Environmental change and biological diversity : Present, past and future

A. S. Raghubanshi, J. S. Singh & B. S. Venkatachala

The present paper reviews the current distribution and factors determining the level of biological diversity. Past climate changes causing mass extinctions, lessons drawn from these past events, and the impact of future climate change on biological diversity in its broadest sense are also considered. Large scale changes in vegetation zones and composition, over extensive parts of the globe are indicated. Displacement of isotherms due to rise in global temperatures would necessitate very rapid species shifts which may be possible only with human assistance except for plants propagated by spores or dust seeds. Rates of migration and behaviour of the migrating species will determine their range shift capabilities. Differences in migration rates may result in new combinations of species because of dissociation of communities into their component species. Species rigidly associated to a particular set of environmental conditions may well become extinct. Characteristics such as large population size, broad geographical distribution and high dispersal potentials will protect species from extinction. Increased pressure from invaders, increased frequency of epidemics and alteration of productivity and species distributions are indicated. Elevated sea water temperatures may badly damage sea flora and fauna as is exemplified by present day El nino effects. Destruction of coastal habitats due to sea level rise may affect birds and fishes using salt marshes, estuaries and islets as breeding ground. Island species will be severely affected both due to reduced area and limitations of latitudinal migration. Changes in precipitation pattern may result in reduced avian and mammalian populations in many parts of the world.

Key-words—Climatic change, Greenhouse effect, Biological diversity, Mass extinctions, Species turnover, Past climatic change.

A. S. Raghubanshi & J. S. Singh, Department of Botany, Banaras Hindu University, Varanasi 221 005, India.
B. S. Venkatachala, Birbal Sahni Institute of Palaeobotany, 53 University Road, Lucknow 226 007, India.

सारांश

बातावरणीय परिवर्तन एवं जैविक विभिन्नतायें : वर्तमान, अतीत एवं भविष्य

ए० एँस० रघुबंशी, जे० एँस० सिंह एवं बेंगलूर श्रीनिवासा वेंकटाचाला

इस शोध-पत्र में वर्तमान वितरण एवं जैविकीय विभिन्नता के स्तर को सुनिश्चित करने वाले कारकों की विवेचना की गई है। अतीत में जलवायवी परिवर्तनों के कारण हुए बृहत् स्तर पर विलोपों, इन्हीं घटनाओं से निष्कर्षित परिणामों तथा भविष्य में जैविक विभिन्नताओं पर होने वाले परिवर्तनों के प्रभाव का गहन अध्ययन किया गया है। भूमण्डल के अधिकतर भाग की संरचना तथा वनस्पतिक मंडलों में अत्यधिक हुए परिवर्तनों को इंगित किया गया है। सम्पूर्ण भूमण्डल के तापक्रम में वृद्धि के कारण समतापीयों के विस्थापन से विभिन्न जातियों में बहुत तीव्र परिवर्तन हो सकता है और ऐसा बीजाणुओं अथवा धूलि-बीजों द्वारा उत्पादित पौधों को छोड़कर मानव द्वारा ही संभव है। प्रवासनी जातियों की प्रगामी दर तथा इनके व्यवहार से इनकी दूर-दूर तक विस्तृत होने वाली क्षमता का नियंत्रण होता है। प्रगामी दरों में विभिन्नताओं के फलस्वरूप जातियों के नव-संयोजनों का प्रादुर्भाव भी हो सकता है ऐसा समुदायों के विघटन से भी सम्भाव्य है। ऐसी जातियाँ जो विशेष परिस्थितियों तक ही सीमित हैं, विलुप्त हो सकती हैं। परन्तु जातियों के विस्तृत एवं घने होने, इनके विस्तृत भौगोलिकीय वितरण तथा अत्याधिक विकीरण से ये विलुप्त होने से बच जायेंगी। आक्रामकों के दबाव, जानपदिक रोगों की बारम्बारता तथा उत्पादकता एवं जातीय वितरण में परिवर्तनों की भी विवेचना की गई है। समुद्री पौधों एवं जन्तुओं पर समुद्री पानी के ताप में वृद्धि का बहुत बुरा प्रभाव पड़ सकता है जैसा कि इस समय अनुभव किया जा रहा है। समुद्र के जल-स्तर में वृद्धि के कारण पक्षियों एवं मछलियों का तटीय साहचर्य नष्ट हो सकता है ये जन्तु लवणी दलदलों, वेलासंगमों तथा छोटे टापुओं को अपने प्रजनन-स्थल के रूप में प्रयोग करते हैं। यही नहीं, अपितु द्वीपों की जातियों पर भी इसका सीधा एवं प्रतिकूल प्रभाव पड़ेगा। कम वर्षा होने से विश्व के अनेक भागों में पक्षियों एवं स्तनधारियों दोनों ही की जनसंख्या कम हो सकती है।

BIOLOGICAL diversity, i.e., species richness and variety of natural communities, is increasingly threatened by the environmental crisis (Pielou, 1975). Public interest in biological diversity has

emerged due to the concern over the imminent extinction of thousands of species as a result of pollution and habitat destruction (Soule & Wilcox, 1980; Ehrlich & Ehrlich, 1981; Ricklefs, 1987). The current frenzy of environmental degradation is unprecedented with deforestation, desertification, and destruction of wetlands and coral reefs occurring at rates comparable to or greater than the major catastrophes in the fossil records and threatening to eliminate most tropical forests and millions of species in our lifetime (Soule, 1985).

The exacerbating anthropogenic forcing and environmental degradation seem to have ushered in an era of mass extinctions. According to the estimates of Myers (1988), from the "hot spot" localities of tropical forests which combine exceptional levels of biodiversity, endemism and threats of imminent destruction, some 17000 endemic plant species (13.5% of all plant species of tropical forest) and 350,000 animal species might soon be lost. In the next few decades 25 per cent of the 250,000 higher plant species will probably disappear, and in the remaining period of 21st century another 25 per cent might be lost (Myers, 1990).

Several authors have considered the significance of future climatic change on species survival (Ford, 1982; Norse & McManius, 1980; Wilcox, 1980; Brubaker, 1986). Peters and Darling (1985) have discussed the possible impact of greenhouse gases and related global warming on the diversity of species inhabiting biosphere reserves.

It is difficult to assess the consequences of a sharp reduction in biological diversity for natural resources and for the intrinsic stability of natural systems. Many consider, with justification, these consequences to be potentially disastrous (Ricklefs, 1987). The ability to predict the change in system function after biological depauperation, requires an understanding of the processes responsible for generating and maintaining diversity in biological communities. We must try to understand how the biological diversity is distributed globally, what factors determine the level of biological diversity, and how was it impacted by the past climatic changes.

WHAT IS DIVERSITY?

Variability of natural communities is well known. For example, the molluscs of a rocky shore in a cold climate may consist of only a few species whereas the trees in a tract of tropical rain forest may have hundreds of species. Among the most fundamental descriptions of the nature of a community, is a measure of its diversity: the number of different species of organisms and their abundance, generally in terms of individuals, but sometimes as genets or modules (Harper, 1981) or biomass (Southwood, 1987). However, despite considerable interest, a generally accepted definition of diversity has not emerged (Peet, 1974). Hurlbert (1971) contended that diversity *per se* does not exist and suggested abandoning the term because of multiplicity of meanings and interpretations attached to it. MacArthur (1972) also considered the term had outlived its usefulness, and Eberhardt (1969), Austin (1964) and McIntosh (1967) all complained of the lack of a definition. Eberhardt (1969) considered that diversity mostly suggests a considerable confusion of concepts, definitions, models, and measures (or indices). Diversity in essence, has always been defined by the indices used to measure it and this has not led to the uniformity which allows a clear statement of ideas and hypotheses (Peet, 1974).

The concept of diversity has developed from the study of species-abundance relations and from attempts to answer questions such as (i) Why are there so many kinds of organisms?, and (ii) Why are there certain numbers of each kind (Morrison & Yarranton, 1973). Diversity thus incorporates aspects of number of species per unit area, and the distribution of individuals among the species. These aspects were separately considered by Williams (1964), who derived a statistic expressive of the mathematical distribution of any element over another. Margalef (1958) proposed that the amount of information contained in its floristic or faunistic structure is an appropriate measure of the community's diversity.

A community is said to have high diversity if it has many species and the distribution of individuals is fairly even among species. Conversely, diversity is low when the species are few and their abundances uneven (Pielou, 1969). Dependence on two rather independent properties of a community results into ambiguity. Therefore, a community with few species but high evenness could have the same level of diversity as another with many species but low evenness. In general, the diversity of a sample is minimal when all the individuals belong to a single species, and maximal when each individual belongs to a different species. Whittaker (1972) distinguished three levels of diversity:

Alpha diversity—Within-habitat or within-community diversity.

Beta diversity—between-habitat or

intercommunity diversity, defined as the change in species composition along environmental gradients, or species turnover.

Gamma diversity—diversity of the entire landscape or a range of communities in a location (i.e., a combination of alpha and beta).

These forms are not always easily distinguished (Peet, 1974). Many alpha-diversity measurements are influenced by habitat variations, which could be interpreted equally well as beta-diversity. The first two (alpha and beta-diversities), nevertheless have proved particularly useful. The concepts of alpha diversity and equitability have been successfully used in understanding the benthic foraminiferal changes in the northern Indian ocean across the Oligocene-Miocene boundary and during the Quaternary (Gupta & Srinivasan, 1989, 1990c). Further, the degree to which diversity is alpha or regional (beta or gamma) is found to have considerable implications for extinction processes (Sepkoski, 1988). According to Sepkoski (1988) the within-habitat diversity doubled from the Cambrian to the Ordovician, and remained relatively steady thereafter; beta diversity also increased subsequent to the Cambrian and remained approximately steady thereafter. The alpha and beta diversities, each account for one-sixth of the early Paleozoic increase in global diversity. According to Niklas (1986) and Niklas *et al.* (1985), there occurred striking increases in angiosperm gamma diversity through the Cretaceous and Cenozoic. Southwood *et al.* (1979) studied the vegetation along a gradient of a secondary succession in southern England and found that alpha-diversity increased and then decreased with succession age, whereas the beta-diversity was proportional to the successional age differences, age being on a logarithmic scale. This suggested that the turnover of plant species declined logarithmically with successional age.

Biodiversity may range from genetic variation at the population level, through alpha, beta and patch diversities to regional community complexity. In the present paper we take a broader view of species diversity by considering turnover of kinds of species and their assemblages in addition to species numbers and abundances. A broader view may be more conducive to investigations for assessing the role of biological diversity in ecosystem functioning. Schindler (1988) has reviewed literature on the effects of acid rain on fresh water ecosystems to show that significant changes in lake metabolism did not occur although changes in species of phytoplankton were dramatic in acidified lakes. There is lack of knowledge on mechanism through which this biological diversity sustains ecosystem functioning in face of such disruptive processes as acid rain.

