaviour of its components. Davis (1969, 1976, 1981) showed the great influence of differential migration rates (at the species level) on the vegetational composition of North American ecosystems, during the Holocene recolonization. Later, differences in response time (time lag) were added as a significant factor (Davis 1984). The time lags are relatively short for some components (insects, birds), but can last a century or more in plants. These diferences depends on life histories, generation times, behaviour, means of dispersal, competitive ability, and others, and are decisive to determine the community composition at a given site, at a given time (Davis 1984, Wright 1984).

In the light of this evidence, the environental variations, and the specific differences in response, Davis (1984) proposed that ecosystems never attain an equilibrium, being in constant adjustement to the external changing conditions. This continuous disequilibrium hypothesis is sometimes criticized, on the basis of findings that indicate long periods of environmental and ecological stability (Watts 1970, 1979). The alternation of stable and unstable phases is also proposed; but stability cannot mean constancy, because fluctuactions are always present. Mor consistent with palaeoecological evidence is the idea of dynamic equilibrium (Delcourt & Delcourt 1983), according to which

ecosystems experience minor variations controled by a fluctuacting environment. In any case, palaeoecology offers some support to an earlier theoretical proposal of Hutchinson (1979). According to him, a possible mechanism for maintaining high diversity in an ecosystem is the slow and continuous environmental oscillation. This would produce constan internal reorganizations, preventing or reducing extinction.

In sumary, both continuous disequilibrium and dynamic equilibrium can be observed in the Quaternary fossil record. Alternation is also possible, and may be described by the superimposition of diversity spectra B and C in Figure 2.

The concept of climax is rarely used in palaeoecology for an obvious reason: it cannot be deduced from palaeoecological data. Flenley (1979) believed that the idea of climax derives from short periods of observation and does not exists in practice.

Predictability and models

Models are a common way to express theoretical statements and views. A frequent failure of ecological models is the attempt to describe the ecosystem from within living communities are systems included in a bigger one, which, in turn, is a part of others of higher hierarchy, and so on. If we consider the ecosystem as the first level of our interest, the climatic system is the second, and the astronomical (the Solar) system, the third. Since lower levels are influenced by higher ones, generalizations must not be restricted to the study of a single system. Such a narrow view can show randomness in an actual cyclic phenomenon. For instance, a biotic seasonal change is not evident if the observation time is less than one year. On the other hand, if we know the annual rhythm of the climatic system, a correlation between it and the community behaviour reveals the real relation: the internal ecosystem phenomenon is governed by a superior (climatic) system, imposing its cycles. This imposition is commonly called forcing, and proceeds always from higher to lower hierarchies.

Rhythms in climatic change

In ecology, predictability is strongly related with the existence of rhythms. Thus an environment is called predictable if the living beings in it are adapted to its variations, and can absorbe them. Evolution incorporated the shorter, less energetic, and more frequent cycles (Margalef 1986), but: what about long-therm climatic variations? The first stage of the answer is the search for cyclicity in the Quaternary climatic variations.

Initially, only four glacial epochs were recognized in the Pleistocene, whose beginning was situated about 600 000 years BP (Cooke 1973). Subsequent studies showed the existence of about twenty of these events, in the last 2 million years (van Donk 1976, Fink & Kukla 1977). According to Flint (1971), glacia-

tions started at least 10 million years ago, in the Late Tertiary. Some high-altitude evidence supports this (Bandy et al. 1969, Margolis & Kennett 1970, Kvasov & Verbitsky 1981), so that the number of glaciations should be larger. In addition, each glaciation possesses minor fluctuations called stadials (glacier advances) or interstadials (glacier retreats). According to Garner (1974), about a hundred of these minor oscillations occured in the Pleistocene (the last or three million years). Thus, the environmental variations have been the rule, and not the exception, for the present ecosystems.

Two types of mechanisms can generate climatic variations (Mitchell 1976): the stochastic internal processes of the climatic system, and the external, forcing factors. The climatic system consists of the atmosphere, lithosphere, cryosphere, hydrosphere, and biosphere. Interactions among them, as well as thermodynamic adjustements by heat transfer, albedo variations, energy dissipation, geographical changes, local turbulence, and others, are complex, possessing high uncertainity levels. External mechanisms, on the contrary, are deterministic, at the ecological level. Daily variations in sunlight or the influence of the Moon on tides and precipitation (Brier 1964), are good examples of the latter.

Variations of terrestrial orbital parameters, caused by gravitational effects of the planets on the Earth, was proposed as a forcing mechanism of the Quaternary climatic changes by M. Milankovitch, in 1941. The perihelion length varies with a periodicity of about 22 000 years, while the Earth's obliquity varies with a period of some 40 000, and the eccentricity of the orbit possesses a variation period of about 100 000 years. Solar radiation is affected by these parameters and, therefore, their oscillation must have an effect on the climate of the Earth. This prediction, based on astronomical calculations, was later supported by good statistical agreement between isotopic temperature records and the computed cycles (Hays et al. 1976). The lack of satisfactory causal mechanisms favoured the appearance of other hypotheses, in which the internal, stochastic mechanism of the climatic system are able to produce glacial-interglacial alternance (Kaminz & Pisias 1979, Lorenz 1976). However, several physical models were developed in support of the Milankovitch theory (Schneider & Thompson 1979, Denton & Hughes 1983), which is, at present, the more popular one (Pisias & Imbrie 1986, Martinson et al. 1987). This deterministic hypothesis emphasizes the good agreement between facts, with a logical cause-effect relationship, whereas the stochastic factors are considered to be the cause of minor variability. Some writers even refer to the internal mechanisms as simple control exercises (Fairbridge 1976). In effect, when shorter time intervals are considered, a more confusing picture emerges. It has been proposed that most of the Holocene climatic variations are related to the 11-year sunspot period (Currie 1974, Mitchell 1976, Svenonius & Olausson 1979). Some evidence was found for the coincidince of the Little Ice Age with a pronounced minimum in the sunspot cycle (Eddy 1976). The Little Ice Age was earlier considered to be a glacier advance restricted to the tempe-

rate zone (Robock 1979, Williams & Wigley 1983), but recent findings favour a global climatic fluctuation (Hastenrath 1981, Clapperton 1983, Thompson et at. 1986, Rull 1987, Rull et al. 1987), extending from approximately the 15th to the 19th centuries. According to Denton & Karlén (1973), a cycle of about 2 500 years exists for the Holocene climatic oscillations. The Little Ice Age may be then considered the last of these periodic variations. The causes proposed, however, are not always rhytmic mechanisms; variations in the C-14 (Denton & Karlén 1973), and volcanic dust concentrations (Robock 1979) in the atmosphere are the most popular, and the second is the more generally accepted one, because phases of higher volcanic activity (Hirschboeck 1979, Porter 1986), owing to global tectonic events (Flohn 1979, Taira 1983), have been reported.

In summary, macroscale climated events are caused, to a great extent, by ciclic astronomic variations, while microscale phenomena, although influenced by rhythmic factors, are more affected by internal stochastic mechanisms (Imbrie 1985).

Palaeoecological paradox

Whether the environmental changes and fluctuation are predictable (in the ecological, not human sense) or not, is our next question of interest. A previous remark is essential: a great amount of palaeoecological information about climatic variations is directly derived from fossils, that is, the biotic responses to an assumed change are the evidence of it. If, for instance, fossils of a temperate community are found in an 18 000 year-old sediment layer in a present-day subtropical zone, a shift to low temperatures can be inferred, at that date. This involves two basic premises which are not necessarily true (Davis & Botkin 1985): the organisms react rapidly to environmental changes, and the living communities are always in equilibrium wiht the environment. The foregoing discussion is hopefully enlightening about this, but a more general consideration must be kept in mind. If the environment is deduced from organisms, attempts to analyze biotic responses become a sort of circular reasoning, with potentially dangerous consequences. To break the circle, independent evidence of shorter response time must be taken into account. Fortunately, a wide range of them exist (Flint 1976, Wrigh 1984), and often support the results bases on fossils. It is necessary to pay attention, not only to response time, but also to the nature of evidence, if invalid arguments are to be avoided.

Rhythms and biotic responses

With the formerly stated limitations in mind, two types of environments, one oceanic and other continental, will be analyzed.