CURRENT SPECIES DIVERSITY GRADIENTS

Variations in species diversity have been examined with respect to geography, climate and soil. Species diversity increases from the poles to the tropics as documented for a variety of organisms including mammals, birds, fishes, insects, other invertebrates and plants (Abbott, 1968; Black *et al.*, 1950; Darlington, 1959; Fischer, 1960; MacArthur & Wilson, 1967; Pianka, 1966; Price, 1975; Simpson, 1964; Stehli, 1968; and others); diversity is greater on continents than islands (MacArthur & Wilson, 1967); in temperate regions there is an increase in diversity from maritime to continental climates (Whittaker & Niering, 1965; Whittaker, 1960, 1965); Monk (1965, 1967) has reported higher diversities on calcareous soils than on acidic soils; and Frydman and Whittaker (1968) found that diversity was correlated with soil fertility. Resource based models of community structure predict that species richness should be higher in fields with greater range of resource availability (Tilman, 1982).

In certain narrowly defined groups, the latitudinal gradient in species diversity is reversed with species richness increasing poleward within a latitudinal belt before decreasing again at still higher latitudes; for example, in penguins in the southern hemisphere and in alcids in the northern hemisphere (Stehli, 1968); and also, in the sublittoral and shallow shelf infauna (Thorson, 1957). Fresh water planktonic communities are more diverse in the temperate regions compared to their counterparts in the tropics. Ichneumonid wasps are more diverse in the temperate regions than in the tropics (Owen & Owen, 1974), the same seems to be true also for burrowing animals (Klopfer, 1962).

Species diversity tends to decrease with elevation. However, this pattern is by no means universal (Diamond, 1988a). For example, the diversity of plant species along the Western Andean slopes of northern circle is extremely low at sea level, increases from middle to high elevations, and then decreases at still higher elevations. In the Mediterranean zone of California the species diversity reaches a maximum at middle elevations (Cody, 1975).

Levels of alpha diversity appear to be similar in tropical alpine, temperate alpine and arctic communities (Hanselman, 1975). Nevertheless, among mountains, regional or gamma diversity appears to be greater in tropical alpine than in temperate alpine or arctic regions. This is evident

from relatively high levels of endemism and vicarious species complexes on tropical mountains (Smith & Young, 1987).

Another apparent gradient in the diversity of terrestrial species groups is from a high diversity in large continental landmasses to a low diversity in small oceanic islands (MacArthur & Wilson, 1967). Species richness in mammals in the interior of North America is greater compared to that in the peninsulas around the periphery of the continent (Simpson, 1964). This peninsular effect is also shown by the deciduous trees of Canada; there are 31 species in the Atlantic provinces and 50 species in a comparable area at the same latitude (north of 43.5°N) in Ontario (Hosie, 1969).

Species diversity in marine animals, in bivalves and in polychaetes of soft sediments decreases from tropical shallow seas, through successively lower values in the deep sea on the continental slope, in tropical estuaries, in boreal shallow seas and in boreal estuaries (Sanders, 1968). A diversity contrast between boreal shallow water communities of these animals occurring in a continental climate (off the new England Coast) where diversity is low and in a maritime climate (off the State of Washington) where diversity is comparatively high was reported by Sanders (1968).

Study of the relationship of species diversity to environmental conditions has not led to widely acceptable generalities, however (Whittaker, 1972), in some cases diversity is highest in more mesic communities, in others it is not. In forest-grazing land of parts of Kumaun Himalaya, Saxena and Singh (1980) reported maximum floral diversity on the aspects which had intermediate temperature and moisture conditions and it declined towards the cooler (and wetter) and warmer (and drier) exposures. Whittaker (1975) has reported that maximum diversities are in the middle part of the moisture gradient for larger vegetation units in the temperate zone. Terborgh (1973) also stated that the general case in temperate North American vegetation is to have greatest species numbers in the middle part of moisture gradient, rather than in wetter or drier areas. But several contradictions are also available (Whittaker, 1972; del Moral, 1972). Zobel *et al.* (1976) reported increase in plant diversity in forest communities of the Central Western Cascades of Oregon away from the moderate environmental conditions, towards both cooler and more xeric environments.

A few broad trends which emerge from the literature survey can be summarized as below:

  (i) A gradient of increasing diversity is usually seen from the poles to the equator.

  (ii) Diversity usually decreases up the slope of a mountain.

 (iii) Terrestrial communities normally have greater diversity per unit area compared to marine communities.

  (iv) Islands usually have lower diversity per unit area compared to continents.

  (v) Habitats with extreme environmental conditions such as hotsprings, deserts and polar deserts usually have very low species diversity.

  (vi) In benthic communities in the oceans, shallow regions have low diversity while deeper regions have high diversity.

FACTORS CONTROLLING SPECIES DIVERSITY

It is important to understand the factors that govern diversity gradients as any change in the climate is likely to affect the causal factors. Several explanations have been offered within the past three decades to explain the observed patterns in the distribution of species diversity (Connell & Orias, 1964; Darlington, 1957, 1959; Dobzhansky, 1950; Dunbar, 1960; Fischer, 1960; Hutchinson, 1959; MacArthur, 1965; Pianka, 1966; Whittaker, 1972, 1977; Ricklefs, 1979; Rosen, 1981; Thiery, 1982; Cracraft, 1985; Turner *et al.*, 1988). Most of these usually explain only the patterns observed in a particular situation. Complex biological patterns such as those of diversity hardly result from single causal factor. The effect of one factor may be overridden or modified by others. Diamond (1988a) has argued that some of the determinants of species diversity, such as predation, herbivory, disturbance, seasonality, and environmental predictability, control diversity in a nonmonotonic way, so that an increase in those factors may yield either an increase or a decrease in diversity.

There appear to be nine more or less distinct hypotheses regarding observed patterns of species diversity.

1. Time hypothesis

The history of geological disturbances indicates that all communities tend to diversify in time, and therefore older the community more species it is likely to have. Biotic diversity is a product of evolution and therefore is dependent on the length of time through which the biota has developed in an uninterrupted fashion (Fischer, 1960). Communities have been evolving in the tropics for a very long time without interruptions. Thus a constant favourable environment and a relative freedom from

climatic disasters like glaciation has led to greater diversity in warm, humid tropics. On the other hand glaciation and other catastrophic climatic events have repeatedly destroyed biota in the temperate region. There has thus been relatively little time for communities to evolve in the higher latitudes.

The time stability hypothesis is difficult to test (Peters, 1976; Abele & Walters, 1979). The evidence relating to this hypothesis as summarised by Elton (1958) and discussed by Deevey (1949), however, indicates that most continental habitats are ecologically saturated. Some palaeontological data support the time hypothesis. Planktonic fossil foraminifera exhibit a declining trend in species richness from equator to the poles for at least 270 million years (Stehli et al., 1969). Evidence for this hypothesis also comes from a study of the number of insect species associated with different tree species in Britain. There appears to be a fairly strong positive correlation between the number of insect species associated with a tree species and the time for which the tree species has been growing in Britain after recolonisation following the last glaciation (Birks, 1980). Lake Baikal in USSR is also an example which supports time hypothesis. There are 580 species of benthic invertebrates in the deep waters of this lake (Kozhov, 1963). A comparable lake in glaciated northern Canada, Great Slave lake, contains only four species in the same zone (Sanders, 1968).

Simpson (1964) has argued that the warm temperate regions have remained undisturbed long enough (from the Eocene to the present) to become both ecologically and evolutionarily saturated. However, there are fewer species in this zone than in the tropics, indicating that factors other than time stability are needed to explain differences between tropical and temperate diversities. For North American mammals, the recently glaciated zone shows a fairly flat diversity profile, in contrast to a steep gradient in species diversity expected from the evolutionary time theory (Simpson, 1964). Further, Newell (1962) stresses that temperate areas at intermediate latitudes were simply shifted laterally along with their flora and fauna during the glacial periods and therefore they may have had as long a time to adapt as have the nonglaciated areas.

2. Spatial heterogeneity hypothesis

According to this hypothesis, more spatially complex environments favour coexistence of more species. In other words, the more heterogeneous and complex the physical environment, the more complex and diverse will be the plant and animal communities.

Pianka (1966) distinguishes two sub-categories of this hypothesis, one on a macro- and the other on a micro-scale. Simpson (1964) has shown that the highest diversities of mammals in the United States occur in the mountain areas of high topographic relief These areas contain many different habitats and hence more species. Also, mountainous areas experience more topographic isolation of populations and so may promote speciation (Krebs, 1985). MacArthur (1965) has argued that there may be more land bird species in the tropics both because of an increase in the number of species per habitat as well as increase in the number of habitats per unit area.

Microspatial heterogeneity, on the other hand, operates on a more local scale and the size of environmental elements correspond roughly to the size of the organisms populating the region (Pianka, 1966). Elements of the environmental complex in this class might be soil particle size, rock and boulders, karst topography, or the pattern and complexity of vegetation. Habitats with a more complex or variegated structure contain more species than do simpler habitats. Thus, within any group of taxa there are generally fewer species in a rock desert than in an adjacent grassland, fewer in grassland than in an adjacent savanna, and fewer in the savanna than in an adjacent tropical rain forest (Diamond, 1988a). MacArthur and MacArthur (1961) measured bird species diversity on a series of sites and attempted to relate this to foliage height diversity. Foliage height diversity is a measure of stratification and evenness in the vertical distribution of vegetation, and according to MacArthur and MacArthur (1961), foliage height diversity is a good predictor of bird species diversity.

Structural diversity of habitats tends to increase from the poles to the equator with polar ice caps and the equatorial tropical rain forest forming the extreme ends of the gradient. However, vegetation spatial heterogeneity is clearly dependent on other factors and explanation of animal species diversity in terms of vegetation complexity at best puts the question of the control of diversity back to the control of vegetation diversity (Pianka, 1966).

3. The competition hypothesis

As advocated by Dobzhansky (1950) and Williams (1964), the natural selection in the temperate zones is controlled mainly by the exigencies of physical environment, whereas biological competition is a more important component of evolution in the tropics (Pianka, 1966). As competition increases, organisms become more specialized and niche sizes decrease causing

the species diversity to increase (MacArthur, 1965, 1972). The evolutionary impetus to reduce competition results in more niche overlap and thus higher diversity (Klopfer & MacArthur, 1960). Niche theory predicts that when species coexist, their niches should either become narrower or the overlap become greater compared to the allopatric situations. Coexistence of species is made possible because of niche shift also called character displacement (Fenchel, 1975; Giller & McNeill, 1981; Nilsson, 1965), reduction in niche width or increase in niche overlap. Roughgarden (1974) showed decrease in niche breadth in species rich communities of Anolis lizards.

According to Dobzhansky (1950), in the humid tropics catastrophic mortality (density-independent), such as that due to drought and cold, seldom occurs. Catastrophic mortality usually causes selection for increased fecundity and/or accelerated development and reproduction, rather than selection for competitive ability and interactions with other species. Therefore, tropical species will be more highly evolved and possess finer adaptations than temperate species, due to their more density-dependent mortality and the increased importance of competitive interactions.

The importance of interspecific competition, however, is being seriously questioned in recent years (see Shoener, 1983; Connell, 1983; Strong *et al.*, 1984) especially by those working with insects where competition does appear to be relatively weak and unimportant.

4. Predation hypothesis

According to this hypothesis, as predators increase in numbers, they reduce population sizes of their prey, thus allowing for more prey species to coexist (Paine, 1966; Janzen, 1970). Paine (1966) argues that there are more predators and parasites in the tropics than elsewhere and these hold down their prey populations to such low levels that competition among prey organisms is reduced. The reduced competition allows additions of more prey species, which in turn support new predators. It is interesting to recall the review on extinct terrestrial vertebrates by Webb (1987). It was suggested that the extinction of large herbivores in mid-Cretaceous led to that of the large carnivores. However, reassembly was from the top down and each new dynasty emerged from insectivors or small carnivores which gave rise to wholly new groups of dominant herbivores.

5. Climatic stability hypothesis

Stable climates allow the evolution of finer specializations and adaptations because of the relative constancy of resources than do areas with more erratic climatic regimes. This also results in smaller niches and more species occupying the unit habitat space. Thus more stable the environmental parameters, the more species will be ·present. Biological communities would be evolving faster in the wet tropics because of the uniformly suitable conditions for life throughout the year. However, rainfall and temperature can be shown to vary less in the humid tropics than in the temperate zones, but rigorous correlation with faunal diversity has not yet been possible (Pianka, 1966). Climatic factors thus could determine directly the vegetation complexity, while being only indirectly related to the faunal diversity of the area.

The factor of climatic stability can be combined with the time factor, with which it has much in common. The stability-time hypothesis (Sanders, 1968) states that the longer a community has maintained stability and not been subject to major disturbances the more species will accumulate.

6. The productivity hypothesis

It has been suggested that combined with the factor of climatic stability, increased productivity would increase species diversity (Connell & Orias, 1964). The productivity hypothesis states that everything being equal, as environments increase in productivity, diversity will increase. However, many different relationships exist between species numbers and the productivity of their resources (Ricklefs, 1979; Krebs, 1985; Begon *et al.*, 1986), and a variety of theoretical explanations have been advanced to support different relationships between resource productivity and species diversity (Connell & Orias, 1964; Pianka, 1972; Riebesell, 1974; Tilman, 1982). In at least one case, the same data have been used to support both increasing and decreasing relationship between productivity and species diversity. Brown and Gibson (1983) interpreted the data of Whiteside and Harmsworth (1967) on Chydorid Cladocera to mean that species diversity and productivity have a negative correlation, while Krebs (1985) using the same data indicated otherwise.

Productivity-diversity relationships may be classified broadly into two types: increasing, and unimodal (Abrams, 1988). Since a certain level of resource productivity will allow some consumers to exist, diversity must increase with productivity for low levels of productivity. As productivity continues to increase, diversity may remain the same or increase (both called increasing productivity-diversity relationship), or diversity may decrease, resulting in a unimodal relationship. There are cases

in which diversity increases with productivity over the range of productivities measured; see for example Pianka's (1967) data relating number of lizard species to length of the growing season, Brown's (1975) analysis of North American desert rodent communities, and Belovsky's (1986) summary of generalist herbivore species number vs. productivity. Kirchner (1977) found that fertilizing a shortgrass prairie with nitrogen or increasing productivity by watering increased plant species diversity. Tilman (1982) présents data on several plant communities illustrating unimodal productivity-diversity relationships. A similar pattern was observed by Abramsky and Rosenzweig (1983) for diversity in desert rodent communities. Richerson and Lum (1980) on the other hand, found no evidence for an effect of productivity on diversity in an extensive analysis of California land plant communities (Abrams, 1988).

7. Temporal heterogeneity hypothesis

Pianka (1966) has argued that the longer growing season of tropical regions allows the component species to partition the environment temporally as well as spatially, thereby permitting the coexistence of more species. Such temporal partitioning of environmental resources is also exhibited by the warm and cool season plants of mixed-grass prairie (Singh et al., 1983). Different photosynthetic adaptation of plants to cool and moist (C_3) and to warm and dry (C_4) conditions permits temporal separation of species into warm season and cool season guilds. This confers upon the constituent species the ability to avoid competition. This seasonal expression causes plant diversity to vary with time, the mid season, experiencing maximum diversity as the recruitment of the community is completed and the resource tends to be more equitably shared among the constituent species at that time.

8. Lithospheric complexity and environmental harshness hypothesis

Cracraft (1985) presented an alternative conceptualization of biological diversification and its causes. He considers "the rates of speciation and extinctions are diversity independent. The rate of speciation is hypothesized to be mediated by the rate-change of lithospheric evolution operating through geomorphological complexity. Increased complexity presents more opportunities for vicariousness and long-distance dispersal to produce isolation and differentiation". He further formulates a deterministic theory of extinction which relates

"an increased probability of extinction to an increase in the gradient of environmental harshness. The latter is a measure of the physiological stress to which populations are exposed" Since rate of biological diversification is a function of balance between rates of speciation and extinction, lithospheric complexity together with environmental harshness is responsible for species diversity gradients. Latitudinal and longitudinal gradients of diversity (Simpson, 1964; Wilson, 1974; MacArthur, 1969; Cook, 1969) parallel the gradients in topographic complexity which is taken to be an approximation of lithospheric (geomorphological) complexity and environmental harshness. An increased diversity with increasing depth in benthic invertebrates is related to opportunities that complexity creates for geographic isolation and differentiation.

The theory does not claim to explain all observations, neither it attempts to account for the greatest amount of variance seen in large scale diversity gradients (Cracraft, 1985). But Cracraft supports testability of the theory because it has considerable empirical support.

9. Species-energy hypothesis

Recently, Turner et al. (1988) have tried to explain the steep decline in the number of species from tropics to pole by 'the weather', that is, latitudinal decline in the input of solar energy. They proposed a new hypothesis, the species-energy hypothesis, which predicts that species richness correlates with the available solar energy as measured by temperature and sunshine hours. Such a correlation has been demonstrated for birds (Wright, 1983), butterflies and moths (Turner et al., 1987) and terrestrial vertebrates (Terentev, 1963). Plant diversity (Richerson & Lum, 1980) and tree diversity (Currie & Paquin, 1987) are found to be related with temperature and rainfall, or with evapotranspiration, which is a function of these two.

Turner et al. (1988) argued that if their hypothesis were correct, "the correlations should exist only during those parts of the year when organisms are actively absorbing energy, and should disappear if energy absorption ceases, ...or even become negative if irreplaceable energy is being expanded, as when an insect hibernates". They provide data for distribution of small insectivorous birds in Britain and show that the diversity of summer visitors correlates only with summer temperature and the same of winter visitors with winter temperature only.

The relationship between energy and species

richness is explained by giving a simple stochastic theory, "Given the observed constant turnover (colonization and extinction) of species in any one area, regions where populations are larger will have more species at equilibrium, as smaller populations become extinct more often". "Greater energy supplies might increase populations of birds indirectly, through overall productivity, or directly on account of the lower metabolic energy required to maintain body functions when the air is warmer".

PAST CLIMATIC CHANGES AND DIVERSITY

The present biological diversity on the Earth has taken a long time to evolve. Signor (1990) has reviewed the history of vascular plant diversity to show that the Devonian appearance of seed plants accelerated the diversification to a Late Devonian peak of over 40 genera; thereafter following a slight decline, the diversification resumed in the Carboniferous, and the number of species increased to over 200. The increase in the number of plant species occurred gradually between the mid-Carboniferous and the end of the Permian. The slight reduction (about 20%) in diversity at the end of the Permian was followed by a rapid increase to pre-Mesozoic levels, subsequently diversity increased slowly to about 250 species in the Early Cretaceous. Coniferophytes, cycads and cycadeoids replaced the previously dominant groups and dominated the plant biota until the Middle Cretaceous. The mid-Cretaceous coincided with the final phase of plant diversification and the appearance of angiosperms. The latter, having the highest rate of diversification among the major plant groups, diversified slowly at first but more rapidly in the Cenozoic, and they now constitute more than 80% of the plant species on earth. According to Knoll (1984), there were about 25,000 species of flowering plants in the Early Cretaceous, this number swelled to 100,000 species by the Late Cretaceous, and today there are about 200,000 species. However, extinctions and reconstitution of biotic communities have repeatedly occurred in the geological past as illustrated through the following examples. There is a spectrum of minor extinction events, many of which indicate the biological system being in profound stress, in addition to five major extinction events during past 600 million years (Raup, 1986). Apparently, relatively long periods of stability alternated with short-lived extinction events. Raup and Sepkoski (1984, 1986) analysed the numerical patterns of extinction in the marine fossil record and identified 10 mass extinctions since the Late Permian from family data and 8-12 extinctions

from generic data. They inferred that extinctions are driven by some environmental process (implicating extraterrestrial or geophysical driving mechanisms) with a periodicity of approximately 26 Ma. However, proposed cyclic nature of extinctions has generated a lot of debate (Davis *et al.*, 1984; Quinn, 1987, Quinn & Signor, 1989; Patterson & Smith, 1989) which is still inconclusive.

Major extinctions have occurred at geologic time boundaries, such as Frasnian/Fammennian, Ordovician/Silurian, Permian/Triassic, Triassic/Jurassic and Cretaceous/Tertiary Plants seem to have survived the great mass extinction events better than animals; for example, at the Triassic/Jurassic boundary, gymnosperms of similar morphology dominated the vegetation on either side as did the angiosperms across the Cretaceous/ Tertiary (K/T boundary) (Ricklefs *et al.*, 1990). During each mass extinction episode 25->75 per cent of the extant taxa were lost. The course of Gondwana floral development in India in relation to P/T boundary furnishes an interesting example.