The planktonic fossil assemblages from deep sea cores exerted great influence on palaeoecological study, by extending considerably the record, as

well as by providing much more detail. The latitudinal variations have been much more clear in oceanic than in continental ecosystems (see examples in Funnel & Riedel 1971, Cline & Hays 1976), due to the higher environmental homogeneity of oceans. In addition, it is reasonable to assume a relatively rapid response of living plankton communities to surface temperature changes, because they live in superficial water, and consist of very simple, mostly unicellular, organisms. Local manifestation of the glacial-interglacial succession will be the alternating dominance, or substitution, of assemblages typical for either lower or higher latitudes, in an apparent cyclic way. Within the many examples found, a Caribbean one is selected. Four ecological assemblages of foraminiferal species were recognized in its sediments, through factor analysis (Imbrie & Kipp 1971). Figure 3 shows the variation of tropical and subtropical assemblages. During the glacial epochs, a lower surface temperature occured and subtropical communities dominated, by southern migration of climatic belts. During interglacial apochs, on the contrary, northword displacement of the tropical zone determined a dominance of the tropical assemblage, at the boring site. Thus, at a global level, a glaciation can be viewed as a contraction of Earth's latitudinal climatic belts, whereas an expansion of them was typical of interglacials. Since Quaternary climatic changes were more or less rhytmic, these induced successive contractions and expansions, followed the same tendence.

Very different is the situation in the continents, where topography, land mass distribution, and other local and regional factors create barriers, limiting the extent, and sometimes the possibility, of migration. Furthermore, the existence of particular microclimatic conditions must be also considered. Thus, a terrestrial ecosystem may be limited and, ultimately, it may disappear. According to Heine (1977), the equatorial climatic belt was strongly reduced, and did probably not exist in some areas, during the last glacial maximum. Taking into consideration the evidence of aridity, the continuity in time of tropical humid forests is in some way surprising. The refuge hypothesis becomes thus a logical necessity. If refuges really did exist, the rhythmin these tropical communities did not consist of latitudinal shifts, but centripetal contractions, and centrifugal expansions, with subsequent coalescence, around the refuge areas. But, so far, all that we know is that tropical forests are now substantially greater in extent than during the last glacial epoch (Walker & Chen 1987).

On the basis of these biotic evidences, forcing by climatic factors cannot be discovered. In other words, endogenous rhythms, primarily indiced by periodical environmental causes, would exist. Current evolutionary arguments prevent the acceptance of this hypothesis, but evidence is the only way to reject it. A common feature of endogenous rhythms is their persistence, even when forcing mechanisms cease to occur. An equivalent palaeoecological situation would be the record of biotic oscillations, associated with a consistent lack of indications of climatic change. However, since abscence of evi-

dence is not evidence of abscence, a definite answer seems difficult. The food agreement between oceanic records and well dated continental records may provide some help. In North America, most of the temperature decreases recorded in the sea coincided with evidence of glacial advance (Fullerton & Richmond 1986), but it is not the case in Europe (Sibrava 1986). Taking the Northern Hemisphere globally, a more or less good agreement can be found in the climatic tendencies indicated by either fossils and physical evidence, approximately during the last 800 000 years (Bowen et al. 1986). Since this interval includes nearly half of the recorded Pleistocene glaciations, it favours the view of climate as a forcing mechanism. Thus, Quaternary ecological cycles, as shown in Figure 3, are most probably climatically determined. As a consequence, the Quaternary environment appears to be non-predictable by communities, at a macroscale level.

Modelling

The Quaternary climatic changes and fluctuations, because they are statistically tractable, can be subjected to mathematical modelling. The so-called meta-models, capable of generating external disturbances by itself, testing the ecosystem responses, are thus unnecessary. Disturbances are known, and we must simply incorporate them to suitable simulations. The formerly indicated fit between ecological, climatic, and astronomical cycles is a model, which permits the explanation of community behaviour by searching its causal mechanisms. Other models are predictive (in the human sense), that is, they use available factual information to speculate about the future, by finding tendences. The first step of predictive simulations must be a test, which is only possible when palaeoecological records are considered. Models, to be valid, must correctly reproduce the observed biotic trends. Solomon et al. (1980) used the known palynological information on the forests from Tennesse (Delcourt 1979) to test the fitness of a model of forest evolution (FORET), based on species growth and mortality parameters, and their variation under different climatic situations. By forcing the theoretical model with the known climatic history, an estimated species-biomass diagram was attained, which more or less reflected the observed vegetation trends. A similar model (JABOWA, Botkin et al. 1973), was forced by hypothetical climatic variations of different duration and intensity (Davis & Botkin 1985). Decreases of about 2° C in the mean annual temperature caused the replacement of the dominant taxon by another, with a delay of 100-200 years, after the climatic shift. Smaller temperature decreases did not affect the forest composition, in a palaeoecologically observable way. So, minor environmental variations may not be observed in pollen records. According to these workers, only events like the Little Ice Age or more intense, caused sufficient forest changes to be recorded in the sediments.