A glacigene event initiated the Permian flora in India. The advent of *Glossopteris* association in the earliest Permian thus witnessed a great stress on environment because of extensive glaciation on the Gondwana supercontinent. The cold conditions under which sediments of Talchir Formation were laid allowed limited diversification of plant species in number as well as kind. Major floral elements of this period are represented by leaves of the genera *Gangamopteris* and *Noeggerathiopsis*. Slightly later appeared the genus *Glossopteris* with nearly six species and the only conifer reported is *Paranocladus*. The palynological fossils found dispersed in these sediments also reflect low diversification. Out of nine genera of palynofossils, five refer to saccate pollen, three to a trilete-bearing and one alete spore type (Lele, 1975). These floral elements appear to be organizationally related with some of the Late Carboniferous pollen group and could have evolved from that stock (Vijaya & Tiwari: Ms, 1991).

With the amelioration of the climatic conditions, the flora diversified and some new elements, viz., *Botrychiopsis, Euryphyllum, Rubidgea* and *Buriadia* appeared in the late Early Permian (Karharbari "Formation"). Species of the genera *Noeggerathiopsis, Gangamopteris* and *Glossopteris* also increased in number (Bajpai, 1990). By the end of Karharbari the number of palynotaxa almost doubled, the species multiplied four-fold, pteridophytic spores contributing to about one third of the population.

By the early Middle Permian (Barakar

Formation), the *Noeggerathiopsis-Gangamopteris* association declined and was succeeded by a *Glossopteris* dominated association. The genera *Botrychiopsis, Rubidgea* and *Buriadia,* which developed only locally became extinct. Two new elements, viz., *Rhabdotaenia* and *Walkomiella* appeared, the latter taxon is known through only one record. A well marked change in palynofloral composition at the Karharbari/Barakar boundary has been recorded; the Early Permian monosaccate predominance suddenly declined, the diversity in species of the pteridophytic (including lycopsid) spores increased many-fold and the gymnospermous disaccate striate and nonstriate pollen dominated numerically (Tiwari & Tripathi, 1988). Floral elements suggest a mesic environment that was probably warm temperate with ample water supply and sufficient light intensity (Maheshwari *et al.,* in Press). The flora of upper Middle Permian (Kulti Formation) is poorly known.

The Late Permian (Raniganj Formation) had the peak development of *Glossopteris* and some other genera, viz., *Rhabdotaenia, Palaeovittaria, Belemnopteris,* etc. (Maheshwari, 1970). The fossil wood shows well-marked annual rings (Maheshwari, 1972). The climate was warm-temperate with heavy rainfall. On the basis of palynofossil species also, it has been confirmed that the climax of Gondwana vegetation was attained in the Late Permian Raniganj Formation. At the terminal Permian (uppermost Raniganj Formation) the megafossils indicate a rather impoverished vegetation in which leaves had a reduced surface and open venation (Bajpai, 1987, Bajpai & Tewari, 1990).

Relatively more diversified palynofossil-assemblage of the Raniganj Formation reflects the multiple lines of evolutionary trends in pollen and spores. The palynofossil-assemblage is dominated by striate-disaccate pollen *Striatopodocarpites, Protohaploxypinus, Crescentipollenites, Striatites* and *Densipollenites.* The total number of spore-pollen species recorded in Raniganj is 175, out of which 39 species have pteridophytic affinity. 137 species disappeared in the Lower Triassic that included 76 per cent of pollen and 24 per cent of pteridophytic spore species. However, six species of spores and 32 of pollen continued to survive, from Late Permian to Early Triassic, as shown in Table 1 (after Tiwari & Tripathi, 1991, MS).

At the beginning of the Early Triassic (Panchet Group) a change is noticed in the basic composition of the palynoflora. The spore pollen genera consistent in their occurrence in the Early Triassic are *Klausipollenites, Lunatisporites, Lundbladispora, Densoisporites, Playfordiaspora, Alisporites,* and some of the older disaccate-striate taxa (Maheshwari & Banerji, 1975; Tiwari & Singh, 1986). The megaflora shows a continuum in characteristic elements, such as *Schizoneura gondwanensis, Glossopteris* spp. and *Rhabdotaenia* sp. Even the sphenophyll *Trizygia speciosa* has been reported (Bhattacharyya, 1963).

Some of the Lower Triassic forms, e.g., *Playfordiaspora, Lundbladispora, Lunatisporites,* etc made sporadic appearance in the uppermost Upper Permian strata, while a few of the dominant Upper Permian forms, e.g., *Striatopodocarpites* and such others continued, in diminishing order of diversification, into the Lower Triassic (Vijaya & Tiwari, 1987; Srivastava & Jha, 1990). The early part of the Lower Triassic is marked by 84 distinct species which were either absent in the Upper Permian or appeared inconsistently only at its closing phase. Among the new-comers of Triassic palyno assemblage, pteridophytic spores are represented by 48 species and the gymnospermous pollen by only 36 species. The taeniate pollen perhaps increase consistently at the cost of striate pollen (Tiwari, personal communication).

Thus a major change is recorded in the pollen-spore constituents and, implicity, in the vegetation at the P/T boundary. It is necessary to work out leaf floras with this objective to record climatic signatures both at the transition as well as in the Early Triassic.

The mass extinction at the K/T boundary has been a subject of numerous studies. There are those who believe in a gradual extinction (thousands to million of years) through long-term global cooling and marine regression, while others advocate catastrophic (months to years) extinction. The three most commonly cited causes of mass extinction are: (i) change in sea level, (ii) climatic deterioration, and (iii) collision with extraterrestrial bodies.

Alvarez *et al.* (1980, 1984b) proposed that the impact of a 10 km diameter asteroid caused mass extinction at the end of the Cretaceous. The dust clouds blocked out solar radiation, photosynthesis was checked, and earth's surface was cooled to lethal limits. Massive wildfires were also caused by the impact (Saito *et al.,* 1986; Wolbach *et al.,* 1988). Evidence cited in support of asteroid impact hypothesis includes a worldwide layer of clay deposits enriched with siderophilic elements, mainly iridium, osmium isotope ratios, shocked quartz and spherules interpreted to be microtaktites (Bohor *et al.,* 1987; Kerr, 1988). Hut *et al.* (1987) have postulated multiple small impacts, instead.

The K/T extinction event seems to have been preceded by several million years of global cooling

Table 1—Distribution of spore-pollen taxa through Permo-Triassic period of India

PALYNOTAXA/AGE	PERMIAN	TRIASSIC
Acanthotriletes filiformis	———	
Alisporites gracilis	———	
Altimonoletes flavatus	———	
Anapiculatisporites consonus	———	
Anapiculatisporites veritas	———	
Apiculatisporis inconspicuus	———	
Apiculatisporis levis	———	
Apiculatisporis secretus	———	
Barakarites dubius	———	
Brevitriletes communis	———	
Calamospora aplata	———	
Calamospora exila	———	
Corisaccites alutus	———	
Corisaccites distinctus	———	
Crescentipollenites ampulus	———	
Crescentipollenites gondwanensis	———	
Crescentipollenites hirsutus	———	
Crescentipollenites implicatus	———	
Crescentipollenites sellingi	———	
Cuneatisporites exiguus	———	
Cuneatisporites rarus	———	
Cyclobaculisporites indicus	———	
Cyclobaculisporites minimus	———	
Cyclobaculisporites minutus	———	
Densipollenites brevis	———	
Densipollenites densus	———	
Densipollenites magnicorpus	———	
Densipollenites minimus	———	
Distriamonocolpites ovatus	———	
Distriatites bilateris	———	
Distriatites insolitus	———	
Distriomonosaccites ovalis	———	
Divarisaccus invasus	———	
Divarisaccus lelei	———	
Ephedripites ellipticus	———	
Eupunctisporites grabus	———	
Fusacolpites fusus	———	
Gbosbiasporites didecus	———	
Ginkgocycadophytus cymbatus	———	
Gnetaceaepollenites grandis	———	
Gnetaceaepollenites sinuosus	———	
Gondisporites raniganjensis	———	
Gondisporites reticulatus	———	
Gondwanaeplicates bharadwaji	———	
Guttulapollenites hannonicus	———	
Hamiapollenites incestus	———	
Hennellysporites diversiformis	———	
Hindipollenites globosus	———	
Hindipollenites indicus	———	
Hindipollenites rajmahalensis	———	
Hindipollenites oblongus	———	
Horriditriletes brevis	———	
Ibisporites diplosaccus	———	
Indospora clara	———	
Indospora laevigata	———	
Indospora macula	———	
Lacinitriletes badamensis	———	
Laevigatosporites colliensis	———	
Laevigatosporites punctatus	———	
Labirites alutas	———	
Labirites angustus	———	
Labirites kajoraensis	———	
Labirites lepidus	———	
Labirites minutus	———	
Labirites parvus	———	
Labirites rotundus	———	
Labirites singularis	———	
Leiotriletes brevis	———	
Lophotriletes frequensis	———	
Lophotriletes novus	———	
Mammialetes mammus	———	
Marsupipollenites striatus	———	
Marsupipollenites triradiatus	———	
Microbaculispora gondwanensis	———	
Microfoveolatispora foveolata	———	
Pityosporites papillonis	———	
Plicatipollenites reticulatus	———	
Plicatipollenites triangularis	———	
Potonieisporites raniganjensis	———	
Praecolpatites sinuosus	———	
Punctatosporites morosus	———	
Raniganjiasaccites ovatus	———	
Rhizomaspora costa	———	
Rhizomaspora fimbriata	———	
Rhizomaspora indica	———	
Ricaspora granulata	———	
Scheuringipollenites ovatus	———	
Striatites rhombicus	———	
Striapollenites obliquus	———	
Striapollenites saccatus	———	
Striasporis striatus	———	
Striatites alius	———	
Striatites barakarensis	———	
Striatites ganjerensis	———	
Striatites multistriatus	———	
Striatites notus	———	
Striatites obliquus	———	
Striatites obtusus	———	
Striatites ornatus	———	
Striatites rhombicus	———	
Striatites subtilis	———	
Striatites tectus	———	
Striatites tentulus	———	
Striatopodocarpites copiosus	———	
Striatopodocarpites crassistriatus	———	
Striatopodocarpites ovalis	———	
Striatopodocarpites ovatus	———	
Striatopodocarpites subcircularis	———	
Striatopodocarpites tiwarii	———	
Striatopodocarpites tojmensis	———	
Striatosporites braziliensis	———	
Striomonosaccites ovatus	———	
Thymospora raniganjensis	———	
Trochosporites tripus	———	
Tumoripollenites baculatus	———	
Varireticulates varius	———	
Verrucosisporites diversus	———	
Verrucosisporites donarii	———	
Verticipollenites crassus	———	
Verticipollenites debilis	———	
Verticipollenites finitimus	———	
Verticipollenites gibbosus	———	
Verticipollenites oblongus	———	
Verticipollenites secretus	———	
Verticipollenites subcircularis	———	
Vesicaspora distincta	———	
Vesicaspora lutens	———	
Vesicaspora ovata	———	
Vestigisporites disectus	———	
Vestigisporites monosaccatus	———	
Virkkipollenites mehtae	———	
Virkkipollenites obscurus	———	
Virkkipollenites triangularis	———	
Welutischapites extansus	———	
Welutischapites tenuis	———	
Weylandites lucifer	———	
Brevitriletes unicus	———	———
Callumispora gretensis	———	———
Crescentipollenites fuscus	———	———
Crescentipollenites santhalensis	———	———
Cuneatisporites mirabilis	———	———
Cyclogranisporites gondwanensis	———	———
Densipollenites indicus	———	———
Densipollenites invisus	———	———
Faunipollenites perexiguus	———	———
Faunipollenites varius	———	———
Horriditriletes curvibaculosus	———	———
Inaperturopollenites nebulosus	———	———
Labirites incertus	———	———
Labirites raniganjensis	———	———
Labirites rarus	———	———
Lophotriletes rectus	———	———
Parasaccites korbaensis	———	———
Playsaccus fuscus	———	———
Plicatipollenites indicus	———	———
Scheuringipollenites barakarensis	———	———
Scheuringipollenites maximus	———	———
Striatopodocarpites brevis	———	———
Striatites communis	———	———
Striatites solitus	———	———
Striatites varius	———	———
Striatopodocarpites decorus	———	———
Striatopodocarpites diffusus	———	———
Striatopodocarpites labrus	———	———
Striatopodocarpites magnificus	———	———
Striatopodocarpites oblongatus	———	———
Striatopodocarpites perfectus	———	———
Striatopodocarpites rarus	———	———
Striatopodocarpites rotundus	———	———
Striatopodocarpites venustus	———	———
Striomonosaccites circularis	———	———
Verrucosisporites gondwanensis	———	———
Virkkipollenites densus	———	———
Weylandites indicus	———	———
Alisporites asansolensis		———
Alisporites damudicus		———
Alisporites grobus		———
Alisporites indicus		———
Alisporites landianus		———
Alisporites plicatus		———
Aratrisporites fischeri		———
Biretisporites dubius		———
Biretisporites sp.		———
Callumispora fungosa		———
Chordasporites raniganjensis		———
Convertubisporites contactus		———
Convertubisporites densus		———
Crescentipollenites bengalensis		———
Cyathidites australis		———
Cycadopites follicularis		———
Cyclogranisporites triletus		———
Decisporis panchetensis		———
Decisporis rudis		———
Decisporis variabilis		———
Densoisporites complicata		———
Densoisporites contactus		———
Densoisporites playfordii		———
Decisporites triassicus		———
Dictyophyllidites decus		———
Dictyotriletes invisus		———
Divaripunctites bifurcatus		———
Divaripunctites globosus		———
Divaripunctites plicatus		———
Falcisporites nuthalensis		———
Falcisporites stabilis		———
Faunipollenites microcarpus		———
Goubinispora indica		———
Goubinispora morondavensis		———
Granuloperculatipolis flavatus		———
Granuloperculatipollis problematicus		———
Guttatisporites ambiguus		———
Indotriradites cuspidus		———
Indotriradites mammilatus		———
Indotriradites wargalensis		———
Klausipollenites schaubergeri		———
Klausipollenites sulcatus		———
Labirites levistriatus		———
Labirites triassicus		———
Laricoidites intragranulosus		———
Lophotriletes minimus		———
Lunatisporites asansoliensis		———
Lunatisporites damudicus		———
Lunatisporites diffusus		———
Lunatisporites noviaulensis		———
Lunatisporites ovatus		———
Lunatisporites pellucidus		———
Lunatisporites rhombicus		———
Lundbladispora baculata		———
Lundbladispora brevicula		———
Lundbladispora densispinosa		———
Lundbladispora microconata		———
Lundbladispora obsoleta		———
Lundbladispora raniganjensis		———
Lundbladispora warti		———
Orbella indica		———
Osmundacidites senectus		———
Pilasporites plurigenus		———
Pinuspollenites thoractus		———
Playfordiaspora cancellosa		———
Pretricolpopollenites bharadwaji		———
Pyramidosporites racemosus		———
Rhizomaspora bibaria		———
Rhizomaspora divaricata		———
Rhizomaspora triassica		———
Rimaspora plicata		———
Simeonospora kblonovae		———
Striatites levistriatus		———
Striatites panchetensis		———
Striatopodocarpites multistriatus		———
Striatopodocarpites raniganjensis		———
Subverrisporis rudis		———
Verrucosisporites bosei		———
Verrucosisporites densus		———
Verrucosisporites morulae		———
Verrucosisporites narmianus		———
Verrucosisporites triassicus		———
Verrucosisporites warti		———
Weylandites circularis		———

(After Tiwari & Tripathi, 1991 : MS).

Table 2—Distribution of fossil spore and pollen taxa through Eocene-Oligocene Epoch in India

PALYNOTAXA/AGE	EOCENE	OLIGOCENE
Araliaceoipollenites rugulatus		
Arecipites indicus		
Asperitricolporites pilosus		
Caprifoliipites descretus		
Cupanieidites flabelliformis		
Dicolpopollis kalewensis		
Favitricolporites ornatus		
Neocouperipollis cymbatus		
Palmaepollenites baculatus		
Proteacidites debaanii		
Retibrevitricolpites foveolatus		
Retitricolpites florentinus		
Rhoipites baculiferus		
Rhoipites communis		
Schizosporis rugulatus		
Spinainaperturites densispinus		
Stephanocolpites globatus		
Striatricolporites obscuris		
Symplocoipollenites gracilis		
Tricolpites brevicolpus		
Tricolpites fissilis		
Triorites pseudoreticulatus		
Triorites tubiferus		
Araliaceoipollenites matanomadhensis		
Arecipites bellus		
Baksipollis primitiva		
Cupuliferoipollenites ovatus		
Dandotiaspora plicata		
Dermatobrevicolporites dermatus		
Dracaenoipollis circularis		
Intrapunctisporis apunctis		
Lakiapollis ovatus		
Neocouperipollis brevispinosus		
Neocouperipollis kutchensis		
Osmundacidites kutchensis		
Palmaepollenites nadhamunii		
Palmaepollenites ovatus		
Palmaepollenites plicatus		
Pellicieroipollis langenheimii		
Polybrevicolporites nadhamunii		
Pseudonothofagidites kutchensis		
Pseudonothofagidites kutchensis		
Retistephanocolpites flavatus		
Retitetrabrevicolporites globatus		
Retitribrevicolporites matanomadhensis		
Seniasporites verrucosus		
Striacolporites cephalus		
Striacolporites ovatus		
Symplocoipollenites kutchensis		
Tricolpites reticulatus		
Umbelliferoipollenites ovatus		
Verrucolporites verrucus		
Cricotriporites cauveriensis		
Paleocaesalpiniaceaepites miocenicus		
Proteacidites bellus		
Retitricolpites hispidus		
Stephanocolpites tetracolpites		
Tricolpites pilosus		
Marginipollis kutchensis		
Favitricolporites magnus		
Symplocoipollenites punctatus		
Psilatricolporites operculatus		
Proxapertites operculatus		
Anacolosidites trilobatus		
Cupanieidites flaccidiformis		
Engelbardtioidites minutiformis		
Myricaceoipollenites dubius		
Polycolpites pedaliaceoides		
Proteacidites terrazus		
Proxapertites hammenii		
Psilodiporites hammenii		
Rhoipites conatus		
Favitricolporites magnus		
Iugopollis tetraporoides		
Spinizonocolpites echinatus		
Palmaepollenites kutchensis		
Araliaceoipollenites mannargudii		
Tricolpites longicolpatus		
Margocolporites sitholeyi		
Mauritiidites densispinus		
Striatopollis bellus		
Tricolpites margocolpites		
Caryapollenites cauveriensis		
Marginipollis concinnus		
Myricipites barrisii		
Palaeocoprosmadites arcotense		
Biretisporites convexus		
Cheilanthoidspora monoleta		
Cyathidites australis		
Cyathidites minor		
Laevigatosporites lakiensis		
Lygodiumsporites lakiensis		
Palaeomalvaceaepollis mammilatus		
Palaeosantalaceaepites minutus		
Proxapertites microreticulatus		
Striatriletes microverrucosus		
Striatriletes susannae		
Todisporites kutchensis		
Barmocolpites ramosus		
Margocolporites sabnii		
Proteacidites granulatus		
Sapotaceoidaepollenites obscurus		
Subtriporopollis scabratus		
Araliaceopollenites descretus		
Bombacacidites triangulatus		
Compositoipollenites tricolporatus		
Graminidites granulatus		
Leptolepidites chandrae		
Palaeomalvaceaepollis rudis		
Podocarpidites cognatus		
Polypodiaceaeisporites chatterjii		
Polypodiisporites constrictus		
Polyporina multiporosa		
Proxapertites scabratus		
Punctatisporites sarangwarensis		
Retitricolpites delicatus		
Toroisporis dulcis		
Triporopollenites exactus		
Trisyncolpites ramanujamii		
Verrupolyporites globosus		

Legends :

Cauvery Basin	———————
Kutch Basin	– – – – – – –
Godavari Basin	··············
Ranges Extended on the basis of their occurrence in Miocene	—·—·—·—·—

Data after : Venkatachala (1973), Venkatachala & Rawat (1972, 1973), Kar (1985), Venkatachala & Sharma (1984).

and substantial sea-level lowering. Hallam (1987) has argued, on the other hand, in favour of terrestrial causation of end-Cretaceous mass extinction event. He concludes that these extinctions were not a geologically instantaneous event and were selective in character. According to Hallam (1987), the last few hundred thousand years of the Cretaceous were marked by environmental changes more dramatic than experienced for a long time previously or subsequently. A substantial and rapid fall of sea level could have had both direct and indirect influence on the organic world, e.g., marine invertebrate mass extinction episodes occurring in the Phanerozoic due to reduction in neritic habitat area. Sea-level fall could also have caused increases in seasonal extremes of temperature on the continents, thereby increasing the environmental stress. Increased volcanic activity over an extended period and on a large enough scale would lead to the production of immense amounts of acid rain, reduction in alkalinity and pH of the surface ocean, global atmospheric cooling resulting from expelled ash, and ozone layer depletion (Hallam, 1987). Crowley and North (1988) have suggested that terrestrially induced climate instability may be a viable mechanism for causing rapid environmental change and biotic turnover in earth's history. Moses (1989) has reviewed and compared the impact and tectonic explanations. He has suggested that extraordinary tectonism, including volcanism, sea floor spreading and sea level changes which took place prior to and at the K/T boundary, caused changes in biogeochemical cycles and climate leading to mass extinctions.