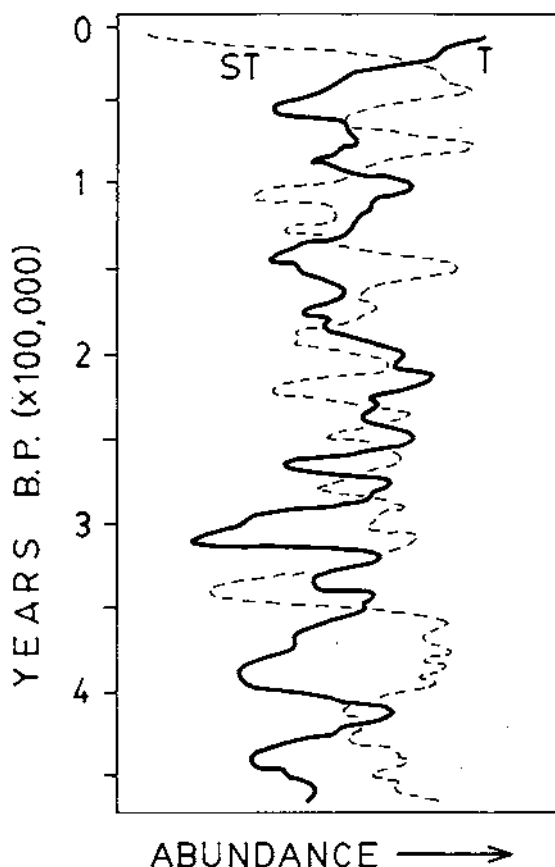These kind of models are still being tested and improved. Their basic struc-

Figure 3. Variations in the relative abundance of tropical (T), and subtropical (ST) foraminiferal assemblages in a deep sea core from the Caribbean. Redrawn from Imbrie & Kipp (1971).

ture seems suitable, but some details must be changed or added, according to successive tests (Solomon et al. 1980). An important failure seems the consideration of only individual (specific) responses. Biotic relationship as copetition, herbivory, predation, and others, are not considered among the deterministic variables. Community responses are not a sum of individual responses. If we ignore these facts, the results of model studies are only of partial ecological interest. The work of Green (1981) is an example of detailed successional and population dynamics information, available from modelling. Using spectral analysis, he found a good association between the Holocene forest history (palynologically deduced) of some Canadian forests, and a harmonic function of a 350-year period. Climatically triggered fires marked the end of each cycle, which was recurrent between, at least, 4 450 and 2 100 years BP. A crooscorrelogram response model was succesfully used to determine successional

patterns. The model also explained some of the effects of changing fire frequency, suggesting mechanisms by which fire, competition, and climate, combine to produce long-term compositional changes.

Final comments

Ecology is not an environmental science, because it is concerned with the whole biosphere, at the community organization level. Biosphere is a mixture of spatial gradients, and temporal trends. The thought on which ecology is based is that neither trends nor gradients are at random, having regularities, and organization levels. Ecological theory is the arm by which ecology attempts to find general rules.

Palaeoecology is not environmental reconstructions. It is a part of ecological study, which possesses a fundamental value for ecological theory, becuse it provides evidence not available from neoecology. Observations at the human scale (microscale) are insufficient to generalize about ecosystem evolution. On the other hand, palaeoecology is a theorizable discipline. Theory gives more stimuling goals than descriptive reconstruction of past environments, or local climatic histories. It is thus necessary, not only to generate more and more information, but also think about it, under an ecological framework.

Hill (1981) posed the question: –Why study palaeoecology?–. The answer seems to me: –For a better understanding of biosphere–, the same than for: –Why study ecology?–.

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