During mass extinction event at the K/T boundary, roughly half of the existing genera perished (Alvarez *et al.*, 1990; Ganapathy, 1980). These included microscopic floating animals and plants, calcareous planktonic foraminifera, calcareous nanoplankton and marine reptiles. The most striking feature of the extinction was disappearance of the planktonic forms and coccolithophorids in the oceanic realm. In this realm, approximately 13 per cent of marine families and about 50 per cent of marine genera died out completely in the Maestrichtian, the final stage of the Cretaceous; the loss may even be as high as 60-75 per cent (Raup, 1986). According to Hallam (1987), the sudden extinction event in bottom-living organisms at the end of the Cretaceous could be related to either the loss of food supply or destruction of chalky substrate habitat. From a study of planktonic foraminifera at K/T transition in Meghalaya, India, Pandey *et al.* (1990) have

suggested that extinction was biological and resulted from predation.

Among the terrestrial vertebrates, dinosaurs were one of only a few groups to be seriously affected by the extinction event. The demise of the dinosaurs probably made possible the Early Tertiary evolutionary radiation of mammals. In terrestrial habitats marsupial mammals were hard hit (Raup, 1986). Species not exterminated during these extinction events included land plants, crocodiles, snakes, mammals and many kinds of invertebrates (Lewin, 1986). Thus a sort of selectivity characterises the major extinctions, however, Raup and Boyajian (1988) have found evidence for a suprisingly uniform extinction pattern in certain marine organisms (Lewin, 1988).

For extinction trends during the Palaeozoic, Sepkoski (1987) opined that whole communities exhibit increasing extinction offshore but the genera within individual taxonomic classes tend to have their highest extinctions onshore. Earlier generalisation that extinction intensity tends to increase offshore from shallow to deep marine environments, result from a concentration of genera in classes with low characteristic extinction rates in nearshore environments (Sepkoski, 1987). Observed rate of extinctions of the genera within individual taxonomic classes is consistent with the ecologic expectation that the organisms inhabiting unpredictably fluctuating environments should suffer more extinction than counterparts living under more predictably equitable conditions.

Kurten (1971) has emphasised the worldwide trend toward glacial conditions during Miocene. Plant fossils recorded from the Miocene sediments do not support Kurten's view atleast for India. The Miocene flora in Kerala-Lakshdweep, Cauvery, Jaisalmer, Cambay, Assam-Arakan and Bengal basins and the Lower and Middle Siwalik was constituted overwhelmingly of tropical evergreen elements, presently known from Indo-Malayan region indicating warm and humid conditions (see Awasthi, 1974, 1982a, b, 1984; Awasthi & Panjwani, 1984; Lakhanpal *et al.*, 1981; Lakhanpal *et al.*, 1984). However, cooling and dry trends occurred in the post-Miocene time as a result of collision of the Indian Plate with the Asian plate, appearance of several physical barriers increased continentality, reduced precipitation, and further rise of the Himalaya. The sudden decline of the rich savanna ungulate fauna in North America during the Miocene suggests that the same cooling and drying trends that produced savanna fauna, when carried further, led to its demise (Webb, 1987). Deterioration of Cenozoic climates during the last few million years when

glaciers began to form in the northern Hemisphere, occurred and the mid-continental North America experienced the final transition from savanna to steppe as the predominant biome. Desertification occurred over a considerable expanse of Mexico and the south-western United States. In the north a unique steppe-tundra biota developed across the land area now partly beneath the Bering Sea but also including adjacent parts of northern Asia and northern North America.

Studies on planktonic foraminifera from Indian Ocean deep-sea cores have revealed that major epoch boundaries are marked by characteristic species: Pliocene/Pleistocene, the last appearance of *Globigerinoides fistulosus*; Miocene/Pliocene, appearance of *Globorotalia tumida*; Oligocene/Miocene, the appearance of *Globoquadrina dehiscens* (Srinivasan, 1989). The intervals of major faunal turnover reflected global climatic events coincident with regional tectonism. Quantitative foraminiferal data integrated with oxygen and carbon isotopic record revealed intervals of major palaeoceanographic events during 22 Ma, 14 Ma, 12-10 Ma, 6.2-5.2 Ma, and 1.8 Ma (Srinivasan, 1989; Srinivasan & Chaturvedi, 1990). Gupta and Srinivasan (1990b) have examined the response of northern Indian Ocean deep-sea benthic foraminifera to global climatic changes during Pliocene/Pleistocene. Four intervals of major faunal and climatic turnovers are recognised: 5.2–5.1 Ma (widespread antarctic glaciation, bottom water cooling, increased upwelling, highest *Uvigerina* abundance and intensified bottom water circulation), 3.9-3.2 Ma (warmer bottom waters, decreased *Uvigerina* and increased *Cibicides* abundance), 3.2-3.1 Ma (bottom water cooling, possible initiation of glaciation in the Northern Hemisphere), and 3.1-recent (major changes in benthic foraminiferal assemblages, warm/cold cycles, major glacial/interglacial intervals, increase in polar ice volume). The Oligocene/Miocene transition resulted in lower alpha diversity of benthic foraminiferal assemblages in northern Indian Ocean (Gupta & Srinivasan, 1989) and reflected significant increase in Antarctic ice.

Turnover of palynotaxa through Eocene/Oligocene in Cauvery, Godavari and Kutch basins in India is illustrated in Table 2 (after Kar, 1985; Venkatachala & Rawat, 1972, 1973; Venkatachala & Sharma, 1984).

Singh (1988) has summarized the history of arid land vegetation and climate. The lowering of world temperature during the Late Cretaceous, Palaeogene and Neogene, reduced precipitation levels all over the globe, curtailing the high rainfall areas. The decline in precipitation prompted the expansion of low-biomass, openland and aridland vegetation, and the evolution of open-land plant taxa. Arid and semi-arid land vegetation which hitherto occupied limited, dry locations thus expanded into areas at the lower spectral end of the precipitation gradient in the low and middle latitudes. During warmer and wetter interglacials tree vegetation was able to encroach into areas formerly occupied by openland vegetation at both high and low latitudes resulting in the advance in tree lines polewards and into former deserts during interglacials. The reverse happened during glacial when openland, treeless herbaceous vegetation returned (Singh, 1988).

Numerous large-scale climatic fluctuations causing a succession of glacial/interglacial cycles, occurred during Quaternary. These climatic oscillations were particularly severe and their impact on biota was drastic particularly in western Europe (Coope, 1987). During shorter interludes the climate of England was occasionally warm enough to support a warm-temperate vegetation. The glacial/interglacial cycles during the Quaternary also changed drastically the distribution and abundance patterns of benthic foraminiferal assemblages in northern Indian Ocean (Gupta & Srinivasan, 1990a). In general, the Early Quaternary was characterised by relatively less diverse assemblages, unstable bottom water conditions, and cooling of bottom waters. The transition between Early and Late Quaternary was marked by warming of bottom waters and more equitable and more diverse assemblages. In Late Quaternary the benthic foraminiferal assemblages were more diverse, more equitable but less abundant reflecting a more uniform and less intensified bottom circulation perhaps due to less glacial activity in Antarctic regions.

The climatic changes during Late Quaternary were abrupt and intense and episodes of wholesale extinction must have been almost synchronous with the events that caused them; namely the sudden rise and fall of the regional temperature (Coope, 1987). On the other hand, species recolonizing these areas show a lag in their response to the climatic stimulus and as a result recovery was rather protracted and gradual (Coope, 1987). Coope (1987) has also suggested that individual species adjust to changing conditions by tracking the appropriate environment geographically rather than by evolutionary change, and species ecologically tied to one another by mutual dependence must have moved at the speed of the slowest member. We have to bear this in mind while speculating on the future climatic change and its impact on biota.

Ritchie (1985) has described the vegetational

changes in Lower Mackenzie Basin of north west Canada. During the late glacial the vegetation was relatively stable, consisting of sparse herb tundra on uplands in a slowly warming climate (Ritchie & Hare, 1971; Ritchie & Cwynar, 1982). During Early Holocene thermal conditions were about 10 per cent warmer than present, a change from tundra woodland at most sites occurred. This was largely brought about by the efficiently dispersed *Populus*. Relatively rapid changes in regional vegetation occurred during 11,800-6,500 years BP; *Juniperus* invaded the poplar woodlands, and later the slower-dispersed *Picea* arrived and formed stands on alluvial sites, largely replacing the poplar. At about 7,500 years BP *Butea papyrifera* spread to the uplands. The accumulated fuel load perhaps caused an increase in fire frequency, which in turn maintained arboreal birch in the area. Fire opened up the woodlands locally and prompted the spread of *Alnus crispa* (Ritchie, 1985).

Vishnu-Mittre (1984) suggests that during the mid-Miocene there existed an incipient latitudinal zonation of vegetation in the Himalaya, then only 2200-2400 m high. There occurred wet tropical forests on the lower slopes, wet temperate forests on the higher slopes, with wet subtropical in between. The palearctic genera occurred in the top two zones as they do today in the eastern Himalaya. There was not much difference in the generic composition between the Neogene floral assemblages of eastern and western Himalaya. However, the specific affinities of the taxa differentiating these floral assemblages are only tentative; indications are that they had a number of common species (Vishnu-Mittre, 1984). At that time the tropical wet evergreen forests of the western Himalaya consisted overwhelmingly of Malayan and southeastern elements (e.g., *Dipterocarpus, Cynometra, Anisoptera, Gluta, Diospyros, Elaeocarpus, Sterculia, Bursera*), while the temperate forests consisted of a number of palearctic genera (e.g., *Pinus, Abies, Picea, Alnus, Betula, Magnolia*). The tropical wet evergreen vegetation of the eastern Himalaya had somewhat different species (Awasthi, 1974; Mohan, 1933). Some of the present-day common tree taxa with which older taxa had affinities were *Calophyllum, Dipterocarpus, Shorea, Kayea* and *Gluta*, etc. It may be pointed out that only the eastern Himalayan region still contains a wet evergreen tropical forest. Several of the modern species, however, were also present during the Miocene.

The following important genera are recorded in:
Palaeocene-Eocene: *Araucaria, Podocarpus, Musa, Pandanus, Nipa, Cocos, Areca, Hyphaene,* *Phoenix, Polyalthia, Homalium, Hydnocarpus, Mesua, Garcinia, Ailanthus, Sterculia, Grewia, Bursera, Walsura, Euphoria, Terminalia, Syzygium, Lagerstroemia, Sonneratia, Barringtonia, Leea, Phyllanthus, Cinnamomum, Artocarpus, Ficus,* etc. (Bande *et al.*, 1988; Lakhanpal *et al.*, 1984)

Miocene-Pliocene: *Polyalthia, Mesua, Calophyllum, Garcinia, Kayea, Dipterocarpus, Anisoptera, Dryobalanops, Shorea, Hopea, Sterculia, Heritiera Pterospermum, Schleichera, Euphoria, Bursera, Ziziphus, Mangifera, Gluta, Swintonia, Lannea, Buchanania, Dracontomelum, Albizia, Afzelia-Intsia, Cassia, Bauhinia, Cynometra, Sindora, Dialium, Millettia, Isoberlinia, Pongamia, Ougeinia, Parinaria, Carallia, Terminalia, Syzygium, Barringtonia, Careya, Lagerstroemia, Sonneratia, Duabanga, Alangium, Chrysophyllum, Sideroxylon, Diospyros, Leea, Cordia, Phyllanthus, Artocarpus, Holoptelea,* etc. (Awasthi, 1974, 1982a, 1982b; Awasthi & Panjwani, 1984; Lakhanpal *et al.*, 1981, 1984).

The Miocene orogeny and perhaps planetary dynamics led to mark climatic changes involving the pluvial cycles, i.e., the repetition of cold (and dry) and warm (and mesic) phase during the Pliocene. These cycles brought about drastic changes in physiogamy and in vegetation, which include the disappearance of some forest types (e.g. tropical wet evergreen *Dipterocarpus-Anisoptera* forests from the western Himalaya), arrival of species from extra-Himalayan regions, relative increase and decrease in the area occupied by different biomes such as forest and steppe, etc. It is, however, difficult either to interpret the sequences of such changes precisely, or to suggest at what rate and at which time the vegetational changes occurred (Vishnu-Mittre, 1984).

By the end of the Miocene (Lower Siwalik), the tropical African elements, such as *Zizyphus mauritiana* had reached the lower slopes of the western Himalaya (Lakhanpal, 1965; Lakhanpal & Awasthi, 1984). In subtropical and temperate belts of Kashmir, a continuous flux between the forests of *Quercus-Carya, Larix, Quercus, Engelhardtia, Quercus-Alnus,* and *Pinus roxburghii* on the one hand, and steppe (Poaceae with or without Cheno-amaranth and *Artemisia*) on the other, occurred from 3.5-2.47 million years B.P. The steppe attained preponderance during the cooling-phase and the forests during the warming phase. *Cedrus deodara,* a Mediterranean species, immigrated during the Pliocene. During Pliocene in the Kashmir valley, subsequent to the decline of *Cedrus-Quercus* forests, *Pinus wallichiana* arrived and expanded. *Pinus wallichiana* declined subsequently to be replaced by *Picea-Cedrus-Quercus* forests.

The subalpine and alpine conditions developed in the Himalaya after the final uplift. At the time, *Quercus semecarpifolia* and *Betula utilis* were the chief subalpine and apline forest-forming species. During the last glaciation (about 0.7 million years ago), the steppes encompassed most of the areas in higher elevations (above 3000 m), but the subsequent warm-phase led to the expansion of junipers in dry areas and of *Q. semecarpifolia* and *Betula utilis* in relatively mesic areas. Similar alternations were found between steppe and *Ephedra* communities in arid parts.

During the Pliocene-Early Pleistocene as many as 25 species in subtropical and temperate zones were found which occur today in the Sino-Japanese region. *Abies spectabilis, Betula utilis, Quercus semecarpifolia, Q. glauca, Cinnamomum tamala, Juglans regia, Machilus duthiei, Pinus wallichiana, Acer oblongum, Alnus nepalensis, Cupressus torulosa, Litsea elongata* and *Mallotus philippensis* are example of trees.

More recently, between about 8,000 and 4,500 years ago, a warm phase which resulted in massive snow-melting and concomitant increase in the sea-level coincided with the invasion of chir pine (*Pinus roxburghii*) forests by oaks (*Quercus* spp.) in the central Himalaya (Vishnu-Mittre, 1984). At this time, in fact, oaks predominated in the entire subtropical and temperate belts of the western Himalaya. In some regions, such as the Kashmir Valley (within about the last 500 years) and Himachal Pradesh (during 1,400-500 years ago) oaks disappeared or were pushed to sheltered areas within the conifer regimes. The present flora of Kashmir Valley is devoid of either oaks or *P. roxburghii* (Puri *et al.*, 1983). In Kashmir, at higher elevations (2000-3000 m), *Pinus wallichiana* (the blue pine) was the main pine species, while in Himachal Pradesh and Kumaon in the lower elevations, the pine was mainly *P. roxburghii.*

It is interesting that the oaks predominated and invaded the pine forests during the warm-phase of the climate, because at present the oak forests are located at higher elevations (hence cooler environment) than the chir pine (*P. roxburghii*) forest (Singh & Singh, 1987).

While reviewing the geologic history of biotic diversity, Signor (1990) has concluded: (i) evolutionary change leading to increased alpha diversity in marine and benthic communities contributed directly to increased diversity on regional and global scales; (ii) coevolutionary interactions between terrestrial plants and animals led to increased species richness in terrestrial communities; (iii) continental drift has been a major force controlling global diversity, both in the marine and terrestrial realms; and (iv) climate and sea level undoubtedly played a role in the short term but are unlikely to control diversity in the long term.

Several insights can be drawn from palaeoecology which are relevant to future global change. Davis (1989) emphasised on four of these: (i) Species respond to climate individualistically; the individual range shifts have caused changes in the composition of plant and animal communities through time; (ii) Biological responses to climatic change often occur with time lags; each species and ecosystem component has its own time constant of change; (iii) Disturbance regimes are an aspect of climate that changes as climate changes; a change in disturbance regime can amplify the results of climatic change arnd produce a much larger change in vegetation; (iv) Multiple impacts will be important, producing effects that are different from any we see around us today. Ricklef's *et al.* (1990) have concluded that, "It is clearly in our best interest at this point to increase our resolution of past mass extinction events so that we may answer such questions as to their causes, time courses, the attributes associated with extinction/survival, the types of refuges within which life forms persisted, and the return of the global systems to pre-event levels of biomass, diversity, and ecological complexity"

FUTURE CLIMATE CHANGE AND SPECIES DIVERSITY

Although man has been altering the environment for nearly two million years, it is only recently that the influence has approached global proportions with almost inevitable changes in the climate (Hansen *et al.*, 1981). Current predictions (Manabe & Stouffer, 1980; Manabe and Wetherald, 1975; Hansen *et al.*, 1984) indicate a steady state increase in global temperatures of 1.5 to 4.5°C by the year 2030 and 6 to 10°C increase between 50 and 60°N over the continents (Manabe & Wetherald, 1986; Mitchell, 1983). The earth's climate has not varied more than 1 or 2°C in the past 10,000 years. Thus warming expected in the next 50 years or so will exceed any climatic change experienced in human history.

As discussed earlier, entire biomes have shifted in response to global temperature changes in the past. Profound changes in response to global warming are suggested in the distribution of major biomes, particularly those of north temperate and boreal regions (Emanuel *et al.*, 1985). It has been suggested that shifts similar to those during

Pleistocene and past Holocene would occur, and vegetation belts would move hundreds of kilometres towards the poles (Frye, 1983). Peters and Darling (1985) assume a 300 kilometre shift towards poles on the basis of models (Miller et al., 1986) and on the positions of vegetation zones during analogous warming periods in the past (Dorf, 1976; Furley et al., 1983). Using two general circulation models, GISS model of NASA and GFDL model of NOAA, M. Davis and C. Zobinski predicted 500-1000 kilometre northward range shifts for eastern hemlock, yellow birch, beech and sugar maple (see Roberts, 1989). Under milder GISS scenario, their predictions showed that in the middle of the century sugar maple would disappear across the southern edge of its current range in 200 to 600 kilometre wide belt. Under the more severe GFDL scenario, sugar maple would die out throughout its entire range, except the Maine, eastern Quebec and Nova Scotia. Similar patterns are also predicted for yellow birch and hemlock but beech would be most affected species under either scenario. Under the GISS model beech would die out over a 1500 kilometre region in the eastern United States.

CGC (1988) speculates 500 km displacement of isotherms of North America for every 5°C rise in global temperature. This change could occur within 100 years (Jaeger, 1988). Fossil records have been useful in assessing the rates at which tree species were able to advance across the landscape during the Holocene. The rates measured by the appearance of pollen in quantity at different latitudes average 10–45 km per century over long time periods (Firbas, 1949; Davis, 1981; Huntley & Birks, 1983). The fastest range adjustment exhibited by spruce into northwestern Canada at 200 km per century (Ritchie & McDonald, 1986). Dispersal rate for beech was about 20 km a century. In the event of several hundred-kilometre poleward shift in temperate belts during the next century, localized populations currently living near their maximum thermal tolerance levels would have to shift northward at a rate of several kilometres per year to avoid being left behind in areas too warm for survival (Peters & Darling, 1985). If the current predictions of rates of species shift of 700 to 900 kilometres per century are correct, beech would have to migrate 40 times faster than it did 15,000 years ago (see Roberts, 1989). Although some species, such as plants propagated by spores or dust seeds, may be able to assume this rate (Perring, 1965), many species would not disperse fast enough to escape the expected climatic change without human assistance (Peters & Darling, 1985).

Dispersal rates are crucial to species ability to colonise suitable habitats. Species having slow migration rates or experiencing geographical barriers may not survive and become extinct. Even behaviour of a species is important for the rate of migration. Many tropical deep forest birds, for example, simply do not cross even very small unforested areas (Diamond, 1975). This is also true for the chaparral birds. These bird species are highly sedentary and refuse to cross strips of nonchaparral habitat wider than 50-100 meters (Diamond, 1988b). Here lies the importance of contiguity of habitat. The current rate at which protected or undisturbed biomes are being fragmented, poses severe problems for future. A direct relationship between fragmentation of ecosystem and many of global changes that have been detected in last few decades seems undeniable. In all cases of major fragmentation of ecosystem, changes in species diversity and species composition are found (Wilson, 1988). Certainly, fragmentation will result in fewer pathways for species migration towards favourable habitats (CGC, 1988).

Given the low rates of plant dispersal, vegetation would not be able to change its geographical distribution as fast as the changes in suitable habitat (CGC, 1988). As a result, there would be lags of decades in adjustment of ecological systems to rapidly changing climatic conditions. CGC (1988) concludes that lags in the match between climate and vegetation will become apparent in the mid-continent long before doubling of carbon dioxide has occurred. Quaternary palaeorecords show that species do not react en bloc to the climatic change but have responded to change individualistically (Coope, 1987; Davis, 1981). Species will perhaps alter their geographical range as each will find conditions intolerable or new territories for colonization. As a result, ecosystems that are of limited spatial extent today may have been much more expensive in the past. CGC (1988) gives example of oak savanna, which today forms the narrow ecotone between prairie and forest in North America, but which covered an area hundreds of kilometres wide during the mid-Holocene (McAndrews, 1967). Species that are rare or geographically localized today, such as bristlecone pine (Pinus aristata), were abundant in the past, while ponderosa pine (P. ponderosa), the dominant tree over large regions of the Rocky Mountains today, was very rare during the last glacial period (Spaulding et al., 1983). Spruce which now characterises the vast boreal biome, was sparse throughout North America in the Early Holocene (Webb, 1987).

The above examples show that existing biomes

will not remain intact under future changes of global climate. Differences in the rate of migration of constituent species will dissociate communities into their component species. The fossil records reviewed in this paper show clearly that communities may be disassembled and species reassembled in new combinations in response to new climatic conditions (Davis, 1981; Graham, 1986; Coope, 1987). The resulting new combinations of vegetation, climate, and soil can result in altered spatial patterns of such fundamental processes as net primary production (Pastor & Post, 1988). More subtle, but still important processes such as evolved host-pathogen relationships may also be disrupted by the stress of new conditions, resulting in increased frequency of epidemics (Leonard & Fray, 1986).

According to Coope (1987), species that could not track the changing positions of suitable environments must have become extinct when major climatic oscillations began in the Late Tertiary. Rigid association with a particular latitude, for instance photoperiodic dependence, would make a species a likely candidate for extinction. For example, the endomychid beetle, *Stenofarsus rotendus*, in Panama is programmed, mainly through its response to day-length, to terminate diapause in April, at the beginning of rainy season (Wolda & Denlinger, 1984). Without changes in its physiology the species could not live in places where the timing of response to day-length and the beginning of the rainy season did not coincide (Wolda, 1987).

Existing data on exotic species may prove particularly useful in predicting species responses to environmental change (CGC, 1988). For example, the population dynamics of successful invaders (Harper, 1977) may provide information needed to predict which species will spread and expand in response to changed future environment. Species may feel pressure from invaders that find the new climatic regime to their liking (Peters & Darling, 1985). For example, *Melaleuca quinquenervia*, a bamboo-like Australian eucalypt, has invaded the Florida Everglades, forming dense monotypic stands where drainage and subsequent fires have disturbed the natural marsh community (Courtenay, 1978; Myers, 1983). Such invasions may become common place in response to large scale climatic changes.

Estimates of vegetation changes in Canada show a large effect of global warming (Warrick et al., 1986; Gates, 1985). The warming would return Canada to warmer summer conditions than those of the climatic optimum over North America about 6000 years ago (Harrington, 1987). At that time the boreal forest extended far north of its present range

(Ritchie & Hare, 1971; Ritchie & Cwynar, 1982; Lamb, 1982). The moist and wet boreal forest will be expected to move northward and will be replaced on its southern flank by cool temperate forest. In Central Canada, except in the far north, large tracts of the boreal forests will be replaced by cool temperate steppe (Harrington, 1987).

According to a recent report by EPA, spruce and northern pine would decline in the southern parts of their range in the east side of United States and expand northward (see Roberts, 1989). New England coniferous forests would be replaced by hardwoods, especially by oak while southern pine might shift into hardwood forests of eastern Pennsylvania and New Jersey. In the southeast, some 18 tree species may become locally extinct, and forest land may become converted into scrub and savanna. In the west side of United States, Douglas fir, ponderosa pine and western hemlock can disperse upslope in the Rockies. In California and Oregon the Douglas fir would shrink in the lowland and be replaced by western pine. In the case of regional drought and increased fire due to change in climate, forest area in the west could be dramatically reduced and some species would go locally extinct. For the United States as a whole, the EPA report foresees a marked loss of healthy forest area and a net reduction in forest productivity for several centuries.

Climatic changes resulting from increase in atmospheric carbon dioxide are expected to alter forest productivity and species distributions. Williams (1985) estimates that a doubling of CO_2 will increase productivity in northern Alberta while reducing it in the dry southeastern part of the province. For Finland, Kauppi and Posch (1985) have estimated that a climatic warming will lead to the greatest absolute increase in yield from the boreal forest in warm southern and maritime regions but the greatest relative increase in north.

Using a linked forest productivity soil process model with climate model predictions corresponding to a doubling of CO_2, Paster and Post (1988) have assessed the possible responses of north eastern North American forests to a warmer and generally drier climate. Their model prediction were: (i) on soils where there was no decrease in soil water availability with a doubling of CO_2, the current mixed spruce-fir-northern hardwood forest was replaced by a more productive northern hardwood forest, and (ii) with increase in the proportion of the growing season with soil water below wilting point, the simulated mixed spruce-fir/northern hardwood forests were replaced by a stunted pine-oak forest.

Peters and Darling (1985) have shown that small

ecological reserves may be especially vulnerable to the effects of climatic change. A likely result will be the extinction of species that such reserves were established to preserve. While discussing the effect of global warming on natural reserve species, Peters and Darling (1985) identified nine types of species and communities which may be particularly affected by warming trends over the next hundred years. These include: (i) peripheral populations located near the edge of a species range, (ii) geographically localised species such as island species, (iii) genetically impoverished species having very small populations and ecotypes, (iv) specialized species requiring narrow range of environmental conditions, (v) poor dispersers, (vi) annuals, (vii) montane and alpine communities, (viii) arctic communities, and (ix) coastal communities. Characteristics such as large population size, broad geographic distribution and high dispersal potential should help protect species and higher taxa from extinction. Palaeorecords show that large body size appears to be a disadvantage, at least for terrestrial animals. No tetrapode greater than 10 kg survived the Late Cretaceous (Padian & Clements, 1985).

Survival of specialist species may be strongly dependent on a single host. A loss or departure of that host due to climatic change will certainly lead to destruction of the specialized species. For example, in fig wasps, whose reproduction is closely tied to the plant in which they hatch, each of the 750 species can grow only on its own species of fig (Kjellberg *et al.*, 1987). Similarly Everglades kite (*Rostrhamus sociabilis*) depends on the apple snail (*Pomacea caliginosa*) for its food. The snails are themselves localised in distribution, and a decrease in their abundance due to drying of the Everglades has threatened the kite with extinction in the United States (Bent, 1961). Large herbivores were the most susceptible to disruption during the revolutions in land plants, notably the Carboniferous-Permian rise of seed plants and the early to mid-Cretaceous rise of flowering plants (Webb, 1987).

Elevated ambient temperatures may affect land bird fauna through the negative response of nestlings to elevated temperatures (Murphy, 1985; Tomback & Murphy, 1981; Barrett & Runde, 1980; Salzman, 1982). Possible effects of elevated sea temperature on marine flora and fauna can be surmised by taking examples from El Nino events. Temperature controls the sea water density and is related to nutrient concentrations, for example, a strong negative correlation exists between temperature and nitrate, there are negligible amounts of nitrate above 15°C (Jackson, 1977, 1983). Tegner and Dayton (1987) observed mass

mortality in sea-urchins during the periods of high temperature. The severe El Nino of 1982/83 caused extensive damage to the fishing industry and to the sea birds and other organisms (Feldman *et al.*, 1984; Schreiber & Schreiber, 1984; Glantz, 1985; Jordan, 1985). Extensive coral mortality occurred all over the eastern pacific (Glynn, 1983, 1984). As a result of nutrient depletion caused by elevated temperatures *Macrocystis* canopies were reduced and considerable mortality and reduced growth rates occurred in kelp forest communities. During the 1982-83 El Nino event in Chile, the northern populations of the alga *Durvillea* disappeared and have not yet recolonized (Tomicic, 1985). The kelp, *Laminaria japonica*, is grown extensively in warm waters (Tseng, 1981) and their sporophytes are temperature sensitive and probably near the limit of the temperatures in which they can survive. An increase in water temperature of only a few degree could eliminate the entire population of this alga.

A rise in sea level resulting from thermal expansion of sea water and melting of glaciers and polar icecaps has been widely discussed (Hansen *et al.*, 1981; Hoffman *et al.*, 1983; NRC, 1983). The Villach conference on the Greenhouse effect in Austria in 1985 predicted a rise in sea level between 20-140 cm in the next 50 years. However, recent estimates predict a sea level rise in the range 30 ± 20 cm (Thom, 1989; Gaughan, 1989). The effect of expected rate of sea level rise in the next century may be somewhat analogous to the effects of sea level rise that occurred at the end of the last ice age, 80 m over an interval of 14,000 years (Bloom, 1988). During deglaciation, major dislocations in estuaries, marshes, and nearshore ecosystems occurred (CGC, 1988). Available information suggests that the predicted rates of sea level rise are near the upper bound of possible rates of intertidal marsh growth (Bormann *et al.*, 1984). Consequently, sea level rise in the next century is likely to drown many if not all salt marsh systems except in areas where the land is rising and reducing the rate of relative sea level change (CGC, 1988).

If predictions of sea level rise are correct, coastal habitats, such as salt marshes and islets used by nestling birds, may be inundated or eroded. Salt marshes and estuaries are very important for many birds and fishes as a breeding ground. Any destruction of these areas will lead to extinction of many of these species. Freshwater lowlands along the coast are likely to suffer from the intrusion of salt water. The cypress trees of the US Gulf Coast, for example, do not tolerate salt water, yet they grow only slightly above sea level (Titus *et al.*, 1984).

Island species are one of the most threatened

communities as latitudinal migration of these species are limited (Peters & Darling, 1985). If latitudinal migration required by them exceeds the size of the island, a climate change would leave little alternative but extinction.

The projected increase in temperature would cause widespread changes in precipitation pattern (Hansen *et al.*, 1981; Kellog & Schware, 1981). It is suggested that there will be an increase in precipitation over India, and decrease in central and south central USA and over much in Europe and Russia (Wigley *et al.*, 1980). Summer dryness may become more frequent over the continents at middle latitude in the Northern Hemisphere. Some models suggest a 40 per cent decrease in rainfall in American Great Plains by the year 2040. In some areas, increased temperature could exacerbate regional drying (Manabe *et al.*, 1981). Breeding success in certain birds may strongly depend on rainfall intensity as shown by *Sterna birundo* in Germany (Becker & Finck, 1985). The same is true for birds in tropical dry forests in Puerto Rico (Faaborg *et al.*, 1984). Drought in the interior of Australia is shown to strongly reduce the number of suitable rabbit warrens and number of rabbits (Myers & Parker, 1975). Similarly red kangaroos, *Megaleia rufa*, are greatly reduced in numbers by a long drought (Newsome *et al.*, 1967). In relatively dry years the size of butterfly populations may be severely reduced (Shapiro, 1979; Pollard, 1982). Thus the changing inter-annual and intraseasonal patterns will undoubtedly affect many floral and faunal components. It is thus important to collect and collate data on distribution ranges and on responses of as many important species as possible through careful survey and experimentation.

